Taxonomy and Ecology of African Plants, their Conservation and Sustainable Use

Proceedings of the
17th AETFAT Congress
Addis Ababa, Ethiopia

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Edited by Shahina A Ghazanfar
and Henk J Beentje

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FOREWORD

The 17th AETFAT Congress was held in Addis Ababa, Ethiopia between 21 and 26 September 2003, organized by the National Herbarium, Science Faculty, Addis Ababa University.

The inspiration to hosting the 17th AETFAT Congress was born with setting the deadline to complete the writing up of the Flora of Ethiopia (started in 1980) before the Congress and sharing the alternate responsibility of hosting the AETFAT Congress between Africa, Europe and the USA. The proposal to host the Conference was presented to the members at the end of the 16th AETFAT Congress, held at the Botanic Gardens, in Brussels, Belgium in August 2000, and was unanimously accepted.

On behalf of both the National Herbarium and myself, I would like to acknowledge the contributions of members of the organizing committee: Dr Ensermu Kelbessa, Ms Sue Edwards, Prof. Ermias Dagne, Prof. Legesse Negash, Prof. Masresha Fetene, Dr Sileshi Nemomissa, Dr Zemede Asafw and Prof. Zerihun Woldu, who put in so much time and effort to organize the Congress. Among the Organizing Committee, I would like to express my special thanks to Dr Ensermu Kelbessa who carried the lion's share of the organization. The technical staff members of ETH, other colleagues and friends who are too many to be listed here have tirelessly worked prior and during the conference and their efforts are also acknowledged.

There were three post-congress tours organized in connection with the 17th AETFAT Congress. The team leaders of the three tours are also highly appreciated; they were: Prof. Ib Friis and Mr Feyera Senbetta to SW Ethiopia (Jimma, Mizan and environs), Dr Ensermu Kelbessa and Mr Nigussu Aklilu to SE Ethiopia (Bale and S of Omar) and Dr Nigist Asfaw and myself to northern Ethiopia (the Simen).

The theme of the Congress was "Taxonomy and Ecology of African Plants, and their Conservation and Sustainable Use". Eight symposia and a workshop on endangered species relating to the theme were presented at the Congress. Seventy-six original research papers were presented orally, and 107 posters on the conservation, floristics, taxonomy, vegetation and ecology, phytogeography, economic botany and forestry in Africa were exhibited and presented. All oral presentations and some of the papers presented in the poster sessions were reviewed with the kind assistance of the organizers of each symposium, to whom the organizing Committee would like to express its gratitude. The organizers and subsequently the editors (unless indicated otherwise) include: Drs Alan Paton & Beatrice Khayota (Symposium 1 on the Taxonomy of African Plants); Drs Gaston Achoundong & Martin Cheek (Symposium 2 on Forests & Forestry in Africa; Profs. Mats Thulin & Ib Friis (Symposium 3 on Phytogeography); Profs. François Malaisse & Zerihun Woldu, and Drs Henk Beentje and Shahina Ghazanfar (eds.) (Symposium 4 on the Ecology of African Vegetation); Drs Paul P. Smith & Pete Lowry (Symposium 5 on the Conservation and Sustainable Use of African Plants); Prof. Sigrid Liede & Dr Ulrich Meve (Symposium 6 on Recent Advances in Species and Generic Concepts); Drs Henk Beentje & Shahina Ghazanfar (Symposium 7 on Progress on African Floras), Profs. Tewolde B.G. Egziabher & James Seyani (Symposium 8 on the Convention on Biological Diversity) and Prof. Inga

Hedberg, Dr Janice Golding and Dr Jonathan Timberlake (workshop on endangered species). A special session on the Flora of Ethiopia was also organized and this session was kindly co-chaired by Mr Asrat Bulbula and Prof. Endashaw Bekele, to both of whom we express our appreciation.

The contributions of organizations, institutions, projects for supporting the conference financially, materially and morally are highly acknowledged. These include: the Swedish International Development Agency (Sida), Sweden; the Ethiopian Science and Technology Commission and the Addis Ababa University, the Ethiopian Airlines, the Biological Society of Ethiopia, the Institute of Sustainable Development, the Walta Information Center, Ethiopia; The Royal Swedish Embassy, Addis Ababa; the University of Oslo, Norway; the University of Copenhagen, Denmark; the Royal Botanic Gardens, Kew, UK, the Missouri Botanical Garden, USA and the Technical Center for Agriculture and Rural Cooperation (CTA).

Finally the support obtained from the Royal Botanic Gardens, Kew in the publication of the Proceedings is highly appreciated. In this connection, the editors of the Proceedings of the 17th AETFAT Congress, Drs Shahina Ghazanfar and Henk Beentje are fully acknowledged for the high standard of editing and for the timely publication.

I hope the production of the Proceedings will be a testimony for the completion of the Ethiopian Flora Project and the successful 17th AETFAT Congress held in Addis Ababa. I am also confident all those individuals involved in developing and carrying out the Ethiopian Flora Project will be proud, as will be those institutions that financed and supported the Project over the last twenty-five years: the Swedish Development Agency, SIDA; the Ethiopian Science and Technology Commission; and the Addis Ababa University.

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XVIITH AETFAT CONGRESS, 21–26 SEPTEMBER 2003 HELD AT ECA, ADDIS ABABA, ETHIOPIA

WELCOME ADDRESS

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Your Excellency, Dr Girma Wolde Giorgis, the President of FDRE; honoured guests; dear AETFAT participants; ladies and gentlemen.

It gives me great pleasure to welcome you all to Addis Ababa on behalf of all my colleagues in the National Herbarium of the Addis Ababa University, and on my own behalf.

It is also a pleasure to ask you to note that we are holding this, the XVIIth Congress of AETFAT in the historic Africa Hall, where the founding and many other meetings of the Organization of African Unity have been held.

The OAU, now transformed into the African Union, represents the political unity of purpose of the nations of the African Continent, just as AETFAT has continued to work for coordination and growth in understanding and capacity to document and carry out research into the plant wealth of the African continent. It is only appropriate that AETFAT, the Association that unites botanists interested in and concerned about the flora of Africa gathers here to meet for the XVIIth Congress, the fourth to be held in Africa. We in Ethiopia have a great respect and administration for AETFAT. This stems among other things from the fact that it was AETFAT that initiated the writing up of the Flora of Ethiopia in the 1970's and we are also happy by the fact that the 17th AETFAT Congress is being held at a period when we are completing the writing up of the Ethiopian Flora. As there will be a session on the Ethiopian Flora on Thursday, the 25th of September, I will not dwell on this point here.

Unfortunately, Africa often suffers from a bad press – the spectres of war and famine tend to be the main images portrayed in the international media. And these images obscure the great wealth in plant resources and the cultures that interact with these resources throughout the length and breadth of Africa. I hope this Congress has provided an opportunity for those that have been in the pre-congress tour to see the western parts of Ethiopia and will provide further opportunities for those who will be participating in the northern and south-eastern tours.

We are indeed gratified to know that among the 175 international participants who registered to come to this Congress, about 75 are from African institutions, based and working in this continent.

The theme of this Congress is "Taxonomy and ecology of African plants, their conservation and sustainable use". A number of symposia relating to the theme, and a workshop on threatened plants are planned for the Congress. Seventy-nine original research papers (in English or French) and a hundred-and-four posters on the conservation, floristics, taxonomy, vegetation and ecology, phytogeography, economic botany and forestry in Africa will be presented during this week, so we will all leave wiser and enriched in our understanding of Africa's rich botanical resources, and of the scientists who study these plants.

The theme for this Congress also reflects AETFAT's concern with the implementation of the Convention on Biological Diversity, the CBD, and particularly the recognition of the importance of understanding of, and working with, local communities and peoples in order for the use of plant resources to be balanced with conservation. The session on Threatened Plants is being given in plenary so that all participants can attend. The search for new drugs and novel foods, along with the increasing number of collectors of specialized plants, particularly orchids and succulents, who will pay very high prices for 'novelties', is a challenge which taxonomic botanists cannot ignore.

Another challenge is that of working towards the aim of all countries in Africa having their own cadre of systematic botanists, able to work in their own countries to provide vital information, and carry out both applied and basic research so that other professionals and policy makers can make rational and informed decisions on the best use of the plant wealth of their countries. We are particularly happy to see that the number of African nationals at this Congress is the highest so far in an AETFAT meeting.

Let me remind you of some statistics relevant to plant resources of Africa.

Africa is the World's second largest continent, with a land mass of 30 million km^2 (North America, the third largest continent, has an area of 24 million km^2).

Africa has a moderately-sized population for its size, viz. about 680 million inhabitants. However, the population density ranges from less than 1 person/km^2 in desert and deep forest areas, to over 500 persons/km^2 in the highly cultivated Nile Delta at Cairo.

Africa is generally the driest continent, but it also includes very moist areas, most notably the Congo basin, the hot and humid rainforest on the slopes of Mount Cameroon and the cool to cold Afro-alpine areas on the high mountains in Eastern Africa. Nearly all these different climates are represented within Ethiopia, and Ethiopia has the largest extent of Afro-alpine areas of all countries in Africa. The post-Congress tours will be going to these areas; the Bale Mountains National Park and surrounding areas in the south east, and the Simien Mountains National Park in the north west. It is pleasure to see that Prof. Olov Hedberg, the father of studies into the Afro-alpine Flora of Africa and founder member of AETFAT is with us in this Congress.

According to the World Conservation Monitoring Centre, the vascular plant flora of Africa is somewhere between 40,000 and 45,000 species. This is approximately one fifth of the World's flora. Only tropical and subtropical Asia (with c. 50,000 species) and Central and South America (with c. 85,000 species) have more. The continent houses a range of conservation hot spots: the incredibly rich Fynbos of the Cape Region of the Republic of South Africa, the unique succulent flora of the Karoo in Namibia at one end of the continent, the complimentary but still poorly known succulent flora of the Somali-Masai vegetation zone of Eastern and the Horn of Africa, the wealth of unique taxa in the Eastern Arc (Usambara) mountains in the east, and the equally unique and rich flora of Mount Cameroon in the west.

The plant resources of the continent directly and indirectly affect the livelihood of a large proportion of the population of the continent. Thus AETFAT has an enormous challenge and opportunity to better understand the diversity, taxonomy, ecology, sustainable use of these plant resources for the benefit of mankind and the plants themselves.

Many thanks for all of you who have travelled from all corners of the world and from distant places as far away as New Zealand to be together and to deliberate on issues that are important to our understanding of the African flora.

The AETFAT Secretariat acknowledges with much gratitude the financial and material assistance provided by the following institutions and organizations. Without their generous help the realization of this XVIIth Congress would not have been possible. In particular, the support for travel and subsistence from the following institutions for African participants is much appreciated.

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I would like you to feel at home and enjoy your stay in Addis Ababa and the different parts of the country you are going to visit.

Thank you.

KEYNOTE ADDRESS

HIS EXCELLENCY ATO GIRMA WOLDE GIORGIS

President of the Federal Democratic Republic of Ethiopia

Distinguished Guests, 17th AETFAT Congress participants, ladies and gentlemen.

It is a privilege for me to be the Guest of Honour on this important occasion at the opening of the 17th AETFAT Congress here in Addis Ababa, the capital city of Ethiopia. I understand that the theme for your meeting is the taxonomy and ecology of African plants for their conservation and sustainable use and that your discussions include issues on forests and forestry, issues which are very close to my heart. During my lifetime I have seen the landscape of Ethiopia literally washed away before my eyes, and one major reason for this has been the drastic depletion of forests and other natural vegetation as more and more land has been brought into cultivation. It is very pleasing that a scientific body of the standing of AETFAT is taking the issues of conservation and sustainable use so seriously.

I have learnt that AETFAT is the French acronym for botanists, mostly from Africa, America, and Europe who have formed the "Association for the Taxonomic Study of the Flora of Tropical Africa". This association was established in 1950 in Brussels, where the 50 years anniversary of AETFAT was celebrated in the year 2000. My government and country, the Federal Democratic Republic of Ethiopia, is pleased that you have chosen our capital city, Addis Ababa, and one of the oldest higher education institutions in Africa, Addis Ababa University, to organise this important gathering, the 17th AETFAT Congress.

The National Herbarium, based in the Department of Biology in the Faculty of Science of Addis Ababa University has served as the Secretariat for AETFAT between 2000–2003 and is the organiser of this event. The National Herbarium, established in 1959, has served as the base for carrying out research into and compiling information on all the non-agricultural plant resources of Ethiopia. It is estimated that there are around 6500 species of higher plants in the country with about 12% of these endemic to the country, i.e. not found growing naturally in any other part of the world. Apart from well-known unique crops, these plants also include some important and decorative trees such as *Erythrina brucei* named after the explorer James Bruce, and *Millettia ferruginea*. The woodlands of Somali Region in the Southeast of the country, and those of the western areas of BenShangul Gumuz also contain many economically important species producing gums and resins that are used locally as well as being exported. The National Herbarium has a specialised library which is consulted by students and many members of the public in order to find out about Ethiopia's rich botanical resources.

One of the major achievements of the National Herbarium is the production and publication of a modern Flora. The Ethiopian Flora Project was developed during the 1970s and started officially in 1980 when generous long-term financial support was obtained from Sida-SAREC, Sweden, through the special efforts of Prof. Olof and Dr Inga Hedberg of Uppsala University. Institutional support in Ethiopia was provided to the project through the Addis Ababa University and the Ethiopian Science and Technology Commission (ESTC). We would like to thank all those involved for their steadfast support and contributions to the successful realisation of this project. The National Herbarium now has 6 books in print of the planned 7-volume work, and all the remaining volumes will be published before the end of this year, 2003. Being printed in Ethiopia has made it possible for all professionals — foresters, forage and range experts, agriculturalists, educationalists, traditional and modern medical practitioners, horticulturists, and the many interested members of the public to obtain copies easily and at a very modest price.

Although a number of dedicated Ethiopians are involved in compiling this information, this would not have been possible without the active international collaboration of AETFAT members based in various botanical institutions in Africa, Europe and the USA. We are also happy to note that the idea to write up a modern Flora was initiated and discussed at the AETFAT Congress held in Geneva in 1970. An international ad hoc committee was established which then worked with a local committee based in the Faculty of Science of Addis Ababa University to develop the project. We would like to acknowledge the support of AETFAT in helping the National Herbarium bring about the realisation of this Project.

It is also a fact that much of the writing up of the Flora of Tropical Africa was initiated during the colonial times. Hence much of the basic botanical and zoological information is held in institutions outside the African continent. It is also true that the north has the technology, the trained expertise and funds while the south has the biological diversity, which urgently needs to be documented and studied for the benefit of all of humanity and the planet Earth. The International Convention on Biological Diversity (CBD) was negotiated in order for there to be common governing principles on how biological resources should be used and how the benefits from their use should be shared between countries. A core principle of the CBD is that states have sovereign rights of their biological resources, and the development of these resources has to be based on the balance between conservation and sustainable use. Ethiopia played a major role in the negotiations of the final text of the CBD and has both signed and ratified this Convention. We believe that your organization, AETFAT, can play a leading role in realising the central aims of the CBD. Specifically, the members of AETFAT could:

> Encourage and work for the repatriation of copies of important specimens and their accompanying information so that local institutions have the capacity to carry out the basic research to understand and document their own country's resources.
>
> Promote the development of a code of conduct for North-South collaboration in botanical research in order to promote and abide by the principles of informed access and benefit sharing as indicated in the Convention on Biological Diversity (CBD), and now suggested to be developed as a Protocol to accompany the CBD.

As you know our country is diverse in geology, topography, and climate, which consequently has produced a unique and diverse flora and fauna. Not only is Ethiopia the home of Arabica coffee, but its people grow a range of unique crops including the cereal tef, and the root crop enset. We hope you will all have the pleasure to sample some of Ethiopia's good food and participate in the unique and distinctive coffee ceremony before you return home. We understand that many of you have also arranged to visit various parts of the country in the pre- and post-Congress tours organised for you. We hope you will return home with your hearts warmed by Ethiopia's traditional hospitality and your minds filled with images of a country rich in cultural diversity based on the use and integration of the local biodiversity into the lifestyles of the local communities.

I would like to thank all of you that are so keen to devote your time for the investigation of Africa's botanical diversity, its conservation and sustainable use. I wish you all to have vigorous and encouraging discussions in all of the symposia. It is my great pleasure to declare the 17th Congress of AETFAT open.

Thank you all very much.

CONSERVING PLANT DIVERSITY IN AFRICA: AN OUTSIDER'S VIEW

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Your Excellency, honoured guests, ladies and gentlemen, friends and colleagues, thank you for the opportunity to speak with you today. It is a privilege to be in this historic room and a great pleasure to be here in this beautiful country for the first time.

I am delighted too to be paying a return visit to Sebsebe Demissew, such a regular and welcome visitor to Kew over the past years. At many levels Sebsebe has made a very real contribution to the development of Kew's current approach to science, to taxonomy and conservation. We thank him for this, as well as him and his team for bringing us together here today for the seventeenth meeting of AETFAT.

Kew has been involved in AETFAT since its inception in more than 50 years ago. Looking back to that first meeting involving 21 botanists from 4 countries representing 5 institutions, I think it is true to say that what began as a fairly strictly taxonomic enterprise then has gradually expanded into something much richer, intellectually broader and more applied, embracing biogeography, conservation and economic botany. Shahina Ghazanfar tells me that at this meeting there are close to 200 participants from 33 countries representing more than 50 institutions from all over the world. The scope of the meeting and the research and interest of the participants is well reflected in the programme with sessions ranging from baseline taxonomic work to molecular systematics, forestry, phytogeography, ecology, conservation and the sustainable use of African plants.

And this is very much something to celebrate, for taxonomy isolated from the world in an ivory tower cannot serve its purpose of providing a backbone of names and relationships in the light of which other information can be connected, interpreted and, most importantly, used. If taxonomy is not relevant to the broader range of plant diversity concerns, and relevant to issues of conservation and sustainable use, then it risks becoming remote from the concerns of everyday life, a science whose outputs no-one wants to read and whose endeavours no-one wants to fund. This threat in itself may be sufficiently powerful to make us constantly reconsider our relevance and focus on how we can make what we deliver more accessible and useful to a wider audience.

But I believe there is another driver behind our move to a broader focus on plant diversity, conservation and sustainable use, and since this driver is one that shows us in a better light than purely mercenary concerns about who will fund or read what we produce, I think it is worth emphasising. The second driver is the fact, or at least the impression that I and many of my colleagues have, that most plant taxonomists are actually conservationists at heart. We respect and delight in what we work on and we see the glory in the world of plants. Almost inevitably, we grow to love the group we study and we find charm in details that non-specialists might overlook. There is little pleasure or job-satisfaction to be derived in describing a new species that is clearly about to become extinct, but it is an experience that is all too familiar to many of you in this room. On the other hand there is a real and lasting sense of achievement to be had from making a contribution, direct or indirect, to the protection of a species, an area of land or a unique assemblage of plants. That is an experience too few of us have had until now but one that I would hope that all of us will have more often in the coming years.

The changes which we have been describing, and which AETFAT has undergone in the course of the past 20 or 30 years, are ones which Kew has undergone more recently. We've realised that asking 'How are we relevant?' is not just of academic interest. On the contrary it is a fundamentally pragmatic question because it comes immediately back to 'Why should we be supported by the public, by Government, by corporations or by foundations?' We need to be able to articulate the importance of our work, and convince people that they should care about the diversity of plants and support the work that we do.

I think too that this question is given even more relevance by the clear realisation that although we view ourselves as friends of long-standing in many parts of Africa we are nevertheless outsiders. As such we must respond to the needs of what the insiders want.

The only real justification for spending the money of British taxpayers, through the work of Kew, in Africa can only be that we are providing something that our African partners and friends tell us that they want. Everything else is secondary.

So this talk is presented today very conscious of Kew's role as an outsider – and even more conscious of my personal status as a relative neophyte in matters of African plant diversity.

It would be arrogant for me, or indeed anyone else from Kew, to try to prescribe how Africa should look after its own plant resources. All I can do is to try to describe how we as an institution are trying to meet those needs that we have been able to identify – and how we are trying to change what we do to be even more helpful. It is then up to you – on a country by country basis – to tell us whether or not we are doing a good and useful job – and how we can do better. So I apologise in advance for talking so much about Kew but at the end of the day it is really the only area in which I have any real authority to speak.

The first point that it is important to make is that over the last few years we have been working towards a new view of Kew as a plant diversity institute, rather than one solely concerned with taxonomy and systematics *per se*. This may seem rather a fine and subtle distinction between two abstract concepts but what I will try to do today is present a picture that shows why this new view matters, and how it might be translated into concrete measures that will have a real impact on conservation and sustainable use – with a particular focus on Africa.

Let's start with something here on our own doorstep in Addis Ababa. I understand that we are on the eve of completion of Flora of Ethiopia – at least for flowering plants. And that the last two volumes are basically very close to completion. The project only began in 1980 and to have come so far so fast is truly remarkable. This is a fantastic achievement that has been brought about through the wonderful leadership of Olov and Inga Hedberg and others in Europe, many people in this room and most importantly many people working in Ethiopia. The legacy has not only been a superb and useful flora – but also a fund of people and expertise developed here in Ethiopia that will be crucially important for the future.

At Kew – although we are not quite as advanced – we look forward to the completion of the Flora of Tropical East Africa – the end really is in sight! With the first publication in 1952, we are making good progress towards its completion – 55 years on – in 2007. I understand that 73% of the flora is complete and the rest is either being edited or the manuscripts are near completion. The deadline for typescript delivery has been set at

December 2005 – as I am sure any contributors here present are already well aware. Recently FTEA has published several families of ferns, something which had not been done earlier, as well as volumes of Compositae and a large glossary. The third part of Compositae is expected to be published in 2004 with several of the larger families such as Labiatae, Asclepiadaceae, Acanthaceae, Scrophulariaceae to follow on soon. It is also extremely positive for this project that there is increasing involvement of African colleagues, see for instance the recent publication of Apocynaceae by Dr Omino, and Gentianaceae by Dr Sileshi. We are also now including, where available, the local uses and the conservation status of the species that are described. There is also a project going on to produce an Index of Collectors, and also to develop a website from where information on the tropical East African flora will be disseminated.

Once FTEA is complete we will be in a position to direct more resources towards the completion of Flora Zambesiaca, another major goal for us, which I hope will be completed during my tenure at Kew.

Obviously, completion of FTEA and subsequently FZ will represent major milestones for all of us, and ones which I intend to pursue with vigour – and then celebrate. It would be wrong, however to assume that the completion of the Floras will represent an end in any sense to Kew's work in these areas of Africa. On the contrary I hope it will allow us to develop new links of work with our partners that respond ever more directly and urgently to their immediate needs. A reminder of Kew's mission serves to support this point and also provide the context for our likely future development.

Our mission is not only about increasing knowledge, by which we mean research, including the production of Floras such as FTEA and FZ, but also about increasing understanding, by which we mean translating the results of that research into a form which is accessible to, and comprehensible by, those who need it, be they reserve managers in Cameroon seeking to ensure the survival of particular species, primary school students in the UK completing an assignment for a school project, or Ugandan farmers looking for alternative cash crops.

Kew's Mission Statement also speaks about "enabling better management of the Earth's environment" and this introduces a further key element – the importance of plant conservation and the sustainable use of plant resources. So the Mission Statement reflects our belief that it is the combination of the two strands: knowledge and understanding, or if you prefer, of research and education, that ultimately yield results in terms of conservation and sustainable use.

But I do not want to give the impression that we are waiting until the research is complete before we embark on translating it into action with regard to conservation and sustainable use. That approach would be deeply flawed for at least two reasons. Firstly, as everyone here knows only too well, the research is never finished. There will always be more that can be added to the body of knowledge concerning how plant species are circumscribed, how they can be distinguished from one another and how they may be related to one another. It is for this reason that we are so keen to make the basic research materials for plant taxonomy more accessible. And this evening some of us will be discussing an initiative aimed at making specimens of African plant types more readily available to facilitate taxonomy.

Second, and perhaps much more importantly, time is not on our side. We do not know how many species of plants are threatened – in fact we do not even know how many species of plant have been described to date. However, we can be fairly sure that many many more species are at risk of severe population decline than are currently inscribed on red data lists, and than there were 50 years ago. We cannot afford to wait until we feel we have the complete picture before we act.

So we have already embarked on a range of projects designed to deliver tangible results in terms of conservation and/or sustainable use. But before I tell you about some of them, I would like to explain a little about the fundamental structural and administrative changes we have made within Kew in order to better position ourselves to deliver on this new agenda. These may be of interest to those of you who are actual or potential visitors or collaborators with Kew, but also of interest more broadly as an illustration that we are serious we are about our change in emphasis and perspective.

Our Science Strategy Review resulted in a variety of administrative changes involving many of the science staff. Among these the changes in the herbarium are probably the most radical, and perhaps of most interest to the AETFAT audience. Basically we have re-organised existing staff so that as well as having teams which focus on a particular family or a group of related families, as we have had for many years now, we also have teams that have a regional remit. So that for the first time in many years most of the staff who work on, say, Brazil, are together as part of an integrated team rather than being scattered across the herbarium and managed by staff who have little or nothing in common with them in terms of research interests.

For Africa in the Herbarium we have two such teams, one for the 'Drylands of Africa' including Ethiopia, and the areas covered by Flora of Tropical East Africa and Flora Zambesiaca. This team is led by Kaj Vollesen. We have a smaller but very active team called 'Wet Tropics of Africa' and led by Martin Cheek. Such a change may seem like common sense to many, but believe me, in a herbarium where many of the current staff were already established experts in their field when I visited as a summer undergraduate intern 30 years ago, you have to have a very good reason to fiddle with long-standing arrangements. So I would like to sketch out for you the rationale behind these changes to long-established structures.

Let's begin with the view from 30,000 feet: a pervasive development in science during the twentieth century has been the relentless trend towards specialisation. As the volume of knowledge expands, individual scientists become most comfortable knowing more and more about less and less. (Until finally, some would say, they know everything about nothing at all.) As a result, many fields that were once coherent are now fragmented, and in biology this trend has also been fuelled by a pervasive reductionism that has sought fundamental insights at the cellular, genetic and molecular level. Tightly focused programmes of research have massively advanced our understanding in many areas but this must be balanced with the recognition that important advances often come where traditionally separate fields overlap.

So what does this mean for Kew? Well, our science programmes address the diversity of plant life, how it came to be, what its current status is and how it can be conserved and used in sustainable ways. Therefore almost all of Kew's scientists are generalists to some degree but, because plant diversity is so vast, there is an inevitable tendency to specialise in particular plant groups. Specialisation has advantages in designing focused research programmes that may make rapid progress, but it also has disadvantages, particularly in supporting the objectives of plant conservation. To undertake basic ecological work, anywhere in the world, it is crucial to be able to identify plant species – not only from flowers and fruits but also from leaves and stems. Even in the UK this can be a significant challenge, but in those parts of the world with high plant diversity it is especially difficult and requires an extraordinary level of general botanical knowledge.

We are fortunate at Kew to have a few such generalists. Some of them are here with us today – I will not embarrass them by naming them. But the point I want to make is that until recently at Kew we were taking their generalists skills for granted. We were directing them to act as specialists while at the same time we were behaving as if their generalist expertise would always be available to us. There were even botanists who would do their general naming of their own collections across the herbarium outside official hours since it was not seen to be part of the their core job and because they felt they could not justify spending part of their working day on it. I believe that this was a fundamental error because it is the presence of these generalists, as much as the breadth and depth of our collections, that makes Kew such a great place to attempt to name a mixed bundle of specimens from any part of the world. And as some of us know only too well, such generalist skills cannot easily be put on ice, if they are not used on a regular basis they may decline rapidly. It is a question of use it or lose it.

So as a result of our science strategy review we are seeking to balance the need for focused enquiry with that of continuing our tradition of generalist plant identification skills. And, as I have said, we have established several teams within the herbarium that have a regional remit. Staff in these teams have or will develop general identification skills, based on their experience in sorting, identifying and curating the great variety of material that comes into Kew. For an institution seeking to promote conservation and sustainable use, developing these generalist skills is just as important as encouraging the publication of specialist papers in *Nature* or *Science*. As usual in life, it's a question of working to get the balance right.

By broadening our plant identification capacity, we believe that Kew will be better able to contribute to conservation assessment in the most biodiverse regions of the world. We hope this will help facilitate the selection, establishment and monitoring of *in situ* reserves, highlight critical groups for future focused study, and in the application of *ex situ* conservation approaches, and be of great practical value to those struggling to conserve and use plant diversity on the ground. In short, we hope that this shift in emphasis will enhance our relevance and the impact of our science in today's world.

So that is the plan. But how will we know if it is working? How will we know if we are succeeding in delivering more of what is needed now? Well, we have recently put in place a series of key performance measures which reflect our pre-occupation with access, relevance and conservation. In part these measures reflect the modern preoccupation with metrics under the old adage "what gets measured, gets done". But more importantly these measures provide us all with a point of reference. Some rules, if you like, for our work. We should always be asking what are the outcomes of what we do.

So what are we doing to deliver against these key measures in ways that will make a real difference in terms of plant conservation and sustainable use?

Well, under the first of our key measures we are seeking to enable greater access to our collections – both in terms of increasing the number of people who visit Kew and study the behind-the-scenes collections, and also increasing the number of collections which have been databased and/or imaged and so can be made accessible at some level via the Internet. Increasing access and use is the key justification for investment in curation.

Also, up till now our specimen digitisation projects have been fairly small scale, and focused on a particular group, which is being monographed or on a particular area – for instance we have databased some 20,000 specimens from Western Cameroon as part of a Darwin Initiative project designed to produce conservation checklists for this area. But over the coming year through a whole series of initiatives, we hope to see a step-change in the rate at which specimens are digitised at Kew so that a very significant proportion of the specimens of most interest to researchers elsewhere – and especially in Africa – can be made available via the Internet.

When I speak of digitisation initiatives to an audience interested in African botany, I can hardly fail to mention SABONET – not a Kew project but one we wholeheartedly support – which has been a fantastic success in terms of increasing access to existing information. Through SABONET over 1.1 million specimens have been databased and the annual rate of databasing of material now stands at 150,000 per year across the 16 participating herbaria. Across these institutions, databasing efforts have focused on grasses, with the result that an excellent dataset is being built up for one of the most useful groups of plants. And in parallel with these efforts SABONET has achieved a significant increase in local capacity to manage and curate herbarium collections. A high percentage of SABONET trainees became permanent members of botanical institutions. And, as we all know, curation is the key to keeping herbarium material accessible to those who need to consult it. The SABONET model is one to be emulated and I understand that BOZONET looks set to deliver similar benefits in East Africa.

Another key measure at Kew relates to our output of research publications. These include Floras, monographs and individual research papers. We are committed to maintaining our current high output so that we continue to make the results of our research available outside Kew. But more than that, we are now committed to making those research results increasingly accessible. Again, the Internet offers exciting new ways to do this. Recently, for example, we have started to pilot ways to make the information contained in Flora Zambesiaca more accessible via user friendly web-based queries and interactive dichotomous keys.

The Flora Zambesiaca started to be written in the 1960s and is the treatment of the species of Botswana, Malawi, Mozambique, Zambia, Zimbabwe and the Caprivi Strip. It is c. 60% complete and contains a wealth of information that we believe will be of use to a much wider audience than at present – provided that we can make it available in a more useable form. I am not going to attempt to explain the process in any detail but basically it is a fairly quick and highly automated method of turning text into a searchable database of information. The pilot version currently available on the web allows the user to look up any name and find the accepted name, full synonymy, geographical distribution and ecology – a fairly traditional use of floristic information. But it also allows the user to produce a checklist of species from a country or division. An added benefit is that once the information is databased, it is then possible to perform statistical analyses and address broader questions, for instance the analysis and classification of distribution patterns across large groups such as the orchids. This web site can be accessed at http://www.kew.org/efloras

All 30 of the published volumes of Flora Zambesiaca have now been databased and the pilot web page for euphorbs and orchids went live in August. We are currently conducting scalability studies and awaiting results of feedback before incorporating the rest of the families. So please do visit this pilot site. Play around with it, see if it delivers information in a form that's more accessible and useful to you than the traditional hardcopy flora format – and please let us know what you think of it.

Another good example of how we've been translating existing information into a more accessible and useable form is Sharon Balding's work using herbarium data to develop a targeted species collection guide, to assist seed collectors in Botswana. In order to compile this document, Sharon databased all of RBG Kew's herbarium collections of species on the SABONET Red Data List for Botswana and also the collections held at the Natural History Museum in London. From these specimen data, localities and times of seeding were extracted and put into a GIS for expedition planning. In addition, specimens were scanned and their images incorporated into the GIS to aid identification. The result is a digital and hard copy guide which tells our partners and seed collectors much of what they need to know about Botswana's 43 Red Data List taxa. An added bonus emanating from this process is that a lot of new information emerged about taxa previously designated 'Data Deficient'. This has resulted in new conservation assessments for a number of species. The immediate objective of this work was to increase the efficiency with which seed could be collected from species targeted for inclusion in the Millennium Seed Bank Project. This is a large scale, collaborative, conservation project and Africa is a major stronghold of its operations.

The Millennium Seed Bank Project International Programme is a ten-year global conservation programme (2001–2010), conceived, developed and managed by the Seed Conservation Department of the Royal Botanic Gardens, Kew in collaboration with partners all around the world with two principal aims:

- to collect and conserve 10% of the world's seed-bearing flora (some 24,000 species), principally from the drylands, by the year 2010;
- to develop bilateral research, training and capacity-building relationships worldwide in order to support and to advance the seed conservation effort.

To date the Millennium Seed Bank Project has developed formal partnerships in 16 countries with around 30 institutions. Many more are being developed. In Africa, the Millennium Seed Bank Project has active programmes in South Africa, Namibia, Botswana, Malawi, Kenya, Burkina Faso, Mali, Egypt and Madagascar.

In each partner country the project focus follows the national priorities determined by partners in the host country. And in terms of which species targeted for collection this invariably means focusing on 'the three E's' – endangered, economic and endemic species. Existing information about these target species varies enormously from country to country. For example in South Africa, where the Millennium Seed Bank Project programme concentrates on rare and threatened species, accurate and accessible information is available for this target group in the form of Pretoria's PRECIS database, extensive field guide literature, local expertise etc. As a result, in 2002/3 more than 90% of the collections made by the South African Millennium Seed Bank Project field teams were target species. In contrast, in Madagascar, where reliable plant species information is very limited, our success rate in collecting target species is much lower.

SABONET's recent Red Data listing programme has provided the Millennium Seed Bank Project with valuable information about rare and threatened species in southern Africa. These are a priority in all our African partner countries, and because of SABONET there is now good information about which species these are for Namibia, Botswana, Malawi and South Africa. However, in order to collect the seed of these species, we also need to know where they occur, what they look like and when they are likely to be in seed. This is where Sharon's work comes in – preparing a summary of current knowledge and analysing it using GIS to extract the maximum value from the data available and summarise it in a handbook together with identification aids for the seed collectors.

This successful approach has recently been repeated for the Malawi Red Data List by Mala Ram, a sandwich student also based in Kew's GIS Unit. The Malawi targeted species collection guide contains locality, phenology and identification information on 191 Red Data List taxa. In addition, Mala has reassessed all 63 data deficient species on the Malawi Red Data List, based on Kew herbarium data. Sixty of these species look as though they have may need different IUCN ratings. The Millennium Seed Bank Project collecting programmes in Malawi and Botswana will start later this year, and these collection guides will again form the basis of expedition planning – so as to make it more efficient and as useful as possible.

In conjunction with its partners the Millennium Seed Bank Project has recently undertaken to expand this methodology to encompass ten other partner countries in Africa. In order to achieve this, a proposal was submitted to the Millennium Commission earlier this year requesting funds to database, scan and carry out conservation assessments on 10,000 Millennium Seed Bank Project target species. The application was successful, and this three-year-project will start in January 2004.

Having developed the tools to locate and recognise target plants, the Millennium Seed Bank Project country programmes are now actively trying to find them. This is important not only to collect seed and conserve these species long term, but also to provide species and population information about target species to those responsible for *in situ* conservation.

For rare and threatened species in South Africa, the Millennium Seed Bank Project together with the National Botanical Institute has been piloting the idea of Threatened Species Dossiers. These attempt to systematically record all that is known about a particular species, and include: information from the literature, field data, and germination/propagation protocols. Most of the information recorded in these Threatened Species Dossiers is new and is generated as part of the Project. Thus, up to date, detailed population data on ecology, habitat, threats etc. is collected by the field teams, germination protocols are developed by MSB staff and propagation protocols are developed by horticultural staff at Wakehurst Place and partner institutions. The aim is that these Threatened Species Dossiers will help local conservation authorities to develop species conservation strategies based on thorough scientific knowledge – not just for *ex situ* approaches but for *in situ* work too. In cases where reintroduction or translocation are considered, the Millennium Seed Bank Project will be in a position to supply not just seed, but information about how to grow and manage the plants as well. We are currently looking at ways of upscaling this activity in the context of the National Botanical Institute's Threatened Species Programme, and are looking at other countries in which this approach might be applied.

In terms of the science needed for conservation, I think this connection between *ex situ* and *in situ* conservation is critically important. Traditionally, botanical gardens have been well known for their role in *ex situ* conservation: both through the *ex situ* conservation of plants in the living collections and also through initiatives such as Kew's Millennium Seed Bank. Such a Noah's Ark approach, which simply ensures survival, is fine as far as it goes. But if botanic gardens stop there then I believe that they are not really fulfilling their potential. Keeping living plants or seed in the garden for purposes of conservation is an important insurance policy, but it is very limited compared to utilising them more broadly not only for exhibits and interpretation, but also for reintroduction and restoration programmes.

In the case of individual living plants growing in the safe-haven of the garden, it is probably only possible to attempt small-scale reintroduction programmes. Nevertheless these can be very important. For example, we are involved in reintroducing the native British lady slipper orchid *Cypripedium* back into its few native localities in Yorkshire. We grow the plants up in the micropropagation unit, get them established, and then plant them out in the wild using genotypes that are as close as possible to those which exist in the wild. We are also working on similar reintroduction projects in other parts of the world.

At broader scale, ecological restoration too, I think, is important and the seed bank that we are developing at Kew needs to connect with restoration initiatives worldwide. To be useful as a bank you not only need the capacity to make deposits, but you also have to make withdrawals. It is important for the Millennium Seed Bank project that we are able to make withdrawals that are able to support restoration and reintroduction programmes. The Threatened Species Dossiers backed up by horticultural skills and knowledge about seed germination and viability represent a step towards making this vision a reality.

Turning now to *in situ* conservation, the old adage that prevention is better than cure is also true with respect to plant conservation, as it is in so many other areas of life. *In situ* conservation is a much more cost effective way of saving ecosystems than restoration. And I am keen that we try to find way to make Kew's expertise helpful in this area.

It is in fostering *in situ* conservation that simple baseline, surveys and inventories have a critical role to play. For example, the new species of *Dovyalis* in the Flacourtiaceae was discovered in the course of fieldwork undertaken by Martin Cheek, Jean Michel Onana and other staff from the National Herbarium of Cameroon. Together with Earthwatch volunteers, Martin and Jean Michel were conducting an inventory of the plants of Mt Oku and the Ijim Ridge, a protected area managed by the Kilum Ijim forest project, funded by BirdLife International. The species is represented by a small population of just a handful of individuals at a single site within the reserve. But having drawn this to the attention of the Kilum Ijim Forest Project and BirdLife International their staff actively sought further trees of this species. A previously unknown population was located some 10km from the first outside the reserve boundary in a patch of forest belonging to an adjacent village. At the time, the project staff were already involved in helping these villagers to draw up a management plan for their forest, so there was a perfect opportunity for them to draw attention to these trees and include them in the management plan. This raised awareness in the village of the importance of the tree and encouraged an active interest in protecting them. Rita Ngolan, currently attending the International Diploma Course in Plant Conservation Techniques has just completed a description of this new *Dovyalis*, along with a conservation assessment. It is listed as critically endangered but almost certainly at lower risk now that the villagers are aware of its significance.

This same team of collaborators from Kew and the National Herbarium of Cameroon have also conducted inventory work in the Bakossi Mountains in Western Cameroon and just last month they heard the very welcome news that the Ministry of the Environment and Forests has taken the first steps towards gazetting this area as a national park. The results of the botanical inventory work were a key component of the evidence submitted to support the award of protected status to this area. So congratulations to Achoundong, Ghogue, Sonke, Zapfack and colleagues and best of luck with the next challenge, to get the same status for Mefou, another of their inventory sites.

If the Millennium Seed Bank Project is one of the flagship conservation projects supported by Kew, then the equivalent for the sustainable use of plant resources must be SEPASAL – the Survey of Economic Plants for Arid and Semi-arid Lands. Again, this is a global project with its centre of gravity placed very firmly in Africa.

SEPASAL is a major database on useful "wild" and semi-domesticated plants of tropical and subtropical drylands, developed and maintained in the Centre for Economic Botany (CEB) of the Royal Botanic Gardens, Kew. It began in 1981 with funding from OXFAM and over the years this has been developed first into a PC database and now into an internet version. The database now contains information on more than 6,200 useful dryland species, excluding major crops. It is widely used by aid and development organisations, government departments and non-governmental organisations to help support sustainable use programmes in drylands. SEPASAL can be accessed on the Internet by following the links from our home page at http://www.kew.org/ceb/sepasal/

A new innovation in the SEPASAL project is “Global Editing” software, developed at Kew, which enables remote data entry into SEPASAL via the Internet, so that contributors can submit updates to information held on SEPASAL, and so that Global Editors with expertise in certain species or regions have editorial control of the data on SEPASAL for “their” species. Other advantages of this approach are that editors and Contributors receive acknowledgement on the Internet pages on their species; editors can add their own data to SEPASAL and can receive data submitted by other researchers and fieldworkers worldwide; and the web will only show data that have been checked and committed by the editor of that species. Global Editing software also enables partner organisations to use SEPASAL as a tool for recording information on plant uses. The first overseas node for SEPASAL has been established at the Kenya Resource Centre for Indigenous Knowledge (KENRIK), as part of a collaboration between the National Museums of Kenya (NMK) and Kew; a second node will soon be established in Namibia with funding from the UK Millennium Commission.

Another project closely linked to SEPASAL started last year under the title African Wild Harvest, a collaboration with the Medical Research Council Resource Centre for Human Nutrition Research (HNR). Its task is to collate from primary scientific papers, widely scattered information on the nutritional content and value of sub-Saharan African wild plants, and to assess its quality. The initial phase is focusing on priority Ethiopian species. Nutritional data are entered into a fully referenced database from which food tables can be developed. The data will be linked to SEPASAL and, in the longer term, it is planned to develop methodologies for assessing the nutritional contribution that wild foods make to the food basket of rural African communities.

Kew is also an active participant in PROTA, Plant Resources of Tropical Africa, which is represented here at this meeting and is an international collaborative programme with the objective to synthesise and distribute the widely scattered information on about 7,000 species of useful plants of Tropical Africa. This EU funded project is co-ordinated from the Netherlands with regional Offices in different countries in Africa. Kew acts as a Country Office collecting information within UK on the uses of plants. It is proposed to publish the resulting information in a series of books as well as via the Internet.

As well as these Africa-wide projects, there are a variety of other sustainable use projects in various African countries. These include: working through the Uganda High Commission with Uganda’s Department of Health and the Department of Agriculture to assist them to identify medicinal plants that could be grown sustainably for trade; working with Nairobi University collating information about 70 of the 300 species of *Plectranthus* that have established traditional uses, especially as dyes and for the treatment of diseases; and working on sustainable use projects in Ghana where many rural communities rely on plant-derived extracts to decrease the damage done by insect pests to their crops.

Kew’s focus has traditionally been on tropical Africa but one of our most exciting collaborations in recent years has been with Tunisia in a British Council/Darwin funded project on conservation of medicinal plants. The overall objective is to collate and conserve information about the current uses of medicinal plants within Tunisia and evaluate the activity of 200 species of these plants. Twenty-five students have been involved in the research, of which ten have gained their PhDs. To increase public awareness within Tunisia about the importance of plants the Department of the Environment agreed to support the development of the first national Botanical

Gardens outside Tunis. The designs for this garden have been completed, the grounds in Monastir cleared and the construction of the gardens started. The aim is to display samples of the medicinal plants in the garden along with signage to explain the traditional and present day uses of the plants.

Overall we are pleased with what has been achieved over the past few years in working on our new approach and in working with our partners.

But the more we do the more we are conscious that it is not enough and that we need to move further in some of the directions we have already identified. We need to try to be more responsive to the needs that our partners identify, and we need to be even more creative in getting the best out of the unique resources that we have at our disposal.

We have already come a long way in recognising that it is part of our mission to transfer the information that we have gathered to places and to people to whom it can be most useful. The baseline data gathering and description of floras, which is a central and underpinning element of our programme will go on, and we will continue to work to present that technical information in diverse accessible forms – as you have seen today with the FZ and the MSB initiatives I described.

But beyond that, and more broadly, I believe the way forward is to transform technical data to a form which can be used by anyone, most of all by those who may not have that technical background and who may not have access to the Internet. Producing simply written, illustrated handbooks and guides is one way. Similarly, people who work with nature do not necessarily need identification books – they know their plants – but they may not necessarily know how common or rare a species is in the world and how best to utilize it in a sustainable manner or how best to protect it. But knowledge of this kind must be made available at a local level in order to bring awareness and understanding of the nature around us, its fragility and the importance of its protection and conservation. Our experience in Cameroon and also in Brazil has convinced us that the most effective way of getting down to this small scale and local level is to work together with local communities – sometimes through the intermediary of an NGO, and sometimes directly. It is at this level that *in situ* conservation actually works or fails to work.

At the other extreme, we are also acutely aware that we need to do more, and do it on a larger scale with broader networks of collaborators, if we are to achieve results on a time-scale in keeping with the urgency of the task that faces us. This is not quite the paradox that it might at first seem. The trick will be to connect the local to the national, and the national to the global, so that success breeds success and builds its own momentum. We hope that our Seed Collector's Handbooks will prove to be a good example of this phenomenon, scaling up from a successful project in a single country to at least ten countries over the next three years.

We are excited too about the potential offered by the Mellon Foundation's interest in an African Types initiative. It may allow us to build on the country-by-country digitisation and data-sharing experience built up over the past few years by the National Botanical Institute in South Africa, by Missouri Botanical Garden, by Kew and by many other institutions focused on African botany and who are all trying to be helpful in their own ways. The outcome could be unprecedented access to essential research materials for African botany – types and original literature.

I have deliberately left till last a topic which I believe has been the most exciting development in plant conservation since the last AETFAT meeting – the Global Strategy for Plant Conservation, ratified in April 2002 by the parties to the Convention on Biological Diversity. This is not just another international agreement, but it sits right in the middle of our plant diversity interests. Importantly, it is also an agreement with specific time-bound targets and as a community we need to make the most of this opportunity.

I am sure that the many plant taxonomists here today will find it particularly pleasing to see that Target 1 is the production of a widely accessible working list of all known plant species as a step towards a complete world flora. I, like others in the room, want the complete world flora but I would like the checklist first – and I think we need it soon. This target recognises the central importance of baseline data for any conservation action and we need to get on and deliver it. Over the summer Kew has been facilitating the stakeholder consultation on Target 1 and there has been a lively discussion on what exactly is meant by a working list, what should be included and so on. I know that many of you participated in the consultation process, which was largely done electronically and so you will be aware that the official deadline for submission of stakeholder reports was a week ago. Alan Paton assures me that we did in fact get the report in to the CBD secretariat just in time last week. But I understand that there is still a chance to have input into the process and Alan will be holding a meeting later this week to discuss the report with anyone interested and make revisions if necessary.

I have dwelt on Target 1 because it is of particular interest to taxonomists but, going back to my premise that most taxonomists are conservationists at heart, all 16 targets laid out in the strategy are exciting, challenging and relevant to us. For example, Target 2, a preliminary assessment of the conservation status of all known plant species, at national, regional and international levels, is one to which all taxonomists can contribute.

In many ways I think Africa is ahead of the game with respect to Targets 1 and 2. Products such as Lebrun and Stork's checklist for Tropical Africa, and the Black Book for South Africa, go a long way to meeting Target 1, and there are no really comparable products on the same scale for Tropical America or Tropical Asia. And the fact that Lebrun and Stork are now documenting Ecology and Distribution for their checklisted species provides a fantastic basis for the production of preliminary conservation assessments.

Target 8 sets out the objective of having 60 per cent of threatened plant species in accessible *ex situ* collections, preferably in the country of origin, and 10 per cent of them included in recovery and restoration programmes. It is another very challenging target but also one where the prospects for success are probably as great if not greater in Africa than in any other tropical region, not least because recalcitrance is likely to be less of a problem in seeds of many African species than in those from other tropical areas.

Stella Simiyu will be speaking on the Global Strategy for Plant Conservation in greater detail tomorrow. She is now the CBD secretariat's point person for the Global Strategy and knowing Stella's energy, enthusiasm and sheer capacity for hard work we are looking forward to seeing great things from this direction over the next year or two. We all need to give her the support she deserves.

If we are to come close to achieving some or all of the targets outlined in the GSPC it will be by virtue of a sustained and continuous effort over many years, and success, if it is to be had at all, will be hard won and likely built on tens of thousands of small local achievements set in the broader context of continent wide and global initiatives. It is also very clear that if we are to realise our goal of conserving the remarkable plant diversity of Africa, it is the people in this room who will be in the front lines of these day to day efforts.

websites

Flora Zambesiaca: http://www.kew.org/efloras/
SEPASAL: http://www.kew.org/ceb/sepasal/

THE ETHIOPIAN FLORA PROJECT

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1 Background

The Biology Department in the Science Faculty was established in the 1950s as a department of the University College of Addis Ababa. In 1959, the National Herbarium (the base for the Ethiopian Flora project) was established.

As most of you are aware, Ethiopia has the whole range of climates in which higher plants can grow – from dry to moist and from hot to cold with altitudinal variation ranging from about 126 metres below sea level in the Danakil Depression up to 4,620 metres above sea level at the Ras Dejen (Dashen) – and this has created favourable conditions for biological diversity. The number of species of higher plants found in Ethiopia is estimated to be around 6,500, with about 10 percent endemism.

Ethiopia is one of the 12 major centres of crop genetic diversity in the world. These are known as Vavilov Centres, named after the Russian scientist who collected and studied crops from around the world and who visited Ethiopia in the 1920s. Over 100 species of cultivated crop and their wild relatives are found in Ethiopia. For some of these crops, e.g. arabica coffee (*Coffea arabica),* teff *(Eragrostis tef),* enset (*Ensete ventricosum*) and anchote (*Coccinea abyssinica*), Ethiopia is the sole centre of genetic diversity. This is because these crops are either grown only in Ethiopia, or if grown outside, e.g. arabica coffee, it is within the last few hundred years. The country is also one of the main centres for a number of major crops, e.g. sorghum (*Sorghum bicolor*), finger millet (*Eleusine coracana*), field pea (*Pisum sativum*), lentil (*Lens culinaris*), chick pea (*Cicer arietinum*), perennial cotton (*Gossypium arboreum*), safflower (*Carthamus tinctorius*), castor oil bean (*Ricinus communis*) and sesame (*Sesamum indicum*). This is because it is either their centre of domestication, or else they came early on in the development of agricultural activities, and have thus developed distinctive variation found nowhere else. For three other major crops, linseed (*Linum usitatissimum*), durum wheat (*Triticum durum*), and barley (*Hordeum vulgare*), Ethiopia is the most important centre because, though these crops were domesticated elsewhere, the modernization of agriculture in their centres of origin has seriously eroded their genetic base in those countries leaving Ethiopia with the main extant gene pool. There are some very promising potential crops; important examples are *Cordeauxia edulis* (the Yeheb nut) and *Vernonia galamensis.*

The Ethiopian Flora Project was started in 1980 as a joint collaborative project between the University of Addis Ababa, Ethiopia and the University of Uppsala, Sweden. Financial support has been given consistently from the Swedish Agency for Research Cooperation with Developing Countries (SAREC), now part of the Swedish International Development Co-operation Agency (Sida).

2 Objectives

The objectives of the Ethiopian Flora Project are:

- write up a Flora of Ethiopia within the shortest time possible, this being the principal objective of the project;
- effect training;
- build-up a National Herbarium and a related library to be used as reference centres for pharmacognosists, agriculturists, foresters, wildlife specialists, etc.;
- promote scientific activities in taxonomic botany, economic botany, forestry, plant ecology, plant physiology, etc.

3 Achievements

1. Write up a Flora of Ethiopia. Publications: the production of publications is one of the most important results of the Ethiopian Flora Project.

The Flora of Ethiopia is planned to appear in 8 volumes:

- **Volume 3**, covering 44 families and 1107 species, was published in 1989. It includes the legumes and the most important trees and shrubs for gums and resins.
- **Volume 2 part 2** was published in 1995, covers 26 families and nearly 700 species of herbs, the Cucurbitaceae and Malvaceae, shrubs, particularly those in the Euphorbiaceae, and trees, not least the Myrtaceae which includes *Syzygium* and *Eucalyptus*.
- **Volume 7** was published in 1995 and contains the grasses (over 600 species) while
- **Volume 6**, which was published in 1997, contains 48 families and 700 species of monocotyledons other than the grasses.
- **Volume 2 Part 1** was published in 2000 and contains 61 families and about 680 species.
- **Volume 4 Part 1** contains 13 families and 294 species. It has been published in 2003, in time to be available for the XVIIth AETFAT Congress held in Addis Ababa.

Volume 4 Part 2 which includes the third largest family, Asteraceae, containing about 450 species, 98 of which are endemic to the Flora area and

Volume 5 covers 28 families and an estimated 600 species.

Both books are being finalised for publication by the end of 2004.

The total number of vascular plant species that have been treated in the published volumes 2, 3, 4.1, 6 & 7 of Flora of Ethiopia and Eritrea is over 4000. The remaining volumes, including the conifers and ferns are expected to cover some 2000 to 2500 more species.

The estimated total number of vascular plants species that are so far known from the Flora area is therefore around 6000. Of these about 10%, 600 species, are endemic to the Flora area.

Contributors

Country	Contributors
Austria	2
Belgium	2
Denmark	2
Egypt	1
Ethiopia	10
Germany	6
Italy	1
Kenya	1
Norway	3
South Africa	2
Sweden	9
Switzerland	2
The Netherlands	5
UK	27
USA	3
TOTAL	76

There are 76 contributors from 15 countries involved in the writing up of the Flora of Ethiopia.

Training

A vital component in the building-up of the National Herbarium, and undoubtedly the most important component of the Project from the Ethiopian side in the context of sustainability, has been the training of human resources. The Herbarium now has, through the Project, a corps of well-trained botanists and support personnel to sustain continued research and publication on various aspects of botany. The National Herbarium in Addis Ababa is generally recognized as one of the best-staffed and most active institution in tropical Africa.

Build-up a National Herbarium and a related library to be used as reference centres for pharmacognosists, agriculturists, foresters, wildlife specialists, etc.:

- **Collections of The National Herbarium**
  The number of specimens in the National Herbarium has increased from about 14,000 in April 1980 to over 76,000 in July 2003. The staff of the Herbarium and other researchers of the Biology Department carry out research on Ethiopian plants utilising these specimens and other facilities provided by the Ethiopian Flora Project.
- **Herbarium Library and acquisition of literature**
  Another component planned as part of the Herbarium's development was the accumulation of literature and other sources of information for a library to adequately support the research activities. The herbarium library has acquired much relevant botanical literature through purchase and as gifts, but this part of the project's objectives has not been as satisfactory as the other components. However, since the National Herbarium has been able to purchase its literature direct, with assistance from the Ethiopian Science and Technology Commission, the volume of books has increased greatly.

Services

The National Herbarium also provides plant identification and consultancy services to development organizations and to researchers. The Ministry of Agriculture is the main user of these services, particularly in crop protection, bee keeping, the countrywide survey of woody biomass and livestock development and research.

Does the completion of the Flora mean the end of the study on the Flora of Ethiopia?

Some might think so. However, the completion of the Flora means the state of knowledge on the plant resources of Ethiopia as we know it today. There are some areas of our country where we had inadequate collections and hence our knowledge is rather incomplete. These include the Ogaden, the Afar and Benshangul Regions. We need to do more. Having a Flora will help us to organize new information i.e. the recognition of new taxa will be easier. Even after the present Flora is completed, the staff of the National Herbarium and others will continue research into the flora of the country and knowledge on the total number of species and the proportion of endemics among them will keep being updated.

The Flora will also provide us basic information from which we can produce more simpler books, guides that both the professional and the amateur can use. Members of the Flora project will do what they can to produce such books with minimal support. The field guides to the orchids of Ethiopia, the flowers of Ethiopia and Eritrea: aloes and other lilies are hopefully just the start.

We would also like to move into new areas of research such as the conservation of threatened plants, identification of important hot spots, and working on the compilation of more information on the different vegetation types in the country. Here we would like to have collaboration with national and international agencies like Sida who are dealing with development activities in various parts of our country. These are things which only could be done once we have the basic information on the flora.

Now high natural forest covers less than two percent of the country, and as much as half of the cultivable land is eroded to varying degrees of severity. And yet indigenous trees are not planted, nor forage for domestic animals cultivated. The environmental degradation seen throughout the country is endangering many species. It is very likely that a number of them have already become extinct. There has not been enough specific investigation to say this for certain, but preparation of the family accounts for the Flora has identified many species that are rare and endangered. For example, there are records of plants found in the last century, which have not been found again despite searches for them.

Now we have information, on the national level, we would also like to collaborate with regional governments in identifying the plant resources in their regions, which would help them in development programs be it in rehabilitation of degraded areas, afforestation programs and for other purposes.

No area of Ethiopia, even Addis Ababa, has its plants very well known. Some of the least known areas are as follows:

- The plants that survive in the desert of the Afar with the Awash River and its associated lakes and the Dallol Depression going to 126 metres below sea level. Although considered one of the hottest places on the earth's surface, drought resistant woody plants including the dum palm (*Hyphaene thebaica*) grow there.
- The lowlands on the western border with Sudan and the south and southeast borders with Kenya and Somalia have mosaics of woodland and grassland, and are also traversed by large river valleys. These areas are all poorly known biologically, but enough has been documented to show that they are rich in

natural resources, particularly plants which support the pastoralist peoples and their herds that have lived long in these areas. The trees in these areas also supply the gums and resins, which Ethiopia has been exporting since pre-Christian times.

- The lowlands of Oromiya Region in Borana and Bale Zones, and the Ogaden and Liben (Borana) areas of Somali Region have been found particularly rich in plants and birds unique to Ethiopia. Although heavily utilized by agricultural man for centuries, the indigenous plant resources of the plateau, particularly the wetlands and areas away from main highways and tracks, although heavily exploited, are still mostly unexplored.

The Flora is published, but should it be kept on our shelves?

Now we have documented the flora we would like and encourage all those institutions and individuals that need these information to get it and use it. We would for example like the flora to reach every high school in the country where staff and students will have access to be information available and will undoubtedly help them to know the resources in their surroundings. Student text books still use examples of plants that are not known to the students. We would like it also to reach to agricultural institutions that would make use of it.

4 Future direction

It is expected that by the end of 2004 the writing up of the Flora will be finalised. This Flora will be revised from time to time taking into consideration new information on the plants found in Ethiopia, especially from those areas in which there has hitherto been little botanical exploration. It is anticipated that the published Flora will help in producing regional Floras, handbooks and field guides, and accounts of economically useful plants (food, medicinal, stimulants, weed, poisonous, ornamental, etc.). The availability of the Flora is also enabling the characterization of the Ethiopian vegetation and detailed ecological studies on selected species and communities.

Acknowledgements

The Ethiopian Flora project would like to acknowledge the following:

The Swedish International Development Agency (Sida) for their continued financial support over the last twenty three years through Sida-SAREC and Uppsala University for providing the base for the Ethiopian Flora project in Sweden.

The Ethiopian Science and Technology Commission and Addis Ababa University on the Ethiopian Side for their continued support.

I would also like to acknowledge to all the partner institutions and individuals that have played active roles in the development and finalization of the Ethiopian Flora Project. The important ones include: Uppsala University, Department of Systematic Botany, Evolutionary Biology Centre, where many of the staff completed their doctorates, and the Royal Botanic Gardens, Kew, UK where a lot of the accounts for the Flora have been prepared; the Botanical Museum of Copenhagen University in Denmark, and the Biology Department of the University of Oslo.

ADDRESS AT THE PRESENTATION OF THE ETHIOPIAN FLORA ON THE 25TH SEPTEMBER, 2003

Håkan Åkesson

Ambassador of Sweden to Ethiopia

Prof Endrias, Commissioner Mulugeta, distinguished guests, ladies and gentlemen,

It is a great honor to be here to attend the launch of the Ethiopian Flora.

During the last 23 years Ethiopian, Swedish and other researchers have devoted a tremendous amount of time and energy to produce something, which will last for generations to come. One cannot overemphasize the importance of having a national Flora. It is a wonderful achievement – and we are very proud to be part it.

Sweden is a country far away from Africa. In my garden here in Addis Ababa there is a sign pointing north, saying "Stockholm 5912 km".

We never had, or wanted to have, any colonies.

We got to know Africa quite late.

But when we finally did – at the end of the 19th century – we immediately felt at home on this beautiful continent. We came to like and respect the Africans.

Ethiopia became the first country on this continent that we got to know well. It also became our first development partner, not just in Africa but anywhere in the world. Relations between our countries have ever since been very special. We understand each other, we work well together.

Last spring, Sweden and Ethiopia finalized a new cooperation agreement, whereby we are further increasing our engagement with the country – in fact we will double it. One of the key areas for our cooperation is rural development. Here, the protection of the environment plays an important role.

We were engaged in the CADU project – probably well-known to many Ethiopians in the audience, we are still engaged in the Wondo Genet College of Forestry and work with the government of the Amhara region in a large rural development program where the sustainable use of natural resources is greatly emphasized.

We are also involved in research cooperation. Here, Ethiopians and Swedes have worked together to find ways to protect the environment and make use of the rich biodiversity of this country. It is, therefore, perhaps, not so surprising that the Ethiopian flora project was initiated by Addis Ababa University and the University of Uppsala in Sweden and became a project financed by SAREC, now part of Sida. Ever since the start, these three institutions have worked in true partnership to produce the flora.

Many people link the University of Uppsala to a well known Swedish scholar, Carolus Linnaeus, who held the title of Professor of Biology at that university from 1741 to 1777. During that time the language of instruction in the Swedish universities was Latin, hence his name, Carolus Linnaeus. He is perhaps best known by his Swedish name Carl von Linné.

I think you can guess why I am talking about this ancient man. You know, of course, of the classification of the flora, fauna and minerals emanating from a system invented by Linné in 1735 in his Systema Naturae. His system for the flora contained 23 classes based on the number of stamens, their size and distribution, plus one class for cryptogams. In his book Philosophia botanica he organized the flora in a natural system with 60 families, a system which is still existing today. Linné published the first comprehensive description of the Swedish flora in 1745.

During his time as a professor at the University of Uppsala he travelled extensively in the Swedish countryside to systematize the Swedish flora and fauna. He also trained an abundance of disciples, which in their turn travelled throughout the world – to Australia and Japan, and to southern Africa.

As modern disciples of Carl von Linné, scholars from the University of Uppsala arrived in Ethiopia in the seventies and eighties. Here, they found not only a country full of beauty and history. They also found a people who – like us in Sweden – are very attached to their land and natural resources. They found good academic institutions and devoted researchers.

Due to the enthusiasm and hard work of these Ethiopians, Swedes and others we now have a national Ethiopian Flora.

I would like to pay tribute to these researchers. Their work is indeed a fine example of the long-standing cooperation that exists between Sweden and Ethiopia. Let their work now be disseminated to schools, libraries, universities and research institutions throughout the country.

Finally, I would also like to pay tribute to all the participants of this congress. You do a tremendously important work for your countries – and for the world community at large. I wish you all the best for the future.

Thank you.

ADDRESS AT THE LAUNCH OF THE FLORA OF ETHIOPIA AND ERITREA, ADDIS ABABA, SEPTEMBER 25, 2003

BERIT OKSSON

Director, SIDA, Department for Research Cooperation, SAREC

Mr Chairman, Professor Endeshaw Bekele and Dr Asrat Bulbula, President of AAU Professor Andreas Eshete, and Commissioner of ESTC, Dr Mulugeta Amha, your Excellencies, dear colleagues.

It is a great pleasure and honour for Sida to be present here today. We are here to recognise the completion of a tremendous undertaking, the work behind the production of the Ethiopian Flora. It is also a great pleasure for me personally. Thirty years ago, I came with my husband and children to live in the Ethiopian highlands, in Chilalo, Arsi some 200 km South of Addis Ababa. It was our good fortune to actually live in the countryside, where we came close to people and close to nature.

Very soon we saw the very varied vegetation with lots of plants we had never seen before. We also understood that there was a lot of local understanding on how plants, trees etc could be used, many for medicinal purpose, others as detergents etc. Everyone knew the use of kosso, and other plant extracts for the cure of stomach ache and other conditions.

In my work as the local dentist, I took a special interest in the Mefaka. The mefaka is a twig of a tree chewed into a toothbrush. I wrote an article of its effectiveness as a tooth brush and wanted to know more about what species was used. People could then point to the tree and give us a local name, but no one could give us a name translated in the dictionary.

We saw as well all the different grasses and came to be very fond of injera, the bread baked on teff, a grass we had not noticed elsewhere. We came to recognise the different qualities of the "netch teff" (a white variety of *Eragrostis tef*) , the "key teff" (a red variety of *Eragrostis tef*) and the "tikur teff" (a darker variety of *Eragrostis tef*) i.e. the white, red and black, all different varieties.

The knowledge on flowers was less specific. My mother asked about the name of different flowers. Her informer invariably replied "Ababa" (meaning flower in Amharic). Not satisfied with this answer she asked again. The patient informer slowly said "netch ababa" (white flower), "key ababa" (red flower) and "semayawi ababa" (blue flower), referring to white, red and blue flowers. One flower however, was known to everyone with a name. That was the yellow Meskal flower (*Bidens prestinaria*), the flower that turns the landscape into yellow fields. I sincerely hope that all of you will get the opportunity to see this enchanting scenery. It is as unique to Ethiopia as the thirteenth month, the month of Meskal, which starts now – on Saturday to be precise.

All these plants are naturally locally well known and have local names but many of them have not been known to the world. The Flora project, for the first time has gathered all these plants, and identified them in a systematic way. It has revealed close to 6000 plants, previously not known to the world, many of them endemic to these highlands. This is a fantastic contribution.

Sida has supported the work since 1980. I think this was a very wise decision, but it was as well a rather risky and courageous one. What convinced us was the fact that it was a joint undertaking based on an Ethiopian request, a request presented by the Ethiopian Science and Technology Commission. Professor Tewolde Berhan and Professor Olle Hedberg had agreed to collaborate.

SAREC was created in 1975 as part of the Swedish development co-operation. Its mandate was, and is, now that we are a Department of Sida, to support developing country access to research findings relevant to development. It was obvious that the overwhelming part of global research efforts was directed at phenomena and problems of the North. Only a fraction is directed to the problems of the developing world where 80% of the people live. Thus, SAREC was mandated to address problems of key relevance to combating underdevelopment and poverty. However, the Swedish bill went further than that. It underlined the importance of research in and by developing countries themselves, not only research on and for development.

The Flora project was among the first that started. Today we are very happy about this heroic decision. I have followed the project since mid-80s when I joined SAREC. I have been thoroughly impressed by the stamina and endurance of all involved. The contribution of Olle and Inga Hedberg goes far beyond collecting and determining plants. They have also engaged in research training of collaborating Ethiopian researchers through links with Uppsala University. Today, there is a cadre of very qualified Ethiopian scientists who themselves train and graduate new researchers at the Addis Ababa University. Professor Sebsebe Demissew, who later will present the Flora, took over co-ordination in 1996. His continued work illustrates beyond doubt the sustainability of the investments in efforts and funds.

We now understand as well that the completion of the Ethiopian Flora deserves a place in Guiness Book of records. Floras in general, I am told, take half a century to be produced. So 23 years of funding is very reasonable. Not the least since the eight volumes contain close to 7000 species. This is about 5 times as many as we can count in our Swedish Flora. It is an unbelievable richness.

Very many people have contributed. I have mentioned the professors Tewolde Berhan G. Egziabher and Olle Hedberg, Inga Hedberg and Professor Sebsebe Demissew. I know that they have benefited from the work of many scientists, also scientists from many other countries. They have benefited from the work of technicians, artists and editors and support staff. Together you have produced a true gift to the world.

You have also demonstrated that researchers in developing countries are important. They are essential not only for following, understanding, selecting and adapting global knowledge to useful applications for development. You have shown that developing country research also contributes to the global pool of documented knowledge.

The Flora has already proved its usefulness. It is used by researchers looking into biodiversity and by researchers analysing the ecological balance and the potential impact of transgenic plants. It is used by the School of Pharmacy in their analysis of medicinal plants. It has also caught international attention.

Now, it is up to all of us to make sure that the Flora is disseminated and brought to use. It should be distributed to schools and students all over the country, to teaching institutions and research universities in the country, in the region and in other parts of the world. It may as well be presented in a lightweight version. Sida will consider supporting a CD-ROM version for those who have access to such technology. But the most important and immediate challenge, is to make the printed volumes available.

It is also up to all of us to see that the endemic plants are protected. Knowledge should be freely available as part of our Global Public Goods and common heritage.

But let us ascertain that the Ethiopian ownership is recognised whenever the plants or their genetic properties are exploited commercially.

We in Sida are very proud to be associated with this tremendous achievement. We would like to congratulate the Ethiopian Science and Technology Commission, the Addis Ababa University, Science Faculty, Department of Biology and its Herbarium. With the completed Flora of Ethiopia and Eritrea, the world is a bit richer. Let us take care of that gift.

Thank you.

Bakker, F.T., van Gemerden, B.S. & Achoundong, G. (2006). Molecular systematics of African *Rinorea* Aubl. (Violaceae). In: S.A. Ghazanfar & H.J. Beentje (eds), Taxonomy and ecology of African plants, their conservation and sustainable use, pp. 33–44. Royal Botanic Gardens, Kew.

MOLECULAR SYSTEMATICS OF AFRICAN *RINOREA* AUBL. (VIOLACEAE)

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Abstract

Rinorea Aubl. (Violaceae) comprises 110–120 species in Africa where the centre of diversity appears to be in the coastal plain and the plateau areas of Cameroon and Gabon. We reconstructed phylogenetic relationships among 30 species of African *Rinorea* and allied genera, based on *cp*DNA *trnL-F* sequence comparison, and using *Hybanthus enneaspermus* as outgroup. Having sampled less than 30% of all currently known species we can already conclude that African *Rinorea* is paraphyletic with respect to the Asian species *R. anguifera* and *R. bengalensis*, and that Madagascan species stem from separate, unrelated progenitors. Within the predominantly actinomorphic grade a main zygomorphic *Rinorea* clade was identified. Shifts in zygomorphy are inferred to have occurred at least once during the evolution of African *Rinorea* with at least three reversals to actinomorphy. The radiation of African *Rinorea* is discussed in terms of habitat fragmentation-driven speciation during and after glacial maxima.

Résumé

Systématique moléculaire des *Rinorea* Aubl. (Violaceae) africains. *Rinorea* Aubl. (Violaceae) comprend 110–120 espèces en Afrique où le centre de diversité semble être la plaine côtière et les régions de plateaux du Cameroun et du Gabon. Les relations phylogénétiques entre 30 espèces de *Rinorea* africains et de genres proches ont été reconstruites sur base de comparaison de séquences *cp*DNA *trnL-F* et en utilisant *Hybanthus enneaspermus* comme groupe externe. En ayant échantillonné moins de 30% des espèces connues actuellement, nous pouvons déjà conclure que les *Rinorea* africains sont paraphylétiques par rapport aux espèces asiatiques *R. anguifera* et *R. bengalensis*, et que les espèces malgaches proviennent d'ancêtres séparés et sans lien de parenté. Au sein du grade principalement actinomorphe, un clade de *Rinorea* principalement zygomorphe a été identifié. Les passages à la zygomorphie se seraient déroulés au moins une fois au cours de l'évolution des *Rinorea* africains et au moins trois inversions vers l'actinomorphie auraient eu lieu. Le rayonnement des *Rinorea* africains est discuté en terme de spéciation provoquée par la fragmentation de l'habitat au cours et après les maxima glaciaires.

Key words: *Rinorea*, Violaceae, phylogeny, *trnL-F*, species radiation, center of diversity

1 Introduction

For many African angiosperm forest genera phylogenetic relationships (both at species and generic level) are poorly known, hampering better understanding of their ecology, biogeography and taxonomy. Molecular systematic studies are needed especially to fill this void and at the same time to provide a framework for identification of areas of endemism and their relationships. In addition, molecular phylogenies can offer an absolute time dimension enabling testing of hypotheses regarding timing of coevolution or effects of climate change on speciation rates (e.g. Becerra, 2003; Linder, 2003).

Rinorea Aubl. (Violaceae) comprises approximately 200 species of woody shrubs distributed in Old and New World tropics (Hekking, 1988). Of these, 110–120 are known from Africa where most species occur from Nigeria to Congo, with the centre of diversity in the coastal plain and the plateau areas of Cameroon and Gabon (Achoundong, 1996). *Rinorea* are the most speciose genus in subfamily Violoideae, the other genera in the tribe Rinoreeae (i.e. *Allexis*, *Decorsella*, *Gloeospermum*, *Hekkingia*, and *Rinoreocarpus*; see Table 1) being mostly monotypic to comprising <10 species. The taxonomy of the African part of this conspicuous genus has long remained elusive until a recent revision comprising two subgenera and 8 sections (Achoundong, in prep.), based primarily on androecium symmetry. The genus has been treated by Hekking (1988) for the Neotropics where 48 species occur, whereas the 5 *Rinorea* species so far recorded from Asia have not recently been treated.

Generally, species of *Rinorea* are considered to be important and sensible bioindicators for forest typification as they are usually locally common to abundant and show close association with different forest types (Kenfack *et al.*, 2003). Distribution areas of forest *Rinorea* are mostly limited to the oldest forest types. The Cameroon coastal plain area contains some local endemic *Rinorea* species with extremely small distribution areas (Achoundong, 1996). Together these observations indicate the poor dispersal capacity of *Rinorea* species and hence the potential suitability of this genus for historical biogeographic studies.

It has never been tested whether all African *Rinorea* species are monophyletic, and what their phylogenetic relationships are with their African and Neotropical allies

TABLE 1. *Rinorea* and its allies within tribe Rinoreeae Reiche & Taubert with numbers of species indicated for Neotropics (NT), Africa, Asia and Australia/Pacific.

Violoideae
  Violeae (worldwide)
    Viola (400 spp.)
    Hybanthus (100 spp.)

Rinoreeae (tropics)	NT	Afr.	Asia	Au./Pac.
Allexis	-	3	-	-
Decorsella	-	1	-	-
Gloeospermum	14	-	-	-
Hekkingia[1]	1	-	-	-
Rinorea	48	120	12	2
Rinoreocarpus	1	-	-	-

[1] A new genus recently described by Munzinger & Ballard (2003).

within the subtribe Rinoreeae. It is estimated that 50 species of *Rinorea* occur in Cameroon and 17 in West Africa. It will be of interest to test whether the species from the central African centre of diversity are monophyletic with respect to species from more peripheral distribution areas such as Liberia, Ivory Coast, Congo (Brazzaville), Congo (Kinshasa) and East Africa. Armed with a (molecular) phylogeny we can address questions such as 1) do centres of diversity (i.e. the Cameroon coastal plain area) and origin coincide? and 2) what was the relative importance of recent radiation and/or dispersal in shaping current distribution patterns?

As mentioned above, African *Rinorea* still awaits full taxonomic revision, the last revisions were by Engler (1902) and Brandt (1914). Considerable work has been done recently by Achoundong (in prep.), focusing specifically on floral symmetry, inflorescence morphology, and phyllotaxis for (subgeneric) classification. Whereas all Neotropical species of *Rinorea* have actinomorphic flowers, most African species are zygomorphic, both with respect to corolla and androecium, a feature unique for the genus within Violaceae.

The great number of African *Rinorea* species possibly reflects an adaptive evolutionary radiation event, sensu Schluter (2000) who emphasises lineage splitting: “the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage”. Because of their close association with different forest types *Rinorea* species could indeed reflect an adaptive rather than a non-adaptive radiation, which Givnish (1997) defined as comprising “speciation without appreciable ecological divergence and evolution of corresponding adaptations (or involve adaptations that are only incidentally related to such divergence)”. This study presents the first (incomplete) molecular phylogenetic hypothesis for *Rinorea*, based on plastid DNA sequences from the *trnL-F* region.

2 Material and methods

2.1 DNA extraction, gene amplification and sequencing

Plant material used is listed in Table 2 together with accession details. Both newly collected material and herbarium specimens were used. Outgroups were chosen on the basis of previous molecular phylogenetic studies in Violaceae (Ballard, unpubl., pers. comm.). Methods for DNA extraction, PCR amplification (*cp*DNA *trnL-F*), BigDye terminator labelled sequencing, sequence assembly and alignment are described in Bakker & *al.* (1998).

2.2 Data analysis

The aligned sequences were subjected to both parsimony and Bayesian analysis, using PAUP*4.0b8 (Swofford, 1998) and MrBayes 3 (Ronquist & Huelsenbeck, 2003) running on a Macintosh G5 computer (see also Huelsenbeck *et al.*, 2002, and Archibald *et al.* 2003 for further information on phylogeny reconstruction using Bayesian statistics). Jackknife analysis was carried out using PAUP* with settings so as to emulate Parsimony Jackknifer (Farris *et al.*, 1996), i.e., percentage of characters deleted in each replicate = 37, ‘fast’ stepwise addition and “Jac” resampling method used. Heuristic searches involved TBR branch swapping, MULPARS, and collapse branches when maximum length is zero. Starting trees were generated by 1000 cycles of random addition sequence (RAS) holding 3 trees at each step, and keeping no more than 100 trees > length 296 steps. Trees resulting from this search were then used as starting trees in a subsequent search during which they were swapped to completion as far as possible.

TABLE 2. List of material used; [1]DNA was extracted from herbarium material; [2]seqence obtained from Harvey Ballard; [3]DNA extraction codes refer to WAG DNA bank.

Species	**DNA extr.**[3]	**GenBank**	**Collection**	**Locality**
Allexis cauliflora	Allex3	AY739760	Tinde van Andel 3244	Cameroon, Kribi, Mahale
Decorsella paradoxa	Deco11	AY739761	Jongkind 5026; WAG	Ivory Coast, Tabou
Hybanthus enneaspermus[1]	Hyba20	AY739762	Jongkind 2845; WAG	Ghana, Volta Region
Leonia glycycarpa	Leon33	AY739763	Lars Chatrou 404; U	Bolivia, UDNA 717
Rinorea albidiflora	albi13	AY739723	Achoundong 2121; YA	Cameroon, Njabilobe, Kribi–Ebolowa road
Rinorea anguifera	—	AY739754	Ballard 319[2]	Malaysia, ?
Rinorea angustifolia	angu10	AY739724	Achoundong 2117; YA	Cameroon, Douala–Edéa road
Rinorea arborea	—	AY739756	J-N Labat 3197	Madagascar, ?
Rinorea bengalensis	—	AY739755	MC ?[2]	India, ?
Rinorea campoensis	camp25	AY739725	Achoundong 2113; YA	Cameroon, Elogbantindi- Bella, SW of Edéa
Rinorea campoensis	camp30	AY739742	Gideon Shu X 8294; YA	Cameroon, Bipindi–Lolodorf
Rinorea caudata	caud7	AY739726	Achoundong 2104; YA	Cameroon, near Edea: 5 km on Edéa–Douala road
Rinorea cf. dimakoensis ined.	dima36	AY739728	Sonke 2591; YA	Cameroon, 10 km E of Kika village; 01°58'N 15°41'E
Rinorea cf. *kemoensis*	kemo29	AY739727	Sonke 2664; YA	Cameroon, ?
Rinorea crenata	—	AY739758	Ballard 94-006 WIS2	Costa Rica, Osa pensisula, SW of Rincon, 8°40'30'N, 83°30'W
Rinorea dewitii ined.	—	AY739744	Achoundong 2123; YA	Cameroon, Njabilobe, Kribi–Ebolowa road
Rinorea exappendiculata	exap46	AY739752	Wieringa 4382; WAG	Gabon, Ngounié, Sindara, ferry port to Ikobey
Rinorea gabunensis	gabu24	AY739741	Achoundong 2118; YA	Cameroon, Douala–Edéa Road
Rinorea gabunensis	gabu42	AY739739	Wieringa 4419; WAG	Gabon, Ngounié, 5km on the road Ikobey–Bakongue
Rinorea gabunensis	gabu40	AY739740	Wieringa 4451; WAG	Gabon, Ngounié, 10km on the road Ikobey–Bakongue

TABLE 2. continued

Species	**DNA extr.**[3]	**GenBank**	**Collection**	**Locality**
Rinorea ilicifolia[1]	ilic28	AY739753	Jongkind 3314; WAG	Madagascar, Mahajanga
Rinorea kamerunensis	kame6	AY739729	Achoundong 2111; YA	Cameroon, Elogbantindi- Bella, SW of Edéa
Rinorea ledermanni	lede22	AY739730	Achoundong 2116; YA	Cameroon, Douala–Edéa Road
Rinorea leiophylla	leio9	AY739736	Achoundong 2115; YA	Cameroon, Elogbantindi- Bella, SW of Edéa
Rinorea letouzeyii ined.	leto44	AY739734	Achoundong2180; YA	Cameroon, Route Bella
Rinorea longicuspis	longc8	AY739731	Achoundong 2112; YA	Cameroon, Elogbantindi- Bella, SW of Edéa
Rinorea longicuspis	longJM	AY739757	Munzinger & Karamoko 38; P	Ivory Coast, Songon-Kassembré
Rinorea longisepala	longs17	AY739732	Achoundong 2109; YA	Cameroon, Elogbantindi- Bella, SW of Edéa
Rinorea meziliana ined.	mezi16	AY739733	Achoundong 2119; YA	Cameroon, W of Song Mbong
Rinorea meziliana ined.	mezi43	AY739751	Achoundong?; YA	Cameroon, Kribi Boaben
Rinorea oblongifolia	oblo18	AY739735	Achoundong 2107; YA	Cameroon, near Edea: 5 km on Edéa–Douala road
Rinorea ovata	ovat26	AY739738	Achoundong 2122; YA	Cameroon, Njabilobe, Kribi–Ebolowa road
Rinorea ovata	ovat01	AY739737	Gideon Shu X 7751; YA	Cameroon, Bipindi–Lolodorf
Rinorea simonae ined.	simo15	AY739743	Achoundong 2110; YA	Cameroon, Bella, Ouest of Edéa
Rinorea sinuata	sinu45	AY739750	Achoundong 2178; YA	Cameroon, Route Song Ibog
Rinorea subintegrifolia	subi21	AY739746	Achoundong 2108; YA	Cameroon, Near Edea: 5 km Edéa–Douala road
Rinorea subintegrifolia	subi02	AY739745	Gideon Shu X 327; YA	Cameroon, Bipindi–Lolodorf
Rinorea verrucosa	verr47	AY739749	Wieringa 4474; WAG	Gabon, Ngounié, 10 km on the road Ikobey–Bakongue
Rinorea woermanniana	woer38	AY739748	Achoundong 2120; YA	Cameroon, Njabilobe, Kribi–Ebolowa road
Rinoreocarpus ulei	Rcarp31	AY739759	Lars Chatrou 403; U	Bolivia, UDNA 716

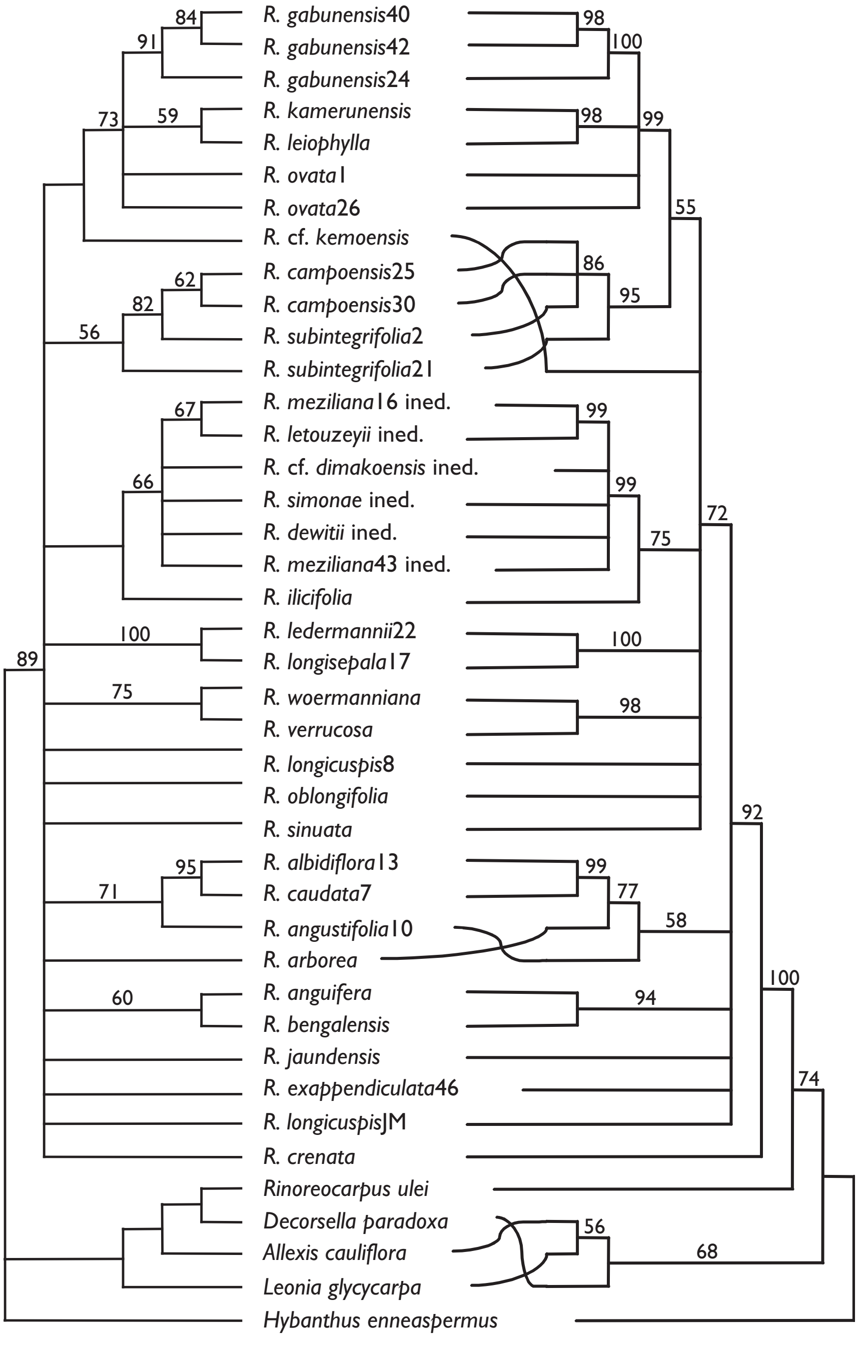

FIG. 1. *Rinorea* trnL-F. Left: semistrict consensus tree resulting from >50,000 equally MPTs found after heuristic parsimony search; jackkinife support values (10,000 reps) are indicated at the branches. Right: Bayesian consensus tree (1,000,000 generations) with posterior probability values indicated at the branches.

Bayesian analysis was performed on the *trnL-F* alignment excluding the recoded indels using MrBayes with the following settings. The maximum likelihood model employed 6 substitution types ("nst=6"), with base frequencies set to the empirically observed values ("basefreq=empirical"). Rate variation across sites was modelled using a gamma distribution (rates="gamma"). The Metropolis-Coupled Markov Chain Monte Carlo search was run with 4 chains for 20,000,000 generations, with trees being sampled every 100 generations. After discarding the first 100,000 trees as "burnin", Bayesian search results were summarized by 50% majority rule consensus yielding posterior probability values as 'clade credibilities'.

3 Results

A trnL-F alignment was created including 41 sequences of which 5 were considered to be outgroup taxa, i.e. *Decorsella*, *Allexis*, *Leonia*, *Rinoreocarpus*, and *Hybanthus enneaspermus* which was actually used to root the resulting trees. The alignment – including the outgroups – contained 1156 characters of which 88 were parsimony-informative. These included 7 phylogenetically informative indels, varying in length up to 56 nucleotides, which were considered to represent single evolutionary events and were scored as single binary characters irrespective of indel length. Parsimony searches conducted using the above-mentioned settings yielded >688,300 MPTs of length 295 steps (CI = 0.875, RI = 0.879) of which the semistrict consensus is shown in Fig. 1a.

Bayesian analysis resulted in convergence and mixing after an estimated 100,000 generations had been completed. As the sample frequency was set at 100 this left 190,000 'burnout' trees. Model parameter values converged at TL = 1.05 (± 2.67), r(C<-->T) = 2.52 (±0.39), r(C<-->G) = 1.11 (± 0.14), r(A<-->T) = 0.48 (± 0.02), r(A<-->G) = 2.11 (± 0.26), r(A<-->C) = 1.12 (± 0.10), pi(A) = 0.37, pi(C) = 0.17, pi(G) = 0.16, pi(T) = 0.30, · = 1, and pinvar = 0.36. The Bayesian trees were summarised by 50% majority-rule consensus with group frequencies considered to represent posterior probabilities (see Fig. 1). Parsimony and Bayesian tree topologies were largely congruent, the latter being far more resolved, which is not unexpected because of the (optimal) model applied. The only incongruence between the parsimony and Bayesian topologies was the placement of *R. arborea*, but the associated posterior probability of its alliance with *R. albidiflora*, *R. caudata* and *R. angustifolia* was only 0.56. Bayesian branch lengths are indicated on the phylogram in Fig. 2. We consider the Bayesian topology as the best representation of our data and will therefore use it as the basis of the following discussion.

4 Discussion

African *Rinorea* is paraphyletic with respect to the Asian species *R. anguifera* and *R. bengalensis* (see Fig. 3). When more Asian species have been sampled we can establish whether they will all be monophyletic with *R. arborea* and *R. anguifera* or not. In addition, as we included only a single species from the Neotropics (*R. crenata*) we cannot rule out whether African *Rinorea* is also paraphyletic with respect to Neotropical species. Furthermore, our data indicate that Madagascar has been 'colonised' twice (i.e. *R. arborea* and *R. ilicifolia*) from Central African ancestors. We can therefore conclude that strictly African *Rinorea* comprises a highly unnatural group, a fact to be considered in future classifications. For *Rinorea gabunensis*, *R. ovata*, *R. subintegrifolia* and *R. meziliana* we sampled plants from multiple locations. The non-monophyletic

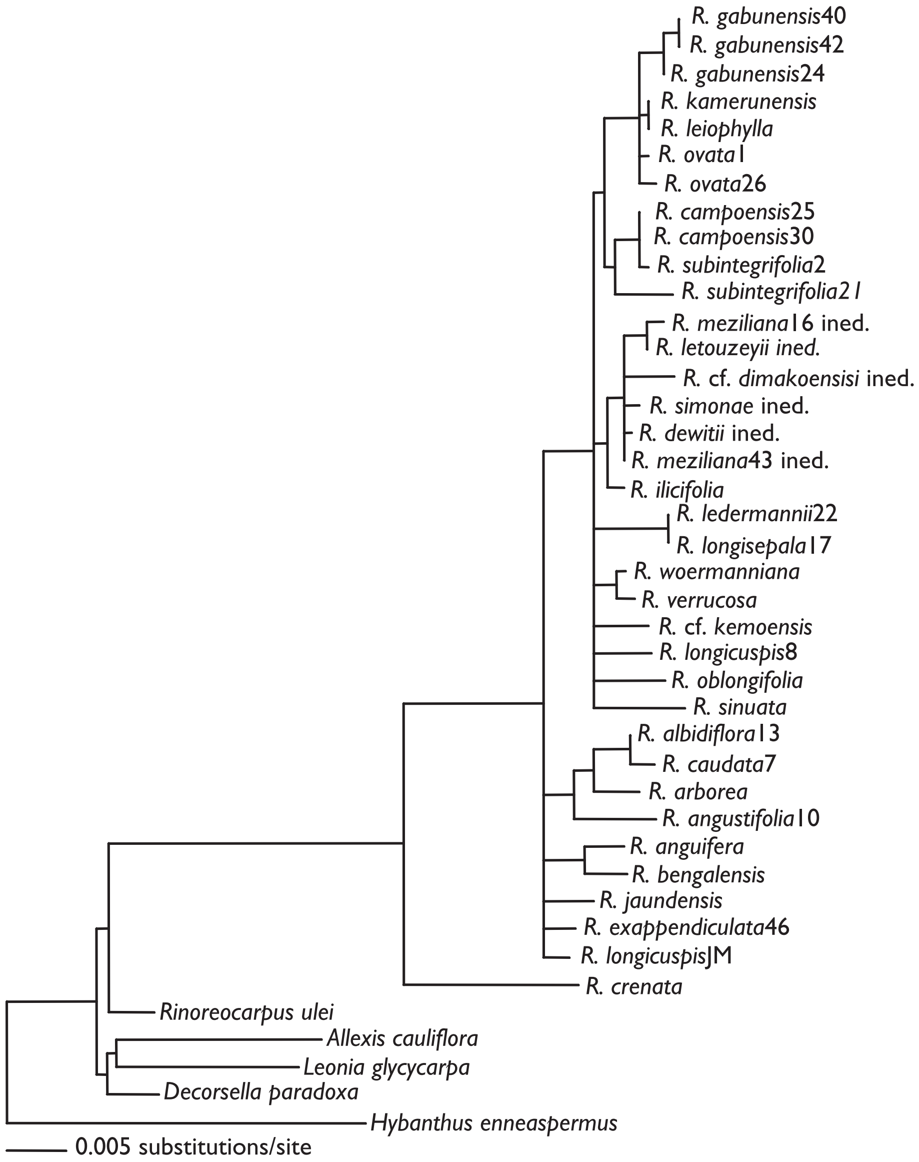

FIG. 2. *Rinorea trnL-F.* Bayesian consensus tree (as in Fig. 1) with branch lengths fitted based on the ML model converged upon in the Bayesian analysis.

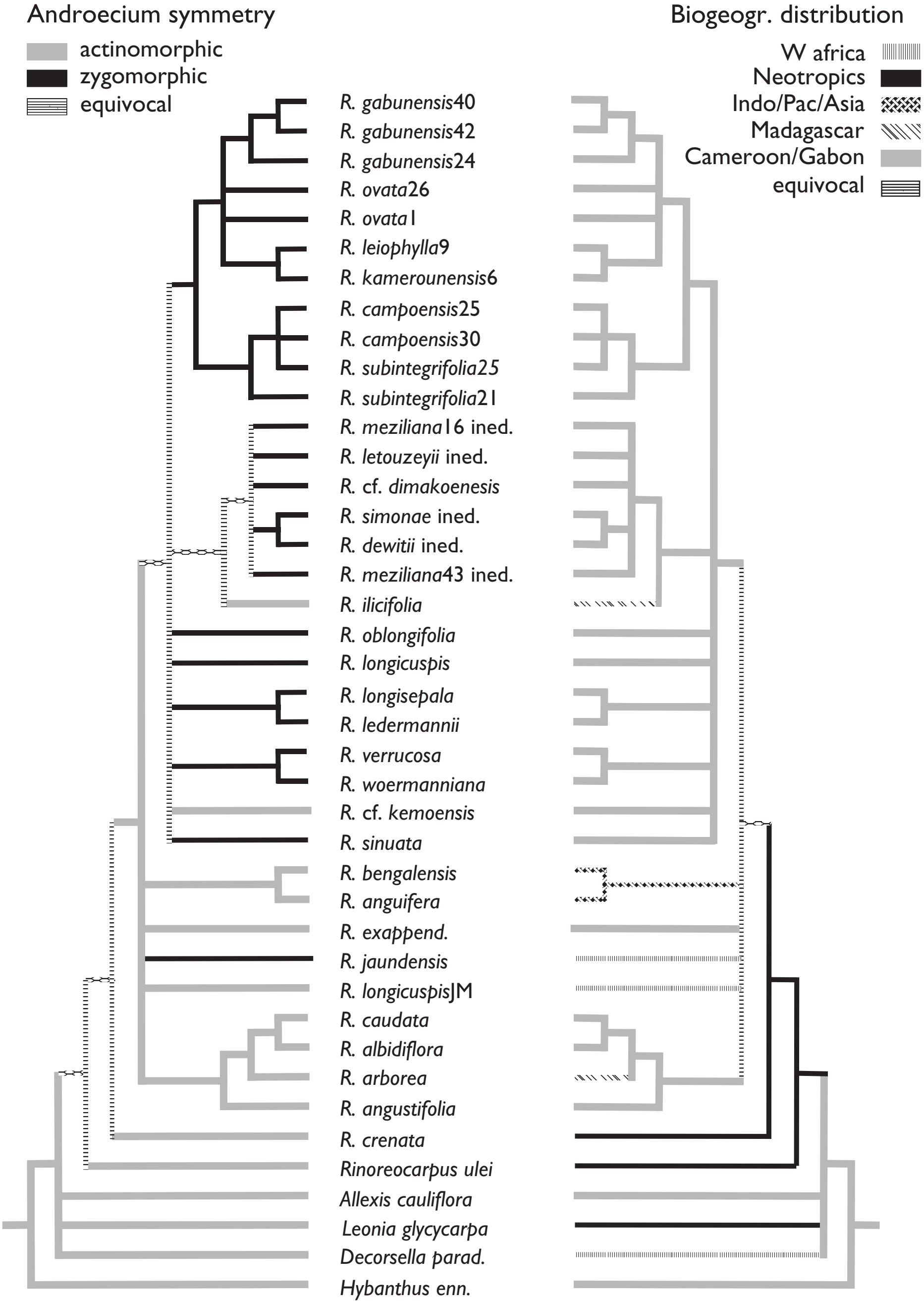

FIG. 3. *Rinorea trnL-F*. Bayesian consensus tree (as in Fig. 1) with optimized androecium symmetry and biogeographic distributions.

grouping of their plastid DNA haplotypes in our phylogeny is indicative of relative young species complexes (e.g. Schaal & Olsen, 2000). We are currently working on a ITS (rDNA) nuclear DNA phylogeny for all accessions in order to enable comparison with the plastid phylogeny presented here and hence identification of possible reticulate patterns due to hybridisation.

Relationships between African *Rinorea* and its African/Neotropical allies were not reliably resolved based on this *trnL-F* data set. Especially the relation between *Leonia*, a strictly actinomorphic woody genus comprising species with indehiscent fruits with mucilaginous seeds, as sistergroup to *Decorsella*, which is strongly zygomorphic, would suggest shifts in floral symmetry occur relatively quickly. The other example in this respect is *Allexis zygomorpha*, the only species from this genus of three with zygomorphous flowers (Achoundong & Onana, 1998). *Rinorea crenata* always resolves as sistergroup of the African *Rinorea* grade. As no other Neotropical *Rinorea* are included in this study it remains to be explored whether additional species-level transatlantic links exist.

The *Rinorea trnL-F* phylogeny with androecium symmetry optimized (Fig. 3) suggests actinomorphic androeciums to be plesiomorphic for African (including Asian) *Rinorea*. Although our species sampling in this study is only 28% of all currently described African *Rinorea*, our *trnL-F* based phylogeny so far indicates that the zygomorphic androeciums species represent the most speciose *Rinorea* clade. The 'zygomorphic clade' does comprise a few 'actinomorphic reversals' (*R. campoensis*, *R. ilicifolia*, *R.* cf. *kemoensis*, see Fig. 3), and hence based on these data we cannot say whether there has been a single shift in floral evolution in African *Rinorea*.

The question can be asked whether the observed correlation between androecium zygomorphy and clade proliferation represents a 'key innovation' triggering off the Central/West African *Rinorea* radiation. The ecological significance of androecium zygomorphy in *Rinorea* is not clear and therefore difficult to relate to pollination biology. As is the case in many angiosperms, field data on pollination are scarce and good understanding of functional aspects of (evolution of) floral morphology is lacking. For African *Rinorea* the only published data on pollination biology are from Munzinger & Pauli (2003) who report that *R. welwitschii* and *R. oblongifolia* are visited by a plethora of bee and wasp species, several of whom could be the effective pollinators. A conspicuous phytophagous interaction between African *Rinorea* and insects was noted by one of us (GA) and reported on by Amiet & Achoundong (1996). The butterfly genus *Cymothoe* Hübner (Lepidoptera, Nymphalidae), of which >70 species occur in Cameroon, is considered to have 'co-radiated' with *Rinorea* species, the larvae feeding on their leaves in a highly host-specific manner. As this type of insect-plant relationship does not appear to interfere with reproductive isolation among *Rinorea* species, we consider it unlikely that the *Cymothoe* species would have triggered the *Rinorea* radiation; rather, the reverse has happened.

Perhaps the low dispersal capacity in many African *Rinorea* species and hence their close association with different forest types (Achoundong, 1996; Kenfack *et al.*, 2003) is indicative of habitat driven speciation, possibly in response to forest fragmentation during glacial maxima with subsequent post-glacial expansion (e.g. Sosef, 1994; Maley, 1987; Leal, 2002). The various local endemic *Rinorea* species known from the littoral plains in Cameroon have been claimed to represent refuge areas during glacial maxima (Achoundong, 1996). In order to test this hypothesis denser species sampling, as well as using additional DNA sequence markers, combined with molecular dating studies would enable age-estimation of the Cameroon coastal plateau clade.

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LES *PHYLLANTHUS* DE MADAGASCAR: PRÉSENTATION DES SOUS-GENRES ET RÉPARTITION DES ESPÈCES

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Abstract

A progress report on the taxonomic revision of the large genus *Phyllanthus* (Euphorbiaceae s.l. or Phyllanthaceae) in Madagascar is given. The background of the collaboration between the University of Antananarivo, Madagascar, and the Royal Botanic Gardens, Kew, is explained, and the experiences, benefits and challenges of PhD studies in Madagascar are discussed. The methods suited for this particular study are laid out and preliminary results presented.

Résumé

Un rapport d'avancement de la révision taxonomique du vaste genre *Phyllanthus* (Euphorbiaceae s.l. ou Phyllanthaceae) à Madagascar est présenté. Les antécédents en terme de collaboration entre l'Université d'Antananarivo, Madagascar, et des Royal Botanic Gardens, Kew, sont évoqués et les expériences, apports et challenges des thèses de doctorat menées à Madagascar sont discutés. Les méthodes appliquées pour cette étude sont exposées et les résultats préliminaires sont présentés.

Key words: Euphorbiaceae, Madagascar, Phyllanthus, taxonomic revision, research challenges

1 Introduction

Madagascar est unique au monde du point de vue de la biodiversité. Elle est connue mondialement pour le haut degré de diversité et d'endémisme de sa faune et flore. D'après Lowry (1992), 75% de ses plantes sont endémiques. Cependant, la connaissance de cette richesse est encore partielle. Suite à la déforestation, notamment par la pratique de la culture itinérante sur brûlis ou «tavy», de vaste superficies des forêts malgaches ont été détruites et les habitats naturels qui restent sont menacés. Aussi, de nombreuses espèces risquent de disparaître avant d'avoir été étudiées.

La collaboration entre l'Université d'Antananarivo, Madagascar et le Royal Botanic Gardens, Kew (RBG, Kew) a été mis en place en 1989. Les activités menées dans le cadre de cette collaboration contribuent à élargir la connaissance de la flore malgache ainsi qu'à donner des formations académiques aux chercheurs malgaches.

Le Missouri Botanical Gardens (MBG) accomplit un programme de formation de para-taxonomistes, une activité couronnée de succès. Le MBG, et récemment le RBG, Kew ont collaboré avec l'Université d'Antananarivo pour former des étudiants afin d'obtenir un diplôme de D.E.A. dans l'option Biologie et Ecologie Végétale. Cependant, il existe une lacune sur la formation de véritables taxonomistes dans les Universités de Madagascar. De ce fait, très peu de chercheurs ou botanistes malgaches peuvent produire des descriptions des flores ou des nouvelles espèces qui sont régulièrement trouvées. Aussi, en 2002 deux étudiants malgaches ont commencé leur doctorat sous le protocole de collaboration entre l'Université d'Antananarivo et le RBG, Kew. L'un travaille sur les Rubiaceae, l'autre sur les Euphorbiaceae *sensu lato* (Phyllanthaceae). Deux autres étudiants ont également commencé leur DEA sur ces deux familles.

Les doctorants résident à Madagascar pour effectuer leurs recherches. Toutefois ils effectuent des stages à Kew et à Paris environ deux mois par an afin de pouvoir accéder aux littérature scientifique et aux échantillons déposés dans ces herbiers, en particulier les types. La supervision des étudiants est conjointement assurée par des chercheurs du RBG, Kew et des enseignants de l'Université d'Antananarivo. La majorité de la supervision est faite au moyen d'échanges de courriers électroniques, au cours des visites de l'étudiant en Europe ou durant les passages du superviseur à Madagascar. Les missions sur le terrain sont souvent menées avec l'un ou l'autre superviseur.

Cette approche présente plusieurs avantages aussi bien pour l'étudiant, que pour l'Université d'Antananarivo ou les RBG, Kew car:

- Les étudiants restent dans le pays et utilisent et développent les ressources internes. Ils stimulent ainsi la vie universitaire par l'introduction de nouvelles méthodes, comme les clés électroniques ou les systèmes d'information géographique (SIG).
- Les missions sur le terrain sont plus faciles à mettre en œuvre et moins chères.
- Les méthodes utilisées n'ont pas besoin de matériels coûteux et ne demandent pas beaucoup d'équipements consommables importés de Kew.
- Les étudiants ne sont pas séparés de leurs familles et augmentent leur chance de développer une carrière dans la recherche à Madagascar.
- Le coût de la vie, les missions sur terrain et les frais universitaires sont moins chers à Madagascar qu'à Kew.
- La collaboration entre l'Université d'Antananarivo Madagascar et le RBG, Kew augmente.

Evidemment cette approche comporte aussi des inconvénients. Très peu de documentation scientifique et des spécimens types est disponible á Madagascar. Tous les deux sont nécessaires afin de pouvoir faire un travail de haute qualité. A long terme, on espère que de plus en plus de littérature, au moins des photocopies, ainsi que des images des spécimens types seront disponibles à Madagascar.

2 Le programme de recherche

Cette publication rend compte de la progression d'un doctorat sur le genre *Phyllanthus* de la famille des Euphorbiaceae *sensu lato* ou Phyllanthaceae. Les *Phyllanthus* malgaches comprennent environ 60 espèces dont 50 sont endémiques de Madagascar. Ils sont des herbes, arbrisseaux, arbustes, et des petits arbres. Ils sont bien représentés dans tout le spectre des formations végétales de l'Ile, des plus humides aux plus arides. La majorité des espèces de Phyllanthus sont endémiques et ont en plus une distribution très restreinte. Au cours des dernières décennies, le genre a fait l'objet de plusieurs études taxonomiques et palynologiques dans différentes parties du monde: aux Caraïbes et Amérique du Nord par Webster (1956–1958, 1967, 1970), en Afrique intertropicale par Brunel (1987), en Nouvelle Calédonie par Schmid (1991) et en Afrique de l'Est par Radcliffe-Smith (1987, 1996).

En ce qui concerne les *Phyllanthus* malgaches, Leandri a commencé des investigations sur *Phyllanthus* à partir de 1933 (Leandri 1933). En 1939, il a regroupé quelques espèces de *Phyllanthus* dans une classification infra-générique, mais la délimitation de chaque groupe n'était pas nette. En 1958, Leandri a traité *Phyllanthus* dans la Flore de Madagascar et des Comores, il en décrit 58 espèces. Or, parmi ces espèces, 4 appartiennent en fait au genre *Margaritaria.* Il a également décrit 7 espèces de *Glochidion* qui est un genre limité à l'Asie, l'Australie et les Iles pacifiques. C'est pour cette raison que Hoffmann et McPherson (2003) ont reclassé ces espèces de *Glochidion sensu* Leandri (1934–1958) dans *Phyllanthus.* Cependant, leurs positions infra-génériques restent encore une question.

L'énorme variation des caractères ainsi que la petite taille des fleurs de *Phyllanthus* découragent souvent les botanistes à les récolter et à les identifier. En outre l'utilisation de la clé de détermination de Leandri (1958) s'avère difficile en raison du chevauchement des valeurs de certains caractères et de la nécessité de disposer simultanément de fleurs mâles et femelles, ce qui n'est souvent pas le cas. C'est pourquoi nombreuses collections de *Phyllanthus* restent indéterminées.

Notre travail a pour but de faire une révision taxonomique des *Phyllanthus* de Madagascar en essayant d'estimer le degré de validité des travaux de Leandri, de tester les classifications infra-géneriques proposées par Webster (1956–1970) et Brunel (1987) et de produire un traitement taxonomique moderne. Cette étude comprendra également l'élaboration d'une nouvelle clé de détermination plus pratique ainsi que la création de cartes de distribution permettant entre autres de pouvoir évaluer le statut de conservation des *Phyllanthus* malgaches.

3 Methodologie

A Madagascar, les spécimens d'herbier ont été consultés dans les herbiers du Parc Botanique et Zoologique de Tsimbazaza (TAN) et du Département de Recherches Forestières et Piscicoles Antananarivo (TEF). Pour faire face au manque de spécimens, et en particulier de types, nous avons également consulté les herbiers du British Museum of Natural History (BM), des Royal Botanic Gardens, Kew (K), l'Herbarium of the Linnean Society (LINN) et l'herbier du Muséum d'Histoire Naturelle, Paris (P).

Afin de d'enrichir les collections déjà existantes dans les herbiers nationaux et de collecter des échantillons complets, des missions de terrain ont été également effectuées dans différentes régions de Madagascar. Les sites de collecte ont été essentiellement la région nord-ouest de Madagascar et l'ouest, le sud-ouest, les Hauts-plateaux et la région est. Nous avons également fait une mission à Mayotte (Iles Comores). Le financement de ces missions provient du RBG, Kew.

Les descriptions des espèces sont enregistrées sous forme de bases de données sous DELTA et MS Access. Les types de chaque taxon sont vérifiés et étudiés dans les herbiers de BM, K, LINN et P. Des lectotypifications sont faites quand c'est nécessaire. Chaque taxon sera illustré afin d'avoir une idée sur son aspect général. La clé des espèces traitera séparément le matériel mâle et femelle pour les espèces dioïques. Les coordonnées géographiques sont traitées sous Arcview afin d'obtenir les cartes de distributions des espèces. Les résultats sont présentés sous la même forme que le traitement pour la version nouvelle de *Flore de Madagascar et des Comores*. Afin de tester la classification actuelle et d'étudier les relations entre les espèces au sein des groupes, une analyse cladistique est faite pour les sections qui sont endémiques ou presque endémiques de Madagascar. Cette analyse est basée sur les données morphologiques.

Les informations sur l'habitat, l'aire de distribution et le nombre de sous-populations seront analysées afin de déterminer la catégorie de menace de chaque taxon selon les catégories standards de l'UICN (UICN, 2001). La connaissance de cette catégorie ou au moins de la distribution et de la menace qui pèse sur l'habitat de chaque taxon sera essentielle pour toutes les institutions oeuvrant dans le cadre de la conservation à Madagascar. Par exemple, contrairement au *Phyllanthus casticum* qui est une espèce commune et très répandue à Madagascar et aux Mascareignes, *Phyllanthus ampandrandavae*, *P. bernieranus*, *P. isomonensis* et *P. tulearicus* sont parmi les espèces endémiques à distribution très restreinte. Leur zone d'occurrence en dehors des aires protégées sont évidemment soumises à des pressions humaines. Les bases de données sur les espèces de *Phyllanthus* de Madagascar seront mises à disposition sur le site Internet du RBG, Kew, et seront accessibles à tous ceux qui travaillent dans la conservation, la recherche scientifique et la gestion des ressources naturelles. Elles pourront également être utiles pour déterminer les espèces cibles pour les projets de conservation, entre autres les projets de collecte des graines pour la conservation *ex situ* (banques des graines).

Les différentes étapes de la méthodologie adoptées sont montrées dans la Fig. 1.

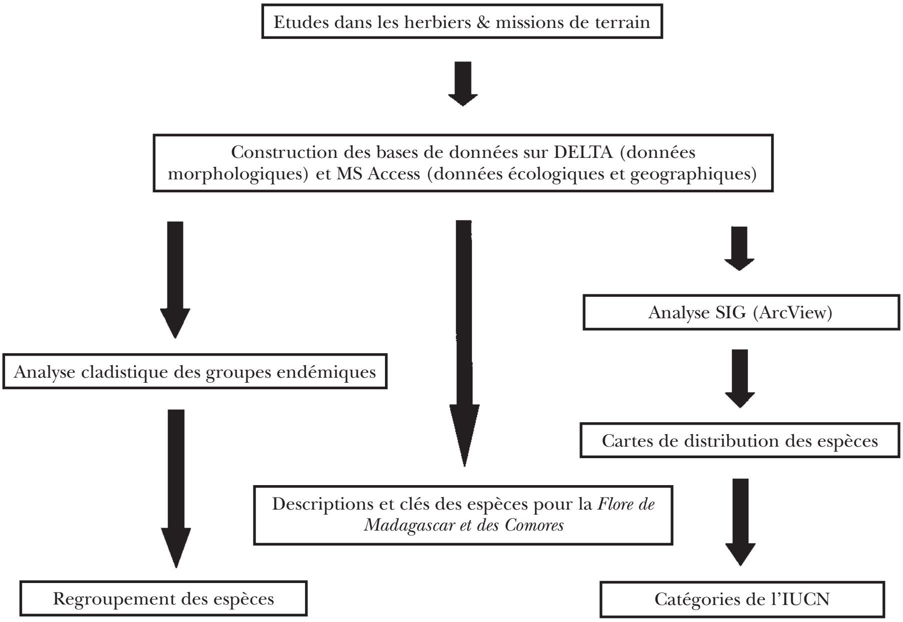

FIG. 1. Les étapes de la méthodologie adoptée.

4 Resultats

Les *Phyllanthus* de Madagascar se présentent sous des formes variées. Ce sont de petits arbres, arbustes ou herbes, monoïques ou dioïques ; les axes sont équivalents ou dimorphes (la ramification est dite phyllanthoïde) et il y a alors différentiation en axe principal orthotrope à croissance continue et en branche plagiotrope à croissance limitée naissant à l'aisselle des feuilles modifiées en écaille ou cataphylles. Les stipules sont présentes. Les feuilles alternes ou souvent opposées ou sub-opposées, sont simples. Les inflorescences sont en cymes axillaires, uniflores ou pluriflores, bisexuées ou unisexuées. Les fleurs sont apétales, unisexuées sans staminodes ni pistillodes, elles ont 5–6 tépales imbriqués ou en deux verticilles; les disques sont présents et formés par des éléments libres qui alternent avec les tépales chez les fleurs mâles ou entiers chez les fleurs femelles. Les fleurs mâles sont souvent caduques, à 2–5(–6) étamines libres ou soudées partiellement ou entièrement, les anthères sont à déhiscence verticale ou horizontale. Les fleurs femelles sont souvent plus grandes que les mâles, les ovaires sont constitués de 3(–6) carpelles soudés, formant 3(–6) loges bi-ovulées; les styles sont au nombre de 3(–6), libres ou soudés en colonne courte ou plus ou moins longue, bifides ou souvent entiers. Les fruits sont capsulaires déhiscents au sec ou bacciformes indéhiscents. Les graines sont au nombre de 6(–12), elles sont triquètres et sont disposées comme des quartiers d'orange. Leur tégument est lisse ou muni d'ornementations.

Une illustration d'une espèce de *Phyllanthus* malgaches est présentée sur la Fig. 2.

Les *Phyllanthus* de Madagascar appartiennent aux sous-genres suivants :

- sous-genre *Gomphidium* (Baill.) G.L.Webster
- sous-genre *Isocladus* G.L.Webster
- sous-genre *Kirganelia* (Juss.) G.L.Webster
- sous-genre *Phyllanthus*

Les caractères morphologiques significatifs de ces sous-genres sont montrés dans le tableau 1.

Sous-genre *Gomphidium* (Baill.) G.L.Webster in J. Arnold Arbor. 48: 338 (1967). – Type: *Phyllanthus chamaecerasus* Baill.

En se basant sur les disques réduits et les styles réduits et entiers, les espéces de *Glochidion* décrites par Leandri (1958) appartiennent à ce sous-genre. Or, *Glochidion* se distingue de *Phyllanthus* par le disque qui n'est jamais présent, la morphologie des graines qui présente une invagination ventrale et les styles entiers. Ces faits ont amené Hoffmann & McPherson (2003) à les transfèrer dans *Phyllanthus*.

Dans ce sous-genre se trouve: *Phyllanthus ankaratrae* (Leandri) Petra Hoffm. & McPherson, *Phyllanthus humbertii* (Leandri) Petra Hoffm. & McPherson, *Phyllanthus lichensilvae* (Leandri) Petra Hoffm. & McPherson, *Phyllanthus marojejiensis* (Leandri) Petra Hoffm. & McPherson, *Phyllanthus oreichtitus* Leandri, *Phyllanthus perrieri* (Leandri) Petra Hoffm. & McPherson, *Phyllanthus sambiranensis* Leandri. D'après leur description *Phyllanthus andalangiensis* Leandri et *Phyllanthus bernerianus* Baill. appartiendraient aussi à ce sous-genre. Ces espèces sont toutes endémiques de Madagascar.

Sous-genre *Isocladus* G.L.Webster in J. Arnold Arbor. 37: 345 (1956). – Type: *Phyllanthus maderaspatensis* L.

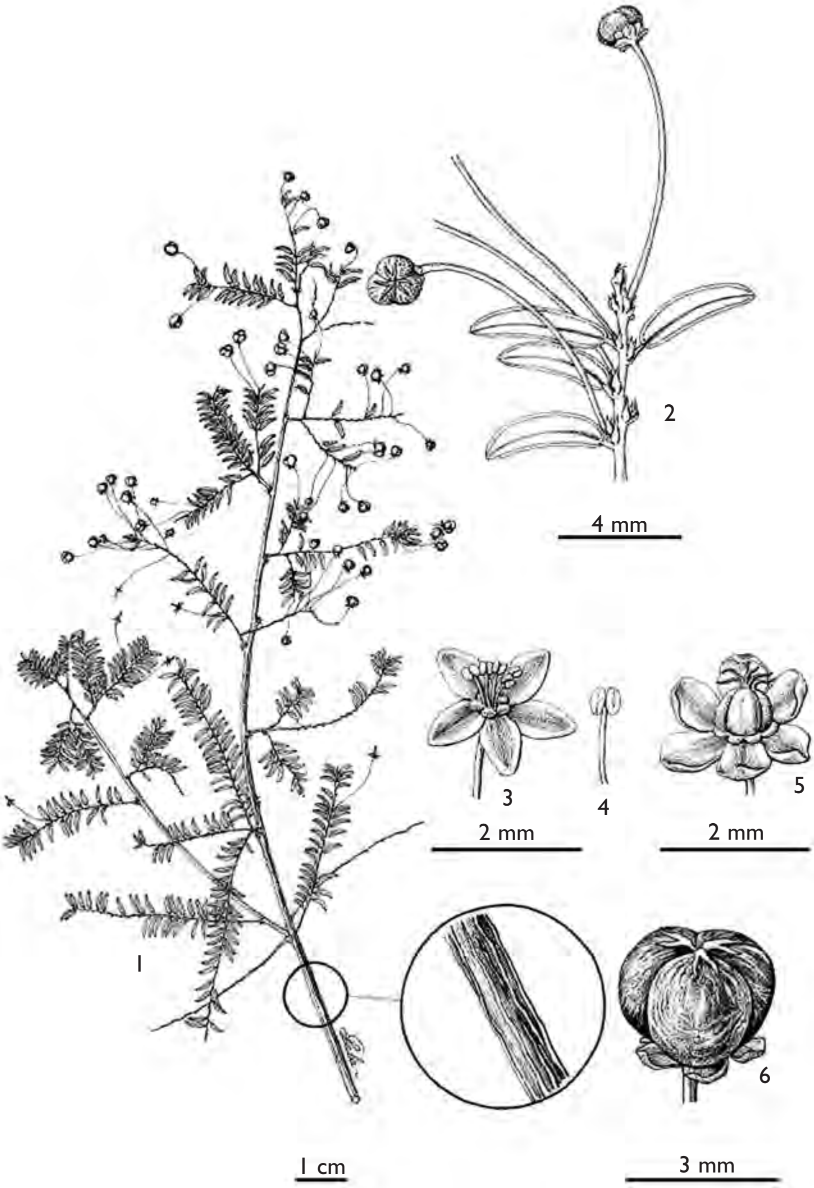

FIG. 2. *Phyllanthus bojerianus*: 1, branches orthotropes et plagiotropes; 2, détail des feuilles et fruits; 3, fleur mâle; 4, étamine; 5, fleur femelle; 6, fruit. Fait par Roger Lala.

TABLEAU 1. Caractères généraux des sous-genres de *Phyllanthus* à Madagascar

Sous genres Caractères	***Gomphidium***	***Isocladus***	***Kirganelia***	***Phyllanthus***
Ramification	Phyllanthoïde pinnatiforme	**Non phyllanthoïde**	Phyllanthoïde **pinnatiforme ou bipinnatiforme**	Phyllanthoïde pinnatiforme
Etamines	3–6 Libres ou entièrement soudées	2–3 Libres ou soudées	4–6 Libres ou **en deux lots**	2–3 Libres ou soudées
Anthères	Libres ou entièrement soudées, **apiculées**, déhiscence en long	Libres, déhiscence en long	Libres, déhiscence en long	Libres ou partiellement à entièrement soudées, déhiscence en long ou **horizontale**
Pollen	3-colporés ou 3-syncolporés, marge constituée de deux murs parallèles exines ruguleuses	3-colporés ou aréolés à orée médiane, exines macro- ou microréticulées	3- ou 4-colporés, exines réticulées	3- ou 4-colporés, exines d'ornementation variée
Carpelles	3	3	**3–6**	3
Styles	Libres ou entièrement soudées, bifides ou **entières**	Libres ou partiellement soudées, bifides	Soudées, bifides	Libres ou partiellement soudées, bifides
Fruits	Capsulaires	Capsulaires	Capsulaires ou **bacciformes**	Capsulaires

A ce sous-genre appartiennent: *Phyllanthus bathianus* Leandri, *Phyllanthus betsileanus* Leandri, *Phyllanthus isalensis* Leandri, *Phyllanthus maderaspatensis* L., *Phyllanthus philippioides* Leandri. A part *Phyllanthus maderaspatensis*, toutes ces espèces sont endémiques de Madagascar.

Sous-genre *Kirganelia* (Juss.) G.L.Webster in J. Arnold Arbor. 37: 344 (1956); 38: 51 (1957). *Kirganelia* Juss., Gen. Pl. 387 (1789). – Type: *Kirganelia phyllanthoides* Desf. (= *Phyllanthus casticum* Willem.).

Il s'agit d'un sous-genre riche à Madagascar. On y trouve: *Phyllanthus analamerae* Leandri, *Phyllanthus ankaranae* Leandri, *Phyllanthus albolapidosi* Leandri, *Phyllanthus angavensis* (Leandri) Leandri, *Phyllanthus bojerianus* Müll.Arg., *Phyllanthus casticum* Willem., *Phyllanthus cryptophilus* (Juss.) Müll.Arg., *Phyllanthus decipiens* (Baill.) Müll.Arg., *Phyllanthus fuscoluridus* Müll.Arg., *Phyllanthus geayi* Leandri, *Phyllanthus goudotianus* (Baill.) Müll.Arg, *Phyllanthus humbertianus* Leandri, *Phyllanthus iratsiensis* Leandri, *Phyllanthus isomonensis* Leandri, *Phyllanthus mananarensis* Leandri, *Phyllanthus mantsakariva* Leandri, *Phyllanthus matitanensis* Leandri, *Phyllanthus mocquerysianus* A.DC., *Phyllanthus multiflorus* Poir., *Phyllanthus nummulariifolius* Poir., *Phyllanthus obdeltophyllus* Leandri, *Phyllanthus pervilleanus* Müll.Arg, *Phyllanthus seyrigii* Leandri, *Phyllanthus tenellus* Roxb., *Phyllanthus vakinakaratrae* Leandri, *Phyllanthus vergens* Baill., et deux nouvelles espèces à décrire.

Certaines des descriptions de Leandri sont basées sur un seul échantillon, ce qui fait qu'il n'a pas pu mesurer l'ampleur de la variations des caractères au sein de ces espèces. Il a ainsi décrit différentes espèces que nous pensons être les mêmes et que nous envisageons de mettre en synonymie. Nous avons par exemple remarqué que la délimitation entre *Phyllanthus casticum* et *Phyllanthus decipiens* n'est pas nette. Sa clé présente des recouvrements entre les caractères végétatifs et floraux. Cet exemple illustre les difficultés qui surgissent lors de l'utilisation de la clé établie par Leandri (1958).

Sous-genre *Phyllanthus* – Type: *Phyllanthus niruri* L.

On y trouve: *Phyllanthus amarus* Schum. & Thonn., *Phyllanthus ampandrandavae* Leandri, *Phyllanthus andranovatensis* Brunel & Roux, *Phyllanthus coursii* Leandri, *Phyllanthus ivohibeus* Leandri, *Phyllanthus lokohensis* Leandri, *Phyllanthus madagascariensis* Müll.Arg., *Phyllanthus melleri* Müll.Arg., *Phyllanthus moramangicus* Leandri, *Phyllanthus niruri* L., *Phyllanthus niruroides* Müll.Arg., *Phyllanthus rangoloakensis* Leandri, *Phyllanthus tampinensis* Leandri, *Phyllanthus urinaria* L., *Phyllanthus vatovaviensis* Leandri, *Phyllanthus venustulus* Leandri. Parmi ces espèces quatre sont non endémiques de Madagascar. Il s'agit de *Phyllanthus amarus*, *Phyllanthus niruri*, *Phyllanthus niruroide* et *Phyllanthus urinaria.*

5 Conclusion

Les résultats préliminaires présentés dans cette publication montrent qu'une recherche de haute qualité peut être menée quand les méthodes adoptées sont adaptées aux possibilités techniques du pays, même si l'accès aux matériaux nécessaires est très limité. L'herbier et les méthodes analytiques basées sur l'informatique sont appropriés. Les pays qui présentent une biodiversité élevée comme Madagascar ont un grand besoin en taxonomistes et nous pensons que notre projet démontre qu'il est possible de satisfaire à ce besoin. Il s'agit d'un processus continu et d'apprentissage profitable pour tous ceux qui sont concernés. Nous espérons que d'autres institutions à Madagascar auront l'opportunité de développer des projets similaires dans l'avenir.

Note: Ce manuscrit a été soumis en février 2004. Depuis, une progression considérable sur la reconstruction de la phylogénie du *Phyllanthus* sensu lato a été faite par Kathriarachchi *et al.* (sous presse). Les relations obtenues sont plus complexes par rapport à celles qui ont été envisagées par Webster (1956–1970). En effet, de nombreux changement de la taxonomie infra-générique sera nécessaire. Ces modifications seront détaillées dans les prochaines publications (Ralimanana & Hoffmann, en cours de prép.).

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PHYLOGENY, MORPHOLOGY AND USES OF *PLECTRANTHUS* (LAMIACEAE)

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Abstract

A phylogeny of basils, *Plectranthus* and allies (Lamiaceae, tribe Ocimeae, subtribe Plectranthinae) based on sequences of the *trnL* intron, *trnL-trnF* intergene spacer and *rps 16* intron of the plastid genome is presented. The aim of this paper is to illustrate the use of a molecular phylogeny to explore the distribution of floral morphology characters and of ethnobotanical use in *Plectranthus* and allies. *Plectranthus,* with around 300 species, is frequently used in traditional medicine in Africa where the genus is most diverse. However, as species are often referred to by more than one name (synonyms) it is difficult for non-taxonomists to synthesise the relationships among the different species. The new phylogeny divides the Plectranthinae into two main clades. The floral morphology of these is different and is likely to favour different pollinators. The floral morphology of *Tetradenia* is very different from the remainder of the Plectranthinae. One main clade of the Plectranthinae is richer in number and diversity of ethnobotanical uses. Although the phylogeny can be used to help direct phytochemistry and drug-discovery research, care has to be taken to check synonomy when using names in some of the existing phytochemical and ethnobotanical literature.

Résumé

Phylogénie, morphologie et usages de *Plectranthus* (Lamiaceae). Une phylogénie des basilics, *Plectranthus* et apparentés (Lamiaceae, tribu des Ocimeae, sous-tribu des Plectranthinae) est présentée. Elle se base sur les séquences de l'intron *trnL*, de la région non codante entre *trnL* et *trnF* et de l'intron rps 16 du génome chloroplastique. L'objectif de cet article est d'illustrer l'utilisation d'une phylogénie moléculaire pour explorer la distribution des caractères de morphologie florale et de l'utilisation ethnobotanique chez *Plectranthus* et apparentés. *Plectranthus*, avec environ 300 espèces, est fréquemment utilisé en médecine traditionnelle en Afrique où le genre montre la plus grande diversité. Néanmoins, les différentes espèces étant souvent désignées par plusieurs synonymes, il est difficile pour les non-taxonomistes de faire la synthèse des relations qui les lient. La nouvelle phylogénie divise les Plectranthinae en deux clades principaux. Leur morphologie florale diffère et il est probable que celle-ci favorise divers pollinisateurs. La morphologie florale de *Tetradenia* est très différente du reste des Plectranthinae. Un des clades principaux au sein des Plectranthinae est plus riche quant au nombre et à la diversité de ses utilisations ethnobotaniques. Bien que la phylogénie puisse être utilisée pour appuyer directement la phytochimie et la recherche en matière de découverte de médicaments, les synonymies doivent être examinées avec attention lorsqu'on utilise des noms repris de certains articles traitant de phytochimie et d'ethnobotanique.

Key words: *Plectranthus*, phylogeny, phytochemistry, *Tetradenia*, uses

1 Introduction

The aim of this paper is to illustrate the use of a molecular phylogeny to explore the distribution of floral morphology characters and of ethnobotanical use in *Plectranthus* L'Hér. and allies (Lamiaceae, Tribe Ocimeae, subtribe Plectranthinae). *Plectranthus* comprises around 300 species and is widespread in the Old World Tropics. The genus has many ethnobotanical uses including traditional medicine in Africa, where the genus is most diverse.

A recent phylogenetic study of Tribe Ocimeae based on three plastid DNA regions reveals *Plectranthus* as currently circumscribed to be paraphyletic (Paton *et al.*, 2004), Fig. 1. Several segregate genera have previously been recognised. Some of these are easily circumscribed using morphology. These include *Aeollanthus* Spreng. (40 species), *Tetradenia* Benth. (20 species) and *Thorncroftia* N.E.Brown (4 species). However, the majority of segregate genera show no clear morphological separation from *Plectranthus*. Such segregates include *Neohyptis* J.K.Morton (1 species), *Englerastrum* Briq. (5 species), *Holostylon* Robyns & Lebrun (4 species), *Leocus* A.Chev. (5 species), *Anisochilus* Wall. (20 species), *Solenostemon* Thonn. (15 species), *Pycnostachys* Hook. (40 species) (Fig. 1). Within Plectranthinae, a clade comprising *Pycnostachys*, *Holostylon, Anisochilus* and species of *Plectranthus* formerly placed in *Coleus* Lour. is supported (BS 97%, Fig. 1). *Pycnostachys* forms a monophyletic group within this *Coleus* clade (BS 96%). A clade which contains *Plectranthus* plus *Tetradenia*, *Thorncroftia*, and *Aeollanthus* is sister to the *Coleus* clade (BS < 50%). *Tetradenia* plus *Thorncroftia* forms a clade with BS 100%. The Madagascan endemic genera *Capitanopsis* S.Moore and *Dauphinea* I.C.Hedge are sisters (BS 76%) (Fig. 1). The lack of resolution at the base of the *Plectranthus* clade (Fig. 1) suggests that further sampling, and perhaps sequencing another gene, is required before changes to taxonomy are made (Paton *et al.*, 2004).

2 Floral morphology

The phylogeny presented in Fig. 1 can be used to study the floral morphology of the Plectranthinae. Generally species within the *Coleus* clade have unequal corolla lips, the posterior (upper) lip being less than 0.8 times the length of the anterior (lower) lip. However, there is no clear discontinuity in this character, with several species, in both clades, having the ratio of the lengths of posterior to anterior lips around 0.8. The functional significance of the size ratio of the corolla lips is not known. Species of the *Plectranthus* clade which usually have large posterior lobes often also show conspicuous nectar guides, but such markings are also seen in the usually small posterior lips of the *Coleus* clade.

Sigmoid corolla tubes are found in all the *Coleus* clade and in the *Plectranthus laxiflorus/P. petiolaris* subclade of the *Plectranthus* clade. In some species of the *Coleus* clade the curves of the tube are shallow and the tube can appear straight. However, careful examination usually reveals the shallowly sigmoid shape of the tube. The

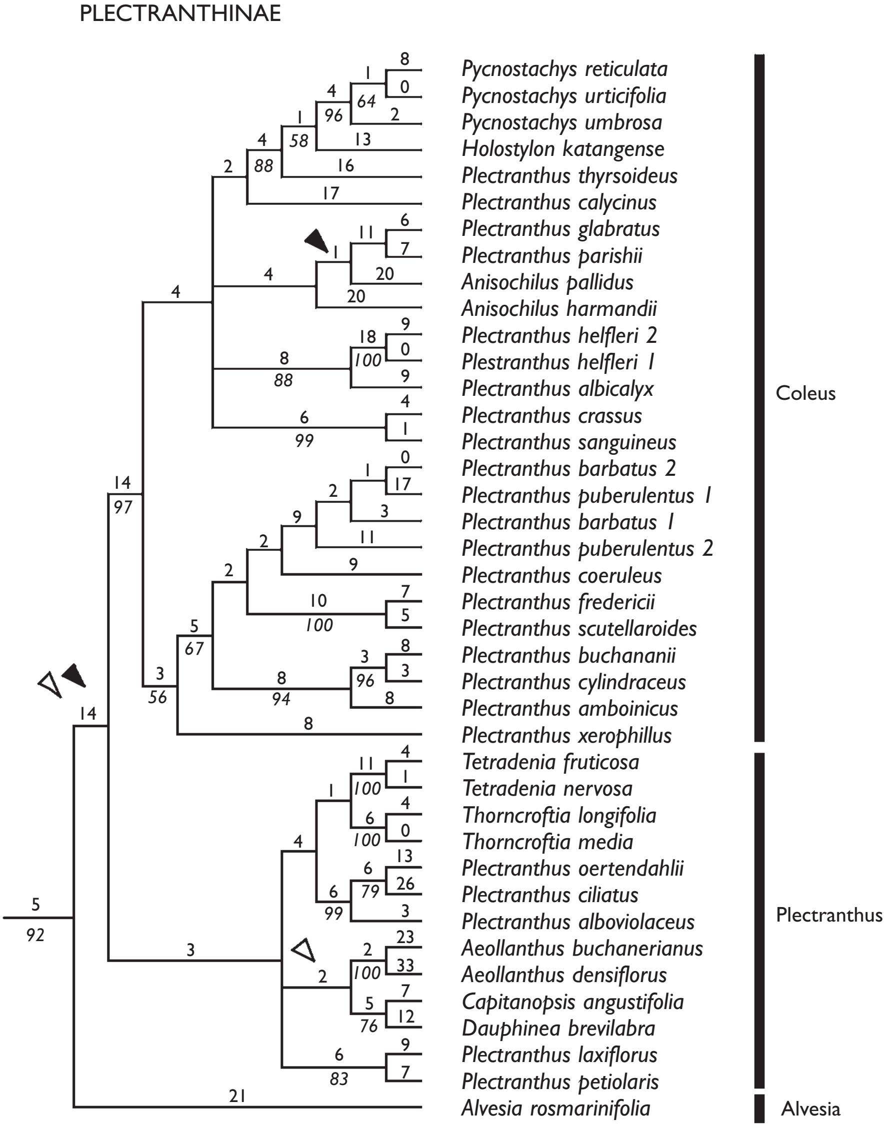

FIG. 1. One most parsimonious tree after successive weighting of molecular data showing branch length (above branches) and bootstrap percentages (below branches, italicized, equal weights). Arrows indicate branches collapsing in the strict consensus trees with successive (unfilled arrows) and equal (black arrows) weights. See Paton *et al.* (2004) for full details of the analysis.

sigmoid tube is always associated with a horizontal anterior corolla lobe. This combination of characters will favour landing insects with flexible probosci. Van der Pijl (1972) suggests that staminal fusion seen in the *Coleus* clade provides a stronger landing platform than would free stamens. Fused stamens have evolved independently in *Syncolostemon* Benth. and *Hemizygia* Briq., members of subtribe Ociminae, sister to the Plectranthinae (Paton *et al.*, 2004). In these genera only the anterior stamens are fused whereas in the *Coleus* clade all stamens are fused together. However, the fusion is not consistent within these clades. Although anterior staminal fusion is synapomorphic for the *Syncolostemon* clade, there is much variation in the degree of stamen fusion from almost complete fusion to fusion at the base only. Staminal fusion is lost several times within the *Coleus* clade e.g. *Plectranthus cylindraceus* Benth. and *P. sanguineus* Britten.

Within the *Plectranthus* clade, with the exception of the *P. laxiflorus* group, the corolla tube is straight or curved distally. Often the anterior lobe is deflexed, a character not seen in the *Coleus* clade. Nilsson *et al.* (1985) suggest that a lack of a firm landing platform in *Plectranthus vestitus* Benth., which has a deflexed anterior corolla lobe, favours hovering insects. Deflexed anterior corolla lobes occur many times in Ocimeae, and within the southern African Plectranthinae this may be associated with long-tongued hovering insects whose behaviour does not require a landing platform (Nilsson *et al.*, 1985). Deflexed lateral corolla lobes seen in *Thorncroftia* may also be associated with a reduction in the landing platform. However, deflexed anterior and free lateral corolla lobes are also found in *Tetradenia* in Plectranthinae and several genera in tribe Ocimeae: *Lavandula*, *Endostemon* and *Puntia*. In *Tetradenia* and *Lavandula* the inflorescence is condensed. The close proximity of the corollas and the spreading deflexed corolla lobes together present a firm landing platform for insects, such as in bees visiting *Lavandula*. In *Endostemon* and *Puntia*, however, the inflorescence is not condensed.

The need for increased sampling and the lack of supported resolution at the base of the *Plectranthus* clade, make it impossible to draw firm conclusions about the direction of evolution between straight tubes with deflexed lobes suiting hovering pollinators, and sigmoid tubes with horizontal anterior lips suiting landing, flexible tongued insects.

The floral morphology of *Tetradenia* is very different from other members of the Plectranthinae. The corolla is 4-lobed due to fusion of the posterior lobes and almost actinomorphic with spreading lobes and stamens, rather than 5-lobed and strongly zygomorphic with a cucullate (boat-shaped) to concave anterior lip. Also the attachment of the stamens to the corolla of *Tetradenia* is regularly spaced at the base of each of the 4 lobes, whereas in the remainder of the Plectranthinae all stamens attach to the corolla at the throat of the tube, at the base of the anterior lobe. Thus *Tetradenia* lacks the characters which could otherwise be used to diagnose subtribe Plectranthinae. Further work is required to better understand the development of the flower in *Tetradenia*. It is possible that the almost actinomorphic form of the *Tetradenia* flower represents the preservation of an earlier developmental stage, before the developing bud becomes zygomorphic.

3 Uses

There are at least 70 species reported to have medicinal or other ethnobotanical uses (Lukhoba *et al.*, in prep.). Our knowledge about the active compounds in species used in traditional medicine is sparse, despite the growing phytochemical interest in the genus. In fact, many of the chemical studies on about 90 species are divorced from the research on their uses. For example, *P. laxiflorus* and *Solenostemon scutellarioides* (L.) Codd., which are frequently cited as having ethnomedicinal uses have surprisingly limited data on their chemical composition. The converse is also true, some species are well researched chemically but have limited ethnobotanical data, for instance *P. defoliatus* Benth*., P. graveolens* R.Br.*, P. grandidentatus* Gürke*, P. argentatus* S.T.Blake*, P. ecklonii* Benth., *P. myrianthus* Briq. and *P. albidus* Baker.

A key barrier to increasing our understanding of the relationships among the different species of *Plectranthus* that have similar uses is nomenclature. In the phytochemical and ethnobotanical literature, reference is often made to a species using a synonym rather than the name accepted by comprehensive taxonomies. For example, after a comparative study of over 700 citations associated with *Plectranthus* we have identified 5 species (*Plectranthus barbatus* Andr.*, P. amboinicus* (Lour.) Spreng.*, P. alpinus* (Vatke) O.Ryding*, P. vettiveroides* (Jacob) N.P.Singh & B.D.Sharma and *P. mollis* Spreng.) that have the most ethnobotanical and phytochemical citations in the literature. However, over 80% of the citations we have used in this study referred to a species by a synonym rather than the accepted name (Lukhoba *et al.*, 2006). For example, *P. barbatus* Andr. is frequently cited as *Coleus forskohlii* (Willd.) Briq. or *Coleus barbatus* (Andr.) Benth. Thus, without detailed taxonomic knowledge, it is very difficult to draw together all the known information about the chemistry (Simmonds *et al.*, submitted) and uses of specific species of *Plectranthus* (Lukhoba *et al.* 2006).

Our preliminary survey of ethnobotanical uses of *Plectranthus* suggests that 70% of recorded medicinal use relate to species found in the *Coleus* clade. *P. amboinicus* and *P. barbatus* exhibit the greatest number of different medicinal uses. Although the monoterpene content of these two species has been well studied the investigations rarely relate directly to ethnobotanical uses. Our knowledge about diterpenoids and flavonoids in these species is still sparse, although our knowledge about the biological activity of these two groups of compounds would suggest that they could more directly relate to the ethnobotanical uses of these species than the monoterpenoids. This hypothesis, however, justifies further investigation.

Paton *et al.* (2004) report on some of the differences in the plant chemistry observed between the *Plectranthus* and the *Coleus* clades. For example, many of the species in the *Plectranthus* clade produce flavones but lack quinonoid diterpenoids, whereas many species in the *Coleus* clade produce quinonoid diterpenoids and lack flavonoids. This information along with the high number of species with medicinal uses in the *Coleus* clade suggests that further research into the chemistry of species in the *Coleus* clade, especially those related to *P. amboinicus* and *P. barbatus* could result in the identification of biologically active compounds as well as other species with potential medicinal properties.

4 Conclusion

The molecular phylogeny of *Plectranthus* has facilitated research into the morphology and chemistry in the Plectranthinae. A meaningful survey of morphology or chemistry would have been difficult prior to this work as existing taxonomies recognised a paraphyletic *Plectranthus* and did not elucidate relationships among the various genera.

The lack of taxonomic knowledge is often a real barrier to the use of the new phylogenies in drug-discovery research. Currently it is often very difficult for non-taxonomists to obtain information that allows taxonomic links between an accepted name and synonomy to be understood. Such links would allow more effective syntheses of chemical and ethnobotanical data. This research has illustrated how, once ethnobotanical data about different species has been corrected for synonomy and then superimposed onto a phylogeny, it can assist us in looking at the taxonomic distribution of medicinally used plants and guide the selection of species for further study.

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A TAXONOMIC STUDY OF THE GENUS *SANSEVIERIA* (DRACAENACEAE) IN ZIMBABWE

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Abstract

A taxonomic study of the genus *Sansevieria* in Zimbabwe is presented, based on gross morphology, leaf epidermal structure and isoenzyme analysis. Specimens analysed were obtained from field collection, herbarium material and cultivated material. Vegetative characters including number of leaves per plant, leaf shape, length, width and reproductive characters of inflorescence type, peduncle, raceme and perianth tube lengths were studied. Scanning electron microscopy (SEM) studies on leaf epidermal surfaces showed variation in epidermal surface ornamentation patterns, shape of the stomata and the degree of adaptation to xeric environments among taxa. Activity of eight isoenzymes was tested in *Sansevieria* leaf extracts. Isoenzyme data confirmed presence of polyploidy and a close relationship between species, suggesting reticulate crossings among ancestral groups. Eight species were delimited on the basis of this taxonomic study: *S. aethiopica*, S. *hallii*, *S. hyacinthoides*, *S. kirkii*, *S. pearsonii*, *S. fischeri*, *S. stuckyi* and an undescribed *Sansevieria* species A. Three species previously recognised as distinct, *S. desertii*, *S. rhodesiana* and *S. pearsonii* were sunk into synonymy of *S. pearsonii.*

Résumé

Une étude taxonomique du genre *Sansevieria* (Dracaenaceae) au Zimbabwe. Une étude taxonomique du genre *Sansevieria* au Zimbabwe est présentée. Elle est basée sur la morphologie générale, la structure de l'épiderme foliaire et des analyses isoenzymatiques. Les échantillons analysés proviennent de récoltes sur le terrain, de spécimens d'herbier et de matériel cultivé. Les caractères végétatifs, notamment le nombre de feuilles par plante, la forme des feuilles, la longueur, la largeur et les caractères reproductifs de l'inflorescence, la longueur du pédoncule, du racème et du tube du périanthe ont été étudiés. Des études à l'aide d'un microscope à balayage (SEM) des surfaces de l'épiderme foliaire ont montré la variation des types d'ornementation, de la forme des stomates ainsi que le degré d'adaptation à des environnements xériques. L'activité de huit isoenzymes a été testée sur des extraits foliaires de *Sansevieria.* Les données isoenzymatiques ont confirmé la présence de polyploïdie et une relation étroite entre espèces, suggérant des croisements réticulés au sein de groupes ancestraux. Huit espèces ont été délimitées sur base de cette étude taxonomique: *S. aethiopica*, *S. hallii*, *S. hyacinthoides*, *S. kirkii*, *S. pearsonii*, *S. fischeri*, *S. stuckyi* et *Sansevieria* species A, non décrite. Trois espèces jusqu'alors reconnues comme distinctes, *S. desertii*, *S. rhodesiana* et *S. pearsonii* ont été mises en synonymie avec *S. pearsonii.*

Key words: isoenzyme, leaf epidermal structure, taxonomy, *Sansevieria*

1 Introduction

Sansevieria belongs to the family Dracaenaceae and consists of xerophytic perennial herbs occurring in dry tropical and subtropical parts of the world. The genus consists of about 70 species ranging from Africa through Asia to Burma and the islands of the Indian Ocean (Purseglove, 1972; Alfani *et al.*, 1989). *Sansevieria* is known variously as the mother in law's tongue, bowstring hemp, snake plant or zebra lily (Agnew, 1974; Koller & Rost, 1988). Local names for different *Sansevieria* species in Zimbabwe include '*mukonje*', '*nyangayapfeni*' or '*sharamhanda*' in Shona, '*isikholokotho*' in Ndebele and '*chikwenga*' in Ndau.

Species of *Sansevieria* are of great economic importance as a source of fibre, medicine, and as ornamentals. Various *Sansevieria* species are widely used to cure earache, toothache, hemorrhoids and other various ailments (Russell, 1982). *Sansevieria* species are major foliage ornamentals mainly due to the variegated and mottled leaves (Bos, 1998). An extremely wide variation in growth form and habit exists within the genus. Alfani *et al.* (1989) pointed out the remarkable variation of the genus in the leaf morphology, reflecting its adaptation to different degrees of drought (Virzo de Santo *et al.*, 1981–1982). The leaves greatly vary in shape and size: species have linear, flat, semi-cylindrical or cylindrical leaves. The mottled, erect and stiff leaves of *Sansevieria* are used a great deal in artistic flower arrangements.

The most extensive taxonomic study of *Sansevieria* to date, largely based on leaf morphology, is that of Brown (1915). He described 54 species and 9 varieties based on living specimens. Forty-three of the species he described were growing in cultivation at the Royal Botanic Gardens, Kew. The species described by Brown (1915) were not all observed in their natural habitat. Some of Brown's descriptions were solely based on cultivated material and others from poor, incomplete herbarium specimens. Information on the inflorescence was often lacking or not seen for some species, for example *S. stuckyi* Godefroy-Leb., *S. singularis* N.E.Br., and *S. zeylanica* Willd.

Table 1 shows the *Sansevieria* taxa that were recognised for Zimbabwe prior to this study. Russell (1982) and Chahinian (1993) however acknowledged that the taxonomy of the genus was not fully understood and that there was need for a detailed study to sort out the taxonomy of the genus in Zimbabwe. The aim of this study therefore was to examine species delimitation within *Sanseveria* in Zimbabwe by investigating macro-morphological variation, analysing the structure of *Sansevieria* leaf surfaces and studying patterns of isoenzyme variation.

TABLE 1. *Sansevieria* taxa recognised prior to the current study.

Species	**Author**	**Type locality**
S. desertii	N.E.Brown (1915)	Bulawayo
S. rhodesiana	N.E.Brown (1915)	Rhodesia (now Zimbabwe) no precise locality
S. aethiopica	N.E.Brown (1915)	near Bulawayo, and in southern part of Zimbabwe
S. livingstoniae	Rendle (1932)	Victoria Falls, Livingstone Island, Zimbabwe
S. hallii	Chahinian (1995)	Beitbridge, southern Zimbabwe
S. conspicua	Russell (1982)	No precise locality
S. stuckyi	Russell (1982)	No precise locality

2 Materials and methods

2.1 Herbarium and field studies

Specimens housed at the National Herbarium, Harare (SRGH), National Botanical Institute, Pretoria (PRE), Royal Botanic Gardens, Kew (K) and the British Museum (BM) were examined during the course of the study. Fieldwork was carried out at 114 Zimbabwean localities between December 1996 to February 1999. Emphasis throughout the study was placed on taking measurements from fresh *Sansevieria* material since many characters in *Sansevieria* change significantly on drying. Table 2 and 3 show the characters studied during the taxonomic study.

TABLE 2. Quantitative morphological characters used in numerical analysis of *Sansevieria* species in Zimbabwe.

Character	Character description
1 Number of leaves	The maximum number of leaves observed in the population
2 Leaf maximum length (cm)	Measured from point of leaf attachment to rhizome up to leaf apex
3 Leaf width at midpoint (cm)	Measured on adaxial surface after leaf had been horizontally cut in the middle
4 Leaf thickness at midpoint (cm)	Distance between the adaxial and the abaxial side through the thickest part of leaf
5 Inflorescence unit length (cm)	Measured from the point where inflorescence attaches to rhizome to the tip of the inflorescence
6 Number of nodal bracts	Numerical count of the bracts along the length of the peduncle
7 Pedicel length (cm)	Measured from point of pedicel attachment to the peduncle to the point of attachment to the perianth tube
8 Perianth tube length (cm)	Distance from swollen base to the tip of perianth tube
9 Inflorescence unit length	Length of the main stalk for the entire inflorescence
10 Internode distance (cm)	Average distance between the three top nodes on the peduncle

TABLE 3. Qualitative morphological characters and the character states measured on the *Sansevieria* specimens analysed.

Character	**Character state**
Phyllotaxy	1 = single leaf 2 = distichous 3 = rosulate
Shape of leaf	1 = cylindrical 2 = semi-cylindrical 3 = linear 4 = flat 5 = flat, rolled base
Leaf surface texture	1 = smooth 2 = slightly rough 3 = rough
Presence or absence of leaf banding	1 = absent 2 = present but faint 3 = present and distinct
Inflorescence type	1 = capitate 2 = racemose

2.2 Phenology studies

The phenology of each *Sansevieria* taxon was studied and observations were made on the time of opening of the flowers and the duration for which they opened.

2.3 Leaf epidermal surface structure

Leaf surface tissue, 4 × 5 mm^2 in size was cut from fresh leaves from various *Sansevieria* species and the white inner fibrous tissue scraped off. Standard scanning electron microscopy (SEM) methods according to Koller & Rost (1986) were used.

2.4 Enzyme electrophoresis

A total of 88 *Sansevieria* specimens were analysed. Eight enzymes were investigated in the leaf extracts; Aspartate aminotransferase (AAT), Aminopeptidase (AMP), Glucose–6-phosphate isomerase (GPI), Isocitrate dehydrogenase (IDH), Malate dehydrogenase (MDH), Phosphoglucomutase (PGM), 6-Phosphogluconate dehydrogenase (6-PGD) and Triose-phosphate isomerase (TPI). Tissue preparation and electrophoretic procedures followed methods modified from Morden, Doebley & Schertz (1987), Wendel & Weeden (1989) and Borgen (1997).

3 Data analysis

Both clustering (UPGMA) and Canonical Discriminant Function analysis (CDA) were performed on the morphological data set using the SPSS 7.0 statistical programme (Norusis, 1988). UPGMA analysis was based on the fifteen morphological characters detailed in Tables 2 and 3 and 35 operational taxonomic units. The number of specimens for each taxa depended on the availability of wild or cultivated material. The CDA analysis was based on the same units, but 13 characters were used as leaf shape and inflorescence type failed the tolerance test in the analysis.

4 Results

4.1 Multivariate analysis

A phenogram (Fig. 1) was produced as the result of the UPGMA analysis. A total number of 8 clusters corresponding to the taxa *S. hyacinthoides*, *S. aethiopica*, *S. kirkii*, *S. hallii*, *S. stuckyi*, *S. pearsonii*, *S. fischeri* and *S.* sp. A. were clear from the phenogram.

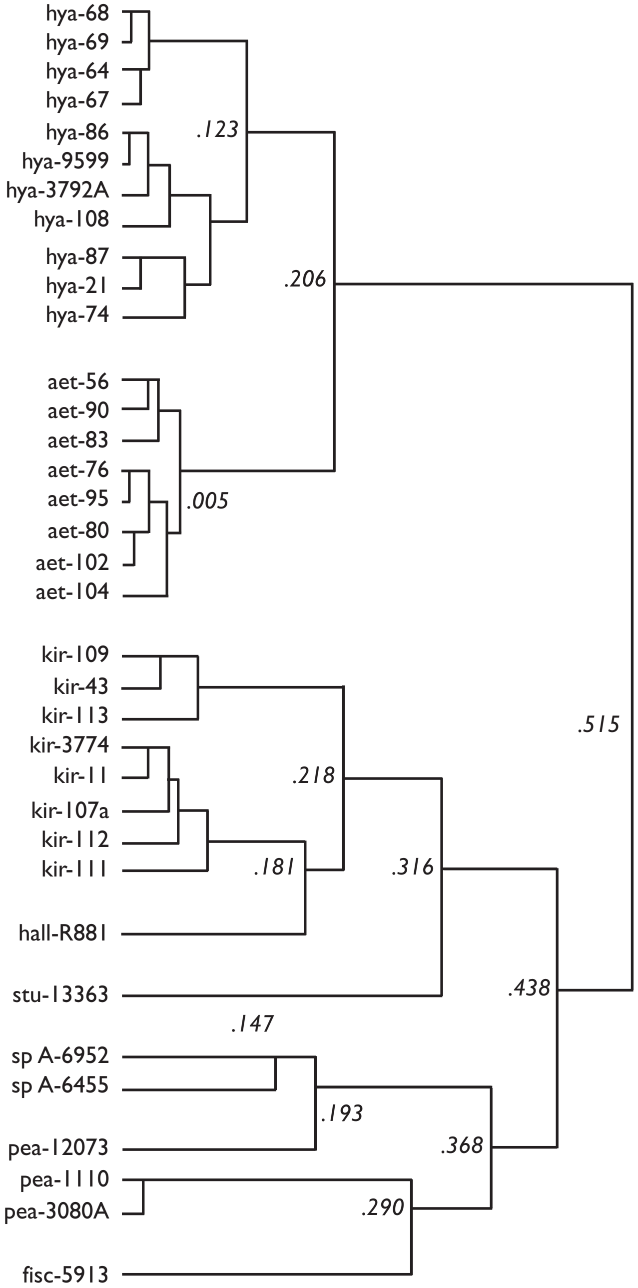


FIG. 1. A UPGMA dendrogram based on 15 morphological characters and 35 individual populations of *Sansevieria*. The individual populations are labelled with population numbers and the first three or four letters of the taxon names (hya = *S. hyacinthoides*, aet = *S. aethiopica*, kir = *S. kirkii*, hall = *S. hallii*, stu = *S. stuckyi*, s.n. = *S.* species A, pea = *S. pearsonii*, fisc = *S. fischeri*). Squared Euclidean Distance was applied.

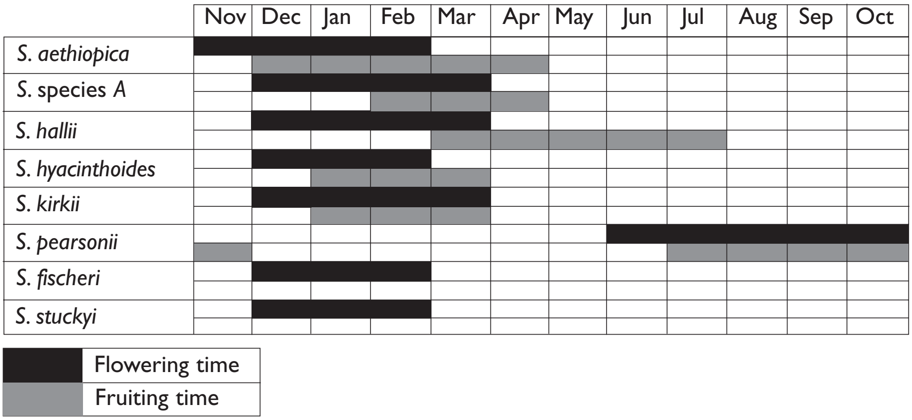
The CDA analysis separated the operational taxonomic units into the same eight distinct groups.

4.2 Phenology

The *Sansevieria* species flowered at specific times of the year as shown in Fig. 2. Flowers generally open in the late afternoon around 15:00 hours, emitting a strong scent, and close in the early hours of the following morning around 07:00 hours. Each flower opens for only one night after which it shrivels. The flowering times overlap with the fruiting times as shown. No fruits were observed for *S. fischeri* and *S. stuckyi*.

Inflorescences in *Sansevieria* include reduced cymes in either spike-like or capitate compound forms. A loose spike-like inflorescence is observed in *S. aethiopica*, *S. hyacinthoides*, *S. pearsonii* and *S.* sp. A, while a capitate inflorescence is observed in *S. hallii*, *S. kirkii*, *S. fischeri* and *S. stuckyi*. Flowers are arranged in fascicles ranging from 2 to 10 per fascicle with a lanceolate bract subtending each fascicle.

The length of the perianth tube is variable between species. The longest perianth tube is observed mainly in the species with capitate inflorescences: *S. hallii*, *S. kirkii*, *S. fischeri* and *S. stuckyi* and also in *S.* sp. A. The colour of the perianth tube ranges from cream in *S. pearsonii*, light green in *S.* sp. A, and light green tinted with purple or pink in *S. kirkii*. Individual flowers have six perianth segments that are fused into a tube, with reflexed lobes during anthesis. The fruit is a berry with one, two or three seeds. The pericarp is green and turns yellow or orange when ripe. It is either smooth or pustulate with blister-like swellings on its surface. A pustulate pericarp was observed on the fruits of *Sansevieria aethiopica*, *S. hyacinthoides*, *S. hallii*, and *S. kirkii* while a smooth pericarp was observed in *S. pearsonii* and *S.* sp. A. Fruits were not seen in *S. stuckyi* and *S. fischeri*.



	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
S. aethiopica	■	■	■	■								
		▨	▨	▨	▨	▨						
S. species A		■	■	■	■							
				▨	▨	▨						
S. hallii		■	■	■	■							
					▨	▨	▨	▨	▨			
S. hyacinthoides		■	■	■								
			▨	▨	▨							
S. kirkii		■	■	■	■							
			▨	▨	▨							
S. pearsonii								■	■	■	■	■
	▨								▨	▨	▨	▨
S. fischeri		■	■	■								
S. stuckyi		■	■	■								

■	Flowering time
▨	Fruiting time

FIG. 2. The flowering times of the *Sansevieria* species.

4.3 Leaf epidermis

The leaf epidermal cell walls showed different ornamentation patterns when observed under scanning electron microscopy. The surface of the cuticle in all the species shows one of three types of cuticular sculpturing. An unornamented surface is observed in *S. hallii*, a surface with micro-ornamentation and the cuticle arranged into striae or reticulate patterns is observed in *S. aethiopica, S. hyacinthoides, S. kirkii,* *S. fischeri, S. pearsonii* and *S.* sp. A, while a papillate surface is observed in one species, *S. aethiopica*. Interpretation could however not be made on the epidermal structure of *S. stuckyi*.

4.4 Isoenzyme variation

Aspartate aminotransferase (AAT), Glucose–6-phosphate isomerase (GPI), Isocitrate dehydrogenase (IDH), Malate dehydrogenase (MDH), Phosphoglucomutase (PGM) and Triose-phosphate isomerase (TPI) gave interpretable banding patterns of the specimens analysed. No interpretable enzyme expression was obtained for Aminopeptidase (AMP) and 6-phosphogluconate dehydrogenase (6-PGD).

The isoenzyme systems investigated (all except AAT) gave a higher number of bands than those expected for diploids. The band patterns obtained for GPI, IDH, MDH, PGM, and TPI show fixed heterozygosity, strongly indicating allopolyploidy (Kephart, 1990). Kephart (1990) stated that patterns observed for polyploids were complex due to the duplication of the entire genome. Isoenzyme data also indicated that all *Sansevieria* taxa are closely related, with *S. pearsonii* in a somewhat distinct position, having unique alleles in the enzymes IDH and PGM. This species is also unique in lacking band expression in 'loci' commonly expressed in other taxa (in the cathodal area of GPI and the anodal area of PGM). The close similarity observed between band phenotypes of the different species, combined with the evidence of polyploidy could be an indication that reticulate evolution has taken place at an early stage during the evolution of the genus *Sansevieria*, and partly accounts for the complicated taxonomy of the genus.

5 Discussion

Maximum number of leaves per plant, leaf maximum length, leaf width and the presence or absence of leaf banding or variegation were important in the delimitation of taxa. These results support the findings of Brown (1915) who delimited *Sansevieria* species on the basis of phyllotaxy, gross morphology and leaf characters. Koller & Rost (1988) put emphasis on leaf shape, leaf colour, variegation patterns and surface texture as important taxonomic characters, based on a study they carried out on 49 *Sansevieria* species. The observed different sculpturing patterns were a diagnostic feature for the different *Sansevieria* taxa. Koller & Rost (1988) suggested that the rough texture on some leaves was caused by the transversely oriented microscopic ridges on the leaf surfaces, which are a result of radial elongation of epidermal cells and that different ornamentation patterns that were observed on the leaf surface were due to different ways in which the copious wax layers are deposited on the leaf surface of different species. The papillae observed to be unique to *S. aethiopica* could be of taxonomic importance in the delimitation of the species. The papillate surface structure makes the species well adapted to the dry, hot low-lying areas of Zimbabwe and Botswana where it occurs.

Brown (1915) treated *S. pearsonii, S. desertii* and *S. rhodesiana* as separate species on the basis of the number of leaves, leaf arrangement in space, and leaf texture. Leaf number in Brown's treatment of the three taxa actually overlaps implying that leaf number is a poor character in the separation of the taxa. Observations made on fresh specimens also gave no evidence to sustain the three taxa *S. pearsonii, S. desertii*, and *S. rhodesiana* as they appeared morphologically similar. The three taxa are therefore included under *S. pearsonii.*

6 Species of Sanseveria from Zimbabwe recognized in this study

Key to the Zimbabwean species

1 Inflorescence capitate; peduncle entirely below the earth surface,
18.5 cm long .... *S. hallii*
Inflorescence paniculate or capitate; peduncle protruding above
the soil surface, 40–109 cm long 2
2 Leaves semi-cylindrical to cylindrical, with longitudinal grooves and
a channel on the face of the leaf 3
Leaves linear, concave, or flat 5
3 Leaves several, up to twelve, distichously arranged; inflorescence
paniculate; perianth tube up to 2.2 cm long .... *S. pearsonii*
Leaf solitary, inflorescence capitate; perianth tube 8.5–12 cm
long 4
4 Leaf up to 147 cm long, with shallow channel at base, narrowing
and tapering into acute apex; peduncle up to 24.2 cm long .... *S. stuckyi*
Leaf with V-shaped channel, which widens into a folded upper
region with an obtuse apex, peduncle 26–33 cm long .... *S. fischeri*
5 Inflorescence capitate .... *S. kirkii*
Inflorescence paniculate 6
6 Leaves linear; 1–2.2 cm wide at midpoint .... *S. aethiopica*
Leaves flat, sometimes folded at base; 6–13.5 cm wide at midpoint 7
7 Leaves distinctly variegated; pedicel 0.3–0.4 cm .... *S. hyacinthoides*
Leaves plain green, sometimes faintly variegated; pedicel 0.85–1.9 cm
long .... *S.* sp. A

Sanseviera hallii *Chahinian* in Sansevieria Journal 5: 7–10 (1995). Type from Zimbabwe, east region, Birchinough Bridge, *Chahinian* 634 (MO holotype, UPS isotype).

Selected specimens from Zimbabwe:

S: Ndanga, Gutu, fl. 22.xii.1951, *Wild* 3711 (K, PRE, SRGH); near Save River, *Richards* R881 (SRGH); along Masvingo–Beitbridge road, just before Lundi River, *Takawira* 72 (SRGH).

E: Umvumvumvu River on Mutare–Birchnough road, *Leach* 10714 (K, SRGH).

Also occurs in South Africa; on steep rocky outcrops.

Sansevieria pearsonii *N.E.Br.* in Kew Bull. 1911: 82–97 (1911) & in Kew. Bull. 1915: 216 (1915); A.A. Oberm. in Flora of Southern Africa 5(3): 8 (1992); Jaarsveld in Aloe 31(1): 11–15 (1994). Type from southern Angola, near the 108.5 km peg on the Mossamedes railway line, *Pearson* 2073 (K!, holotype)

S. desertii N.E.Br. in Kew Bull. 21 (5): 208 (1915); Verdoon in Flowering plants of southern Africa 21: table 806 (1941). Types from Botswana, banks of Botletle River on the Kalahari desert, *Lugard* 9 (K!, syntype); shore of lake Ngami and River Botletle, *Nicolls* s.n. (K!, syntype).

S. rhodesiana N.E.Br. in Kew Bull 21(5): 212 (1915). Type from Zimbabwe, without precise locality (K!, syntype).

S. livingstoniae Rendle in Journ. Bot. 70: 89 (1932). Type from Zimbabwe, Victoria Falls, Livingstone Island, *Rendle* 374 (BM!, holotype).

Selected specimens from Zimbabwe:

N: Hurungwe, Rukomichi River gorge, 16.x.1964, *Bingham* 1373 (SRGH).
W: Hwange, Victoria Falls, fl. 22.viii.1977, *Mshasha* 5 (K, SRGH),
C: Beatrice, fl. 16.vii.1942, *Hopkins* 9189 (SRGH); E: Mutare, fl. 12.vii.1953, *Chase* 5011 (SRGH); S: Save valley, i.1949, *Chase* 1684 (SRGH).
S: Ngundu, Masvingo, fl. 26.vii.1999, *Takawira* 71 (SRGH).
Also in Zambia, South Africa and Angola; in colonies on degraded soils, eroded sandy clays, termite mounds and around rocky outcrops under trees, sometimes in humus, among rocks, on river banks, or tree trunks.

Sansevieria stuckyi *Godefr.-Leb.* ex *Gerome & Labroy* in Bull. Mus. Hist. Nat. 9: 173 (1903); De Wildem. in Notices Pl. Utiles du Congo: 623–625 (1903); Pfennig in Botanische Jahrbucher 102(1-4): 169–179 (1981). Type from Mozambique, Bena, collector unclear, s. n. (P, holotype, K!, isotype).
Selected specimens from Zimbabwe:
E: Burma or Honde Valley, 20.vii.1987, *Richards* DJR 54 (SRGH)
Also in South Africa, Mozambique and Tanzania. In Zimbabwe now locally extinct in natural habitats and not found in the wild.

Sansevieria fischeri (*Baker) Marais* in Kew Bull. 41(1): 58 (1986).
Sansevieria singularis N.E.Br. in Kew Bull. Misc. Inf. 1911: 97 (1911). Types: *Powell* 2; Mwatate, *Powell* 10 (K! isosyntypes)
Selected specimens from Zimbabwe:
N: Chizinga mountain, Umfurudzi, *Jarvis* s.n.
S: Samba Farm near Chiredzi, fl xii.1999, *Jaklitsch* s.n.
Also occurs in Kenya. In Zimbabwe now locally extinct in natural habitats and not found in the wild.

Sansevieria kirkii *Baker* in Kew Bull. Misc. Inf. 1(5): 8 (1887); N.E. Brown in Kew Bull. Misc. Inf. 1915: 255 (1915). Type: from Tanzania, near Pangani, *Kirk* s.n. (K!, syntype); Zanzibar, *Lyne* 3 (K!, syntype); idem, *Sacleux* 1496 (K!, syntype).
Selected specimens from Zimbabwe:
N: Gokwe, Chief Nemangwe area, south of Gwave River in Mopane woodland, fl. 22.i.1964, *Bingham* 1182 (SRGH); Zhombe Mission, 50.5 km along the Gokwe–Kwekwe road, fr. 20.i.1998, *Takawira* 114 (SRGH); Shamva, fl. 26.xii.1921, *Eyles* 3236, (SRGH); Sebungwe, west of Mzola River, xi.1958, *Gillet* s.n. (SRGH).
W: Hwange, Lutope–Gwaai R Junction, fl. 26.ii.1963, *Wild* 6021 (SRGH); Mazabuka, about 3 miles Southwest of Chirundu Bridge, fl. 1.ii.1958, *Drummond* 5419 (SRGH).
C: Makonde, Windale farm, fl. 24.iii.1969, *Pope* 2 (SRGH).

Sansevieria aethiopica *Thunb.* in Prodr. Pl. Cap., 65 (1794) &. in Flora Cap.: 329 (1823); Kunth in Enum. Pl. 5: 19 (1850); N.E. Br. in Curtis's Bot. Mag. 139: t. 8487 (1913); N.E. Br. in. Kew Bull. Misc. Inf. 1915: 230 (1915); Verdoon in Flowering plants of southern Africa 6: t. 212 (1926); Adams in Wild Fl. northern Cape: t. 28 (1976). Type from South Africa, Cape, near Uitenhage, *Thunberg* s. n. (UPS; microfiche in PRE, no. 8576).
S. scabrifolia Dinter in Repert. Sp. Nov. 30: 85(1932). Type: Namibia, Otavifontein, *Dinter* 5377 (B, holotype, PRE!, isotype).
S. zeylanica: Redoute, Liliacees 5: t. 290 (1810); Kunth in Enum. Pl. 5: 19 (1850); Baker in Journ. Linn. Soc., Botany 14: 548 (1875); Baker in Flora Cap. 6: 5 (1896).
Selected specimens from Zimbabwe:

W: near Bulawayo, fr. iii.1900, *Cecil* 103 (K, SRGH); Matobo district, Farm Besna Kobila, fl. i.1955, *Miller* 2055 (SRGH); & same loc., fl. xi.1954, *Miller* 2524 (K, SRGH); Khami, 4.x.1942, *Hopkins* s.n. (SRGH).

S: Gutu East purchase area, fr. 21.xii.1967, *Phaney* s.n. (SRGH); Beitbridge, Shashi Drift, Tuli, near Pioneer Memorial, 14.v.1959, *Drummond* 6153 (SRGH); Gwanda, Stanmore, fr. 20.i.1998, *Takawira* 57 (SRGH).

C: Gweru, Mlezu Farm, SSE of Kwekwe, 20.xi.1965, *Biegel* 542 (SRGH).

Also occurs in Botswana, Namibia and South Africa.

Sansevieria hyacinthoides (*L.*) *Druce* in Bot. Soc. Brit. Isl. Report 3: 423 (1914); Wijnands in Taxon 22(l): 109 (1973) & in Botany of the Commelins*:* 138 (1983); Obermeyer in Flora S. Africa 5(3): 5 (1992).

S. grandis Hook. in Curtis's Bot. Mag. 129: t. 7877 (1903). Type: t. 7877, drawn from specimen sent to Kew from Cuba (iconotype).

S. grandis Hook. var. *zuluensis* N.E.Br. in Kew Bull. Misc. Inf. 1915**:** 251 (1915). Type from Natal, Zululand *Wylie* in NH 12010 (NH, holotype).

S. conspicua N.E.Br. in Kew Bull. Misc. Inf. 1915: 243–245 (1915).

Selected specimens from Zimbabwe:

E: Elim Mission, Nyanga North, vii.1966, *Drummond* 8912 (SGRH); Nyoni Hill, near Tokwe Dam, 7.vii.1968, *Muller* 923 (SRGH); 30 km from Mutare along Mutare–Chimanimani road, fl 10.ii.97, S Mushandike Game Reserve, Masvingo, *Takawira* 34 (SRGH); Ruti Dam site on boundary of Gutu and Sabi, fl. 8.viii.1974, *Ellert* 26672.

Also occurs in South Africa; common on rocky outcrops, on termite mounds or in association with *Colophospermum mopane* or *Aloe* species.

Sansevieria sp. A

Selected specimens from Zimbabwe:

E: Chimanimani, Lower east slopes of Chimanimani mountain ranges, North of Makurupini River, *Muller & Kelly* 5/69. Living plants in cultivation at National Botanic Garden, Harare. Full description of species to be published in a separate paper.

7 Conclusion

Based on vegetative and floral characters morphology, representatives of the genus *Sansevieria* may be referred to eight different species: *Sansevieria aethiopica, S. hallii, S. hyacinthoides*, *S. kirkii*, S. *pearsonii*, *S. stuckyi*, *S. fischeri* and one unnamed species, *Sansevieria* species A. All previously recognised species with a flat variegated leaf and a spike-like inflorescence were placed under *S. hyacinthoides*. This taxon includes accordingly the variegated-leaf taxon from the Great Dyke, the variegated-leaf taxon from Masvingo and that from Murahwa hills, which all show great variation in leaf size, although further delimitation of this complex taxon could not be supported by the numerical analyses. There is therefore a need for a broader study of the *S. hyacinthoides* complex to find useful characters upon which this complex, whose variation is apparent, can be split.

The two similar taxa with giant cylindrical leaves, *S. stuckyi* and *S. fischeri,* have been separated on the basis of floral morphology. Although they both have a capitate inflorescence, they were separated based on the length of the peduncle. All semi-cylindrical leaf species of Zimbabwe that were formally known as *S. livingstoniae*, *S. rhodesiana*, *S. desertii* and *S. pearsonii* have been treated as *S. pearsonii* based on evidence from morphological and isoenzyme data.

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GENERIC RELATIONSHIPS WITHIN THE TRIBE HAEMANTHEAE (AMARYLLIDACEAE) BASED ON PLASTID DNA SEQUENCE DATA

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Abstract

The African tribe Haemantheae (Amaryllidaceae) comprises six genera (*Gethyllis, Apodolirion, Haemanthus, Scadoxus, Clivia* and *Cryptostephanus*) with ± 90 species. A phylogenetic hypothesis for the Haemantheae is presented as a basis for an enquiry into the generic and species relationships within the tribe. DNA sequence data from five plastid regions: the *rpoB-trnC* intergenic spacer, *trnL* intron, *trnL-F* intergenic spacer, the *rps16* intron and the *psbA-trnH* intergenic spacer have been collected and analysed for 43 taxa within this tribe using five Amaryllidacean outgroups. Combined parsimony analysis of all five matrices indicated that *Scadoxus* and *Haemanthus* are monophyletic and resolved as sister clades to one another. The summer rainfall group within the genus *Haemanthus* is monophyletic. The genus *Apodolirion* is embedded within *Gethyllis* as has been previously suggested on morphological grounds. Both *Clivia* and *Cryptostephanus* resolved as monophyletic groups with *Cryptostephanus* placed as sister to *Clivia*.

Résumé

Relations génériques au sein de la tribu des Haemantheae (Amaryllidaceae) basées sur des données de séquençage de l'ADN chloroplastique. La tribu africaine des Haemantheae (Amaryllidaceae) comprend six genres (*Gethyllis, Apodolirion, Haemanthus, Scadoxus, Clivia* et *Cryptostephanus*) et ± 90 espèces. Une hypothèse phylogénique pour les Haemantheae est présentée comme base de recherche des relations génériques et spécifiques au sein de la tribu. Les données de séquençage de l'ADN à partir de cinq régions de l'ADN chloroplastique: la région non codante entre *rpoB* et *trnC*, l'intron *trnL*, la région non codante entre *trnL* et *trnF*, l'intron *rps16* et la région non codante entre *psbA* et *trnH* ont été collectées et analysées pour 43 taxons au sein de cette tribu, en utilisant cinq groupes externes représentants de la famille des Amaryllidaceae. L'analyse de parcimonie combinée des cinq matrices a montré que *Scadoxus* et *Haemanthus* étaient monophylétiques et résolus comme des clades sœurs. Le groupe d'espèces au sein du genre *Haemanthus*, croissant sous le régime des précipitations d'été, est monophylétique. Le genre *Apodolirion* est inclus dans *Gethyllis*, comme la morphologie le suggérait préalablement. *Clivia* et *Cryptostephanus* sont identifiés comme des groupes monophylétiques avec *Cryptostephanus* considéré comme sœur de *Clivia*.

Key words: Amaryllidaceae, Haemantheae, plastid DNA sequences, phylogeny

1 Introduction

Amaryllidaceae is a widely distributed family with centres of diversity in South America, particularly the Andean region, South Africa and the Mediterranean (Meerow & Snijman, 1998). The African tribe Haemantheae, depending on classification, comprises the following main genera: *Haemanthus*, *Clivia*, *Cryptostephanus*, *Apodolirion*, *Gethyllis* and *Scadoxus*. All the genera have berry-like fruits with water-rich seeds (Meerow & Snijman, 1998) which distinguish them from most other Amaryllidaceae.

Apodolirion (six species), which is endemic to southern Africa, is characterized by a solitary flower with a subterranean ovary and chromosome number x=6; three Cape species have been included in the analysis. *Clivia* (five species), found in the Northern Cape and eastern southern Africa, possesses rhizomes and chromosome number x=11; all five species in the genus have been included in the study. *Cryptostephanus* (4 species) from east and central Africa possesses rhizomes and has chromosome number x=12; two species have been included in the analysis. *Gethyllis* (32 species) occurs in southern Africa. Like its closest relative, *Apodolirion,* the plants are characterized by a solitary flower with a subterranean ovary and chromosome number x=6; some species have pubescent leaves; 12 species are included in the study. *Haemanthus* (22 species), endemic to southern Africa has pubescence developed in some species and chromosome number x=8; 19 *Haemanthus* species are included in the analysis. *Scadoxus* (9 species), which is widespread in tropical Africa, is characterised by rhizomes, pseudo-petiolate leaves and chromosome number x=9; two species have been included in this study.

The four most recent infrafamilial classifications of Amaryllidaceae for the six genera in this study of the African tribe Haemantheae, are those of Traub (1963), Dahlgren *et al.* (1985), Müller-Doblies & Müller-Doblies (1996), Meerow (1995) and Meerow & Snijman (1998). Traub (1963) recognised three different tribes: Haemantheae (*Haemanthus* and *Choanthus*), Clivieae (*Clivia* and *Cryptostephanus*) and Gethylleae (*Apodolirion* and *Gethyllis*). Dahlgren *et al.* (1985) recognized only one tribe, Haemantheae, and included *Cyrtanthus* in this tribe. Like Dahlgren *et al.* (1985), Müller-Doblies & Müller-Doblies (1996) also included *Cyrtanthus* in the tribe Haemantheae (*Haemanthus, Scadoxus, Cryptostephanus* and *Clivia*), one of two tribes they recognized, the other being Gethyllideae (*Apodolirion* and *Gethyllis*). In addition they divided the tribe Haemantheae into three subtribes: Haemanthinae (*Haemanthus* and *Scadoxus*), Cliviinae (*Clivia* and *Cryptostephanus*) and Cyrtanthinae (*Cyrtanthus*), infrageneric groupings not recognised by any other author. Meerow & Snijman (1998) recognised two tribes: Haemantheae (*Haemanthus*, *Scadoxus*, *Cryptostephanus* and *Clivia*) and Gethyllideae (*Gethyllis* and *Apodolirion*).

The most recent classification is that of Meerow *et al.* (1999) based on *rbcL* and *trnL-F* sequence data. Here the tribe was demonstrated to comprise six genera (*Haemanthus*, *Scadoxus*, *Clivia*, *Cryptostephanus*, *Apodolirion* and *Gethyllis*). Meerow *et al.* (1999) proposed that *Cyrtanthus* be recognised as a monotypic tribe as its inclusion with Haemantheae received low bootstrap support in their analysis. *Apodolirion* and *Gethyllis* were recovered as sister taxa and were also firmly embedded in Haemantheae. Thus recognition of a separate tribe Gethyllideae was not supported by these molecular data (Meerow *et al.*, 1999) and the more recent analysis of Meerow & Clayton (2004) using *trnL-F* and nr DNA ITS sequences. *Haemanthus* and *Scadoxus*, resolved as sister genera in this analysis (Meerow *et al.*, 1999). In the past they have been treated as one genus (Bjornstad & Friis, 1972), but a cladistic analysis of 25 morphological characters (Nordal & Duncan, 1984) has upheld their delimitation as separate genera.

A separate investigation of the Amaryllidaceae using *matK*, by Ito *et al.* (1999), included 31 taxa of which there were representatives of *Scadoxus, Haemanthus* and *Clivia*. This analysis demonstrated that these three genera form a monophyletic group, with *Clivia* sister to the clade comprising *Scadoxus* and *Haemanthus*.

Of the genera included in the Haemantheae, the widely cultivated genus *Clivia* is of particular interest owing to the recent discovery of a fifth *Clivia* species – *Clivia mirabilis* in the winter rainfall Northern Cape. This has prompted questions regarding the relationship of this taxon to the other four *Clivia* species, which are restricted to the summer rainfall regions of southern Africa: from the Eastern Cape northwards to Limpopo Province and Swaziland (Rourke, 2002).

Using evidence from five plastid DNA sequence regions for 43 of the 90 taxa in Haemantheae, the objectives of this study were to address firstly, the generic relationships in the tribe, with particular emphasis on the relationship of *Gethyllis* and *Apodolirion* to the other members of the group and the status of *Apodolirion* in respect to *Gethyllis*. Secondly to use the phylogeny, in future studies, to comment on the biogeographic implications (summer-winter rainfall taxa relationships) shown by the Haemantheae.

2 Materials and methods

Narcissus (Narcisseae), *Sternbergia* (Narcisseae), *Lycoris* (Lycorideae), *Sprekelia* (Hippeastreae) and *Calostemma* (Calostemmateae) from the family Amaryllidaceae were designated as the outgroup taxa based upon results of a larger analysis of DNA sequence data for the Amaryllidaceae (Meerow *et al.*, 1999). Table 1 lists the taxa and sequence data used in the study and corresponding voucher information.

2.1 DNA extractions, PCR and cycle sequencing

The following five plastid regions: the *rpoB-trnC* intergenic spacer, *trnL* intron, *trnL-F* intergenic spacer, the *rps16* intron and the *psbA-trnH* intergenic spacer were sequenced for 43 ingroup taxa of the Haemantheae and five outgroup taxa. Total genomic DNA was extracted from 1.0g fresh leaf or flower tissue or 0.2–1.0g silica dried leaf or flower material using the 2X CTAB method of Doyle & Doyle (1987). Purification of the DNA was carried out using Qiaquick (Qiagen) purification kits according to the manufacturer's protocol. Twenty to fifty nanograms of total genomic DNA were used as a template for Taq-mediated amplification. One hundred microlitre reactions contained Promega magnesium-free thermophilic buffer (50mM KCl, 10mM Tris-HCl, 01% Triton X100), 3mM $MgCl_2$, 0.004% BSA, 0.2mM each dNTP, 100ng of each primer and 2.5U Taq polymerase.

Thirty cycles of DNA amplification were carried out in a Gene Amp PCR System 9700 (Applied Biosystems Inc.) using the following programme for the *rpoB-trnC* spacer region: first five cycles: denaturation: 94°C for one minute; annealing: 52°C for one minute (with subsequent decrease of one degree per cycle); extension: 72°C for one minute – the next 25 cycles: denaturation: 94°C for one minute; annealing: 48°C for

TABLE 1. Haemantheae and outgroup species used in molecular analyses, with sequence data collected and voucher information. "NBG" indicates Compton Herbarium, South Africa with accession number in brackets; "ex hort NBG" indicates Kirstenbosch Botanical Garden, South Africa with garden accession number; "–" indicates no sequence available; "partial sequence" indicates only a partial sequence available

	voucher/accession	DNA sequence data			
		rpoB-trnC intergenic spacer	*trnL-F region*	*rps16 intron*	*psbA-trnH intergenic spacer*
Apodolirion cedarbergense D.Müll.-Doblies	Dorse & Kragh s.n.; (NBG 160974)	√	√	√	√
Apodolirion lanceolatum (Thunb.) Baker	Nel s.n.; (NBG 90695)	√	√	√	√
Apodolirion macowanii Baker	Dold 447; (NBG)	√	√	√	√
Clivia caulescens R.A. Dyer	Winter; ex hort NBG 573/99	√	√	√	√
Clivia gardenii Hook.	Winter; ex hort NBG 434/99	√	√	√	partial sequence
Clivia miniata (Lindl.) Regel	Winter; ex hort NBG 442/99	√	√	√	partial sequence
Clivia mirabilis Rourke	J.P.Rourke 2220; (NBG)	√	√	√	√
Clivia nobilis Lindl.	Winter; ex hort NBG 735/96	√	√	√	√
Cryptostephanus vansonii Verdoorn	Duncan s.n; (NBG 196209)	√	√	√	√
Cryptostephanus haemanthoides Welw.	Luke & Luke 6398; ex hort Quentin Luke, Kenya	√	√	√	–
Gethyllis afra L.	Graham s.n.; (NBG 190585)	√	√	√	√
Gethyllis britteniana Baker ssp. *britteniana*	Perry 1062; (NBG)	√	√	√	√
Gethyllis campanulata L.Bolus	Snijman 1262; (NBG)	√	√	√	√
Gethyllis ciliaris (Thunb.) Thunb ssp. *ciliaris*	Duncan 364; ex hort NBG 74/93	√	√	√	√

TABLE 1 continued

	voucher/accession	DNA sequence data			
		rpoB-trnC intergenic spacer	*trnL-F region*	*rps16 intron*	*psbA-trnH intergenic spacer*
Gethyllis gregoriana D.Müll.-Doblies	Ex hort E.G.H. Oliver	partial sequence	√	√	√
Gethyllis lanuginosa Marloth	Van Jaarsveld 4377; (NBG)	√	√	√	√
Gethyllis lata L.Bolus ssp. *orbicularis* D.Müll.-Doblies	Lavranos & Bleck 24199; (NBG)	√	√	√	√
Gethyllis linearis L.Bolus	Snijman 857; (NBG)	√	√	√	√
Gethyllis multifolia L.Bolus	Townsend 130; (NBG)	√	√	√	√
Gethyllis namaquensis (Schönl.) Oberm.	Manning 8/2000; (NBG 191661)	√	√	√	√
Gethyllis transkarooica D.Müll.-Doblies	Snijman 1907; (NBG)	√	√	√	√
Gethyllis verticillata R.Br. ex herb.	Tait 76; ex hort NBG 624/96	√	√	√	√
Gethyllis villosa (Thunb.) Thunb.	Williamson 4426; ex hort NBG 768/91	√	√	√	√
Haemanthus amarylloides Jacq. ssp. *amarylloides*	Snijman 599; (NBG)	partial sequence	√	√	√
Haemanthus amarylloides Jacq. ssp. *polyanthus* Snijman	Snijman 1784; (NBG)	√	√	√	√
Haemanthus barkerae Snijman	Perry and Snijman 2252; (NBG)	√	√	√	√
Haemanthus canaliculatus Levyns	Snijman 1266; (NBG)	√	√	√	√
Haemanthus carneus Ker. Gawl.	Wisura 1063; (NBG)	√	√	√	√
Haemanthus coccineus L.	Snijman 1792; (NBG)	√	√	√	√
Haemanthus crispus Snijman	Snijman 1771; (NBG)	√	√	√	√
Haemanthus dasyphyllus Snijman	Snijman 1299; (NBG)	√	√	√	√
Haemanthus graniticus Snijman	Snijman 1782; (NBG)	√	√	√	√
Haemanthus humilis Jacq. ssp. *hirsutus* (Baker) Snijman	Van Jaarsveld 1834; ex hort NGB 479/77	√	√	√	√

TABLE 1 continued

	voucher/accession	DNA sequence data			
		rpoB-trnC intergenic spacer	*trnL-F region*	*rps16 intron*	*psbA-trnH intergenic spacer*
Haemanthus humilis Jacq. ssp. *humilis*	Van Jaarsveld 3325; (NBG)	√	√	√	√
Haemanthus lanceifolius Jacq.	Snijman 1797a; (NBG)	partial sequence	√	√	√
Haemanthus namaquensis R.A.Dyer	Van Berkel 294; (NBG)	√	√	√	√
Haemanthus pubescens L.f. ssp. *leipoldtii* Snijman	Snijman 432; (NBG)	√	√	√	√
Haemanthus pubescens L.f. ssp. *pubescens*	Snijman 1787; (NBG)	partial sequence	√	√	√
Haemanthus pumillo Jacq.	Snijman 668; (NGB)	√	√	√	√
Haemanthus sanguineus Jacq.	Snijman 210; (NBG)	√	√	√	√
Haemanthus tristis Snijman	Manning 2242 (NBG)	√	√	√	√
Haemanthus unifoliatus Snijman	Snijman 181; (NBG)	√	√	√	√
Scadoxus multiflorus (Martyn) Raf. ssp. *katharinae* (Baker) Friis & Nordal	Snijman & Manning 1878; (NBG)	√	√	√	√
Scadoxus puniceus (L.) Friis & Nordal	Wisura 197/70; ex hort NBG	partial sequence	√	–	√
Calostemma purpureum R.Br.	Gibson 51; (NBG)	√	√	–	√
Narcissus sp.	Ex hort Manning	√	√	√	√
Lycoris sp.	Ex hort Manning	√	–	–	√
Sprekelia sp.	Ex hort Manning	√	√	√	√
Sternbergia sp.	Ex hort Manning	√	–	–	√

one minute; extension: 72°C for one minute. For the adjacent *trnL* intron and *trnL-F* intergenic spacer (collectively known as the *trnL-F* region) and *rps*16 intron the following programme was used: 30 cycles – denaturation: 94°C for one minute; annealing: 48°C for one minute; extension: 72°C for one minute. Finally for the *psbA-trnH* intergenic spacer: 28 cycles - denaturation: 94°C for one minute; annealing: 52°C for one minute; extension: 72°C for one minute.

Amplification of the *rpoB-trnC* intergenic spacer was achieved using primers *rpoB*5' and *trnC*5' (Ohsaka & Ohnishi, 2000). In instances where the region could not be amplified in one piece, internal primers (550F: 5' – ATT AAG TAC ATG CCG ATA CG – 3' and 550R: 5' – CGT ATC GGC ATG TAC TTA AT – 3') were designed to allow amplification of the region in two non-overlapping parts. Primers *rps*16F and *rps*162R (Oxelman *et al.*, 1997) were used to amplify and sequence the *rps*16 intron. Primers 'c' and 'f' (Taberlet *et al.*, 1991) were used to amplify the adjacent *trnL* intron and *trnL-F* intergenic spacer between the *trnL* and *trnF* exons and primers *psbAF* and *trnHR* (Sang *et al.* 1997) were used to amplify the *psbA-trnH* intergenic spacer. Internal primers (570F: 5' – ATG TCC AAT AGA ATA TCT CG – 3' and 570R: 5' – CGA GAT ATT CTA TTG GAC AT – 3') were used to amplify the region in two parts where amplification of the entire region was unsuccessful. For each of the above regions amplification primers were then used as sequencing primers.

Amplification products were purified using Qiaquick (Qiagen) spin columns and directly sequenced on an ABI 377 automated sequencer using standard dye-terminator chemistry following manufacturer's protocols (Applied Biosystems Inc). For assembly and editing of the complementary strands Sequencher 4.1 (Gene Codes) was used. For all regions the variation in length among species was minimal, and thus all sequences were aligned by eye.

2.2 Phylogenetic analyses

All cladistic analyses were performed using the parsimony algorithm of the software package PAUP* for Macintosh (phylogenetic analysis using parsimony and other methods v.4.0b; Swofford, 2000). A combined data matrix of the five plastid regions was analysed using 1000 replicates of random taxon addition, tree bisection-reconnection (TBR) branch swapping, with MULPARS on. All character transformations were treated as equally likely (Fitch parsimony; Fitch, 1971). A limit of ten trees was set for each replicate to reduce time spent swapping on large numbers of trees at or near the optimum. To assess internal support, 1000 bootstrap replicates were performed using simple taxon addition and TBR branch swapping with a tree limit of ten trees per replicate.

3 Results

3.1 Combined analysis

Of the 3283 characters included in the combined analysis 236 (7%) were variable and 179 (5%) potentially parsimony informative. Parsimony analysis gave 9010 trees of length 532 and CI = 0.836 and RI = 0.881. One of the equally parsimonious trees was chosen at random and is shown in Fig. 1. Nodes not present in the strict consensus tree are indicated by arrows. Bootstrap percentages are indicated below the branches, but groups with bootstrap percentages <50% have not been reported. *Haemanthus* and *Scadoxus* formed a monophyletic group with bootstrap support of 85%. *Haemanthus* was resolved as monophyletic with a bootstrap percentage of 61% and similarly *Scadoxus* was

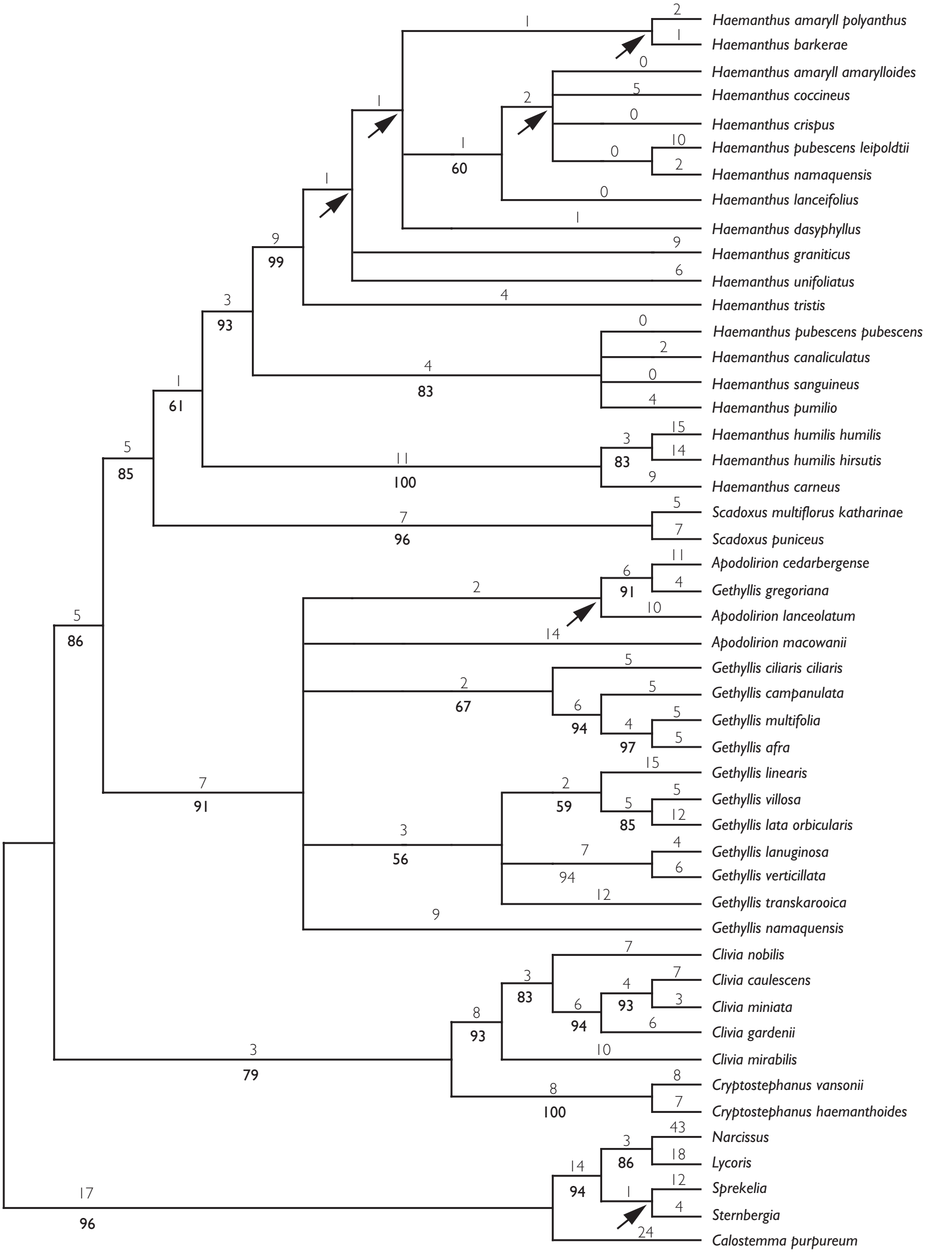

FIG. 1. One of 3055 equally parsimonious trees found from combined analysis of all five plastd matrices. Branch lengths are shown above branches and bootstrap percentages above 50% below.
Tree length: 747; RI: 0.828; CI: 0.772.

monophyletic with a bootstrap percentage of 96%. The summer rainfall taxa of *Haemanthus* (*H. humilis* subsp. *humilis, H. humilis* subsp. *hirsutus* and *H. carneus*) formed a distinct clade with bootstrap support of 100%. *Gethyllis* and *Apodolirion* resolved as a monophyletic group with bootstrap support of 91% with *Apodolirion* embedded within *Gethyllis*. The *Apodolirion* taxa do not group together, however, and of the three taxa included in the study, two occur in the same clade. *Clivia* and *Cryptostephanus* formed a monophyletic group (79% bootstrap support) and resolved as sister to the clade containing *Haemanthus*, *Scadoxus* and the *Gethyllis* – *Apodolirion* clade, the latter clade receiving 86% bootstrap support. *Clivia* was resolved as monophyletic with bootstrap support of 93% and *Cryptostephanus* was also monophyletic with 100% bootstrap support.

4 Discussion and conclusion

In previous classifications *Haemanthus* and *Scadoxus* have been considered to comprise a single genus (Björnstad & Friis, 1972) but subsequently they have been split into two genera based on morphological grounds (Nordal & Duncan, 1984). Differences in the leaf foliage between the two genera include a reduction in the leaf number from more than four in *Scadoxus* to two or four in *Haemanthus*. The strap-shaped leaf in *Haemanthus* has been replaced by a pseudo-petiolate leaf in *Scadoxus* and one chromosome pair has been lost so that *Scadoxus* has a chromosome number of x=9 and *Haemanthus* x=8. The molecular data support this latter circumscription with *Haemanthus* and *Scadoxus* receiving 61% and 96% bootstrap support respectively. Although Snijman (1984) chose not to recognise formal sections in *Haemanthus*, the summer rainfall taxa studied thus far form a distinct clade in this analysis with 100% bootstrap support. *Haemanthus carneus*, *H. humilis* subsp. *humilis* and *H. humilis* subsp. *hirsutus* are summer rainfall endemics of southern Africa (Snijman, 1984). *H. carneus* occurs in the Free State, KwaZulu–Natal midlands and the Eastern Cape near Somerset East and Grahamstown and *H. humilis* subsp. *humilis* and *H. humilis* subsp. *hirsutus* are widespread throughout the inland summer rainfall regions of southern Africa, only nearing the coast around Grahamstown and King Williams Town in the Eastern Cape (Snijman, 1984). All the other taxa of *Haemanthus* included in the study are winter rainfall endemics (Snijman, 1984).

The genus *Clivia* resolved as a distinct clade with *Clivia mirabilis* placed as sister to the clade comprising *Clivia gardenii, Clivia miniata, Clivia caulescens* and *Clivia nobilis*, the latter receiving 83% bootstrap support. *Clivia mirabilis* is the only species in this genus to be found in the winter rainfall region of South Africa (Rourke, 2002), the other four species being confined to the summer rainfall region of South Africa.

Cryptostephanus resolved as a distinct clade, sister to the clade comprising *Clivia*. *Cryptostephanus* is the only genus with a phytomelanous testa (Meerow *et al.*, 1999), while possessing a baccate fruit and a turgid seed, the latter being the case for all the other genera of Haemantheae *sensu* Meerow *et al.* (1999).

As currently circumscribed, *Apodolirion* is distinguished from *Gethyllis* by a difference in the attachment of the anthers. Anthers are uniformly basifixed in *Gethyllis* whereas the inner anthers of *Apodolirion* are basifixed and the outer are somewhat medifixed (Manning *et al.*, 2002). Manning *et al.* (2002) state that this difference is arguably insufficient to separate these genera but have chosen to maintain both *Apodolirion* and *Gethyllis* until strong evidence to refute their monophyletic status became available. Our analysis placed *Apodolirion* embedded within *Gethyllis*, although the taxa included here are not monophyletic within *Gethyllis*. *Apodolirion* and *Gethyllis* share many specialised characters: solitary flowers, subterranean ovaries and elongated berries with numerous seeds. They also share the same basic chromosome number x=6 (Vosa 1986), which is unique in the tribe. The analysis of additional taxa is necessary but it is likely that this clade represents a single genus.

Gethyllis has been divided on the basis of floral morphology into two informal groups, "afra" and "villosa" (Manning *et al.*, 2002). The "afra" group usually has more than six filaments and anthers per flower, the style is straight with a small stigma and the flowers are fleshy, succulent and cup shaped. The "villosa" group has six simple filaments and six anthers, the style is curved sideways and has a large capitate stigma, and the flowers are thin textured and salver shaped. Our results partially retrieved the "afra" group (*G. ciliaris* subsp. *ciliaris, G. campanulata, G. multifolia, G. afra*). The exceptions are *G. gregoriana,* which resolved with *A. cedarbergense* and *A. lanceolatum* in a separate clade, and *G. namaquensis.* The "villosa" group (*G. linearis, G. lata* subsp. *orbicularis, G. transkarooica, G. villosa, G. lanuginosa* and *G. verticillata*) also formed a distinct clade, in support of the informal grouping of Manning *et al.* (2002).

Plastid DNA sequence data have provided significant insight into generic level phylogenetic relationships within the Haemantheae. Increased support for this tree may be achieved through the addition of further DNA sequence data. A nuclear ITS data set is currently being collected to augment this study. Further work on the Haemantheae will include morphological data in combination with molecular data to provide further insights into character evolution and relationships within this tribe.

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THE TAXONOMIC SIGNIFICANCE OF THE FLORAL MORPHOLOGY IN THE LEDEBOURIINAE (HYACINTHACEAE)

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Abstract

The floral parts of *Drimiopsis, Ledebouria* and *Resnova,* members of the subtribe Ledebouriinae in the tribe Massonieae (Hyacinthaceae) were investigated. Preliminary results reveal variation in characters of the perigone, androecium, gynoecium and the pollen not obvious at the macromorphological level. The perigone of the three genera differ in shape and levels of adhesion. *Drimiopsis* filaments differ from those of *Resnova* and *Ledebouria.* The gynoecia differ with respect to the shape of the ovary and the stigma. Both *Ledebouria* and *Resnova* possess a stipe. The pollen grains, though all ellipsoid and monosulcate, show intergeneric variation in shape and ornamentation.

Résumé

La signification taxonomique de la morphologie florale chez les Ledebouriinae (Hyacinthaceae). Les pièces florales de *Drimiopsis, Ledebouria* et *Resnova*, membres de la sous-tribu des Ledebouriinae au sein de la tribu des Massonieae (Hyacinthaceae) ont été étudiées. Les résultats préliminaires révèlent une variation des caractères du périgone, de l'androcée, du gynécée et du pollen difficilement mise en évidence au niveau macromorphologique. Le périgone des trois genres diffère quant à sa forme et à ses niveaux d'insertion. Les filaments de *Drimiopsis* diffèrent de ceux de *Resnova* et de *Ledebournia.* Les gynécées se distinguent du point de vue de la forme de l'ovaire et du stigmate. *Ledebournia* et *Resnova* possèdent un stipe. Les grains de pollen, bien qu'ellipsoïdaux et monosulqués, montrent une variation intergénérique tant dans leur forme que dans leur ornementation.

Key words: *Drimiopsis, Ledebouria, Resnova,* floral morphology

1 Introduction

Although flower morphology (perianth, androecium and gynoecium) has been used to delimit *Drimiopsis* Lindl. & Paxt., *Resnova* van der Merwe and *Ledebouria* Roth within the subtribe Ledebouriinae U. & D. Müll.-Doblies, of the tribe Massonieae (Hyacinthaceae), differing opinions still remain concerning the generic status of *Drimiopsis* and *Resnova. Resnova,* regarded by some as a synonym of *Drimiopsis* (Phillips, 1951; Jessop, 1970, 1972; Dyer, 1976; Arnold & De Wet, 1993; Meyer & Williams, 1997), was recently reinstated as a separate genus (Müller-Doblies & Müller-Doblies, 1997) and has been accepted since by Speta (1998), Watson & Dallwitz (2003), Wetschnig & Pfosser (2003), Lebatha *et al.* (2003) and Manning & Goldblatt (2003). The status of *Ledebouria* has not been challenged since Jessop's contribution (Jessop, 1970; Venter 1993; Stedje, 1998).

An assessment of the taxonomic significance of pollen has largely been neglected in the Ledebouriinae. The pollen grains of the Asparagales, of which the Ledebouriinae are members, are most often monosulcate (Dahlgren *et al.*, 1985; Watson & Dallwitz, 2003). *Ledebouria* pollen has been described on a very minor scale (Venter, 1993).

This paper reports on an analysis of flower characters as an aid in determining taxonomic groupings within the Ledebouriinae.

2 Materials & methods

Table 1 lists the plants investigated. At least 11 *Drimiopsis*, 3 *Resnova* and 6 *Ledebouria* taxa, all currently recognised, were investigated.

Fresh inflorescences were collected in the field and stored in 70% ethanol and then examined with either a SEM or light microscope. The flowers were excised from their inflorescences and then subjected to critical point drying. The unacetylised pollen grains obtained from fresh flowers were air-dried, carbon treated then plated with gold-palladium before viewing with a Philips SL30DX – 4i SEM. Pollen from herbarium material was carbon treated and gold plated for use in SEM. Pollen terminology follows Hoen (2003). Morphological terms follow Radford *et al.* (1974). Some *Ledebouria* data was obtained from Venter (1993).

Data was subjected to a cluster analysis using STATISTICA 6.1 with the following settings: tree clustering; Ward's method of minimum-variance clustering under the amalgamation rule and percentage disagreement as a measure of distance. A data matrix was created based on Table 2, but excluding characters that coded polymorphic for one of the three genera, i.e. 27 characters were analysed.

TABLE 1. Plants investigated. Unless otherwise indicated, all specimens are housed in PUC.

Taxa	Accession number:	Locality
Drimiopsis sp.	Lebatha 048	Charles Craib, South Africa
Drimiopsis sp.	Lebatha 019	Durban, South Africa
Drimiopsis sp.	Lebatha 060	Roosenekal, South Africa
D. atropurpurea	Lebatha 049	Luneberg, South Africa
D. barteri	Lebatha 002	Iringa Distr., Ruaha, Tanzania
D. botryoides subsp. *botryoides*	Lebatha 098	Uzaramo District, Tanzania
D. botryoides subsp. *botryoides*	Lebatha 003	Kiambu District, Kenya
D. botryoides subsp. *prostata*	Lebatha 001	Iringa District, Tanzania
D. burkei subsp. *burkei*	Lebatha 009	Potchefstroom, South Africa
D. burkei subsp. *burkei*	Lebatha 041	Parys Dam, South Africa
D. burkei subsp. *burkei*	Lebatha 055	Waterberg, South Africa
D. burkei subsp. *burkei*	Lebatha 095	Rasesa, Botswana
D. burkei subsp. *burkei*	Lebatha 040	Kosi Bay, South Africa

TABLE 1. continued

Taxa	Accession number:	Locality
D. burkei subsp. *burkei*	Lebatha 046	Vaal River, South Africa
D. burkei subsp. *burkei*	Lebatha 054	Reitvlei, South Africa
D. burkei subsp. *burkei*	Lebatha 056	Waterberg, South Africa
D. burkei subsp. *burkei*	Lebatha 103	Kgale Hill, Botswana
D. burkei subsp. *stolonissima*	Lebatha 037	Strydom Tunnel, South Africa
D. comptonii	Lebatha 079	Mbabane, Swaziland
D. davidsoniae	Lebatha 038	Pilgrim's Rest, South Africa
D. maculata	Lebatha 005	Gaborone, Botswana
D. maculata	Lebatha 006	Gaborone, Botswana
D. maculata	Lebatha 007	Soweto, South Africa
D. maculata	Lebatha 039	Parys Dam, South Africa
D. maculata	Lebatha 033	Mtunzini, South Africa
D. maculata	Lebatha 021	Durban, South Africa
D. maculata	Lebatha 031	Mtunzini, South Africa
D. maculata	Lebatha 062	Mkanga, Swaziland
D. maculata	Lebatha 102	Eastern Cale, South Africa
D. pusilla	Lebatha 078	Mbabane, Swaziland
D. relleiyana	Lebatha 068	Mkhaja, Swaziland
Resnova sp.	Lebatha 086	Roosenekal, South Africa
Resnova sp.	Lebatha 047	Mandini, Swaziland
Resnova sp.	Lebatha 051	Roosenekal, South Africa
Resnova sp.	Lebatha 088	Roosenekal, South Africa
Resnova sp.	Lebatha 052	Waterburg, South Africa
R. humifusa	Wood 774 (K)	Natal, South Africa
R. humifusa	K. Saunders s.n. (K)	Natal, South Africa
R. lachenaliodes	Killick & Marais 2063 (K)	Umtata, South Africa
R. lachenaliodes	Hallack (K)	Transkei, South Africa
R. lachenaliodes	Baur 549 (K)	Bazeia Mts, South Africa
R. lachenaliodes	Tyson 2878 (K)	Clydesdale, South Africa
R. transvaalensis	Van der Merwe, F. 1889-11-36 (PRE)	Amsterdam, South Africa
R. transvaalensis	Van der Merwe, F. s.n. (PRE)	Ermelo, South Africa
R. transvaalensis	Devenish 958 K	Piet Retief, South Africa
Ledebouria sp.	Lebatha 010	Molepolole, Botswana
Ledebouria sp.	Lebatha 059	Pilgrim's rest, South Africa
Ledebouria sp.	Lebatha 050	Piet Retief, South Africa
L. ovatifolia	Lebatha 008	Gaborone, Botswana
L. ovatifolia	Lebatha 055	Waterberg, South Africa
L. luteola	Lebatha 071	Barberton, South Africa
L. marginata	Lebatha 076	Devil se Kantoor, South Africa
L. asperifolia	Lebatha 057	Mbabane, Swaziland
L. asperifolia	Lebatha 080	Mpumalanga, South Africa
L. saundersonii	Lebatha 085	Pigg's Peak, Swaziland
L. inquinata	Lebatha 075	Devil's Kantoor, South Africa

TABLE 2. Data matrix for characters analysed. Only non-polymorphic characters were included in the phenetic analysis. D = *Drimiopsis,* R = *Resnova* and L = *Ledebouria.*

	Character	Character state	Character coding		
			D	***R***	***L***
1	Tepals	isomorphic = 0; dimorphic = 1	1	0	0
2	Tepal number	sextepalous = 0	0	0	0
3	Tepal vitta	conspicuous = 0; faint = 1	1	0	1
4	Outer tepal posture	connivent = 0; recurved = 1; drooping = 2	[01]	1	[12]
5	Inner tepal posture	connivent = 0; recurved = 1; drooping = 2	0	1	1
6	Outer tepal apex margin	conduplicate = 0; flat = 1	0	1	1
7	Inner tepal apex margin	conduplicate = 0; flat = 1	0	1	1
8	Outer tepal longitudinal posture	cucullate = 0; flat = 1	0	1	[01]
9	Inner tepal longitudinal posture	cucullate = 0; flat = 1	0	1	[01]
10	Stamens	connivent = 0; erect = 1; patent = 2	1	1	[012]
11	Stamen arrangement	uniseriate = 0; biseriate = 1	0	1	1
12	Stamen number	sexstaminate = 0	0	0	0
13	Stamen length	as long as pistil = 0	0	0	0
14	Filament shape	deltoid = 0; lanceolate = 1; filiform = 2	0	1	2
15	Filament length	shorter than tepals = 0	0	0	0
16	Anther attachment	dorsifixed = 0	0	0	0
17	Gynoecium	tricarpellate = 0	0	0	0
18	Stigmatic papilla	sessile = 0; stalked = 1	0	1	2
19	Papilla shape	trilobal = 0; round = 1	0	1	1
20	Papilla surface	rough = 0; smooth = 1	0	0	1
21	Style shape	terete = 0; triangular = 1	0	1	[01]
22	Style size	shorter than ovary = 0; as long as ovary = 1; longer than ovary = 2	0	1	[12]
23	Ovary shape	globose = 0; ovoid to oblong = 1; conical = 2	0	1	2
24	Ovary shoulders	absent = 0; present = 1	1	1	1
25	Ovary shoulder ridge	absent = 0; present = 1	0	1	0
26	Ovary expanded and lateral lobes	absent = 0; present = 1	0	0	1
27	Nectaries	absent = 0; present = 1	0	0	[01]
28	Ovary attachment	sessile = 0; stipitate = 1	0	1	1
29	Pollen grain shape, equatorial view	depressed ovate = 0; ellipsoid = 1	0	1	[01]
30	Pollen grain shape, polar view	elliptic = 0; narrowly elliptic = 1	0	1	1
31	Pollen grain shape, lateral view	blunt = 0; tapering = 1	0	1	1
32	Pollen grain types	monosporous = 0; heterosporous = 1	0	0	1
33	Pollen grain equatorial diameter	subequiaxe = 0; breviaxe = 1	0	1	1
34	Pollen distal pole	straight = 0; curved = 1	0	1	1
35	Pollen grain ornamentation	punctate = 0; reticulate = 1; punctate-reticulate = 2	0	1	2

3 Results and discussion

3.1 Perianth

The Ledebouriinae perigone segments are sextepalous and are inconspicuous due to their small stature. In addition they may also be dull-coloured in *Drimiopsis* and *Resnova*. *Drimiopsis* tepals are dimorphic (Fig. 1A) with at least the inner segments permanently connivent. The inner tepals are conspicuously cucullate and wider than the moderately cucullate outer tepals. The tepals of *Resnova* (Fig. 2A) and *Ledebouria* (Venter, 1993) are isomorphic with the inner and outer segments similar in shape and size. Some *Ledebouria* taxa, e.g. *L. apertifolia* (Bak.) Jessop and *L. floribunda* (Bak.) Jessop, possess cucullate tepal apices (Venter, 1993), while most are flat (Fig. 3A). The distinctive vittae of *Resnova* and *Ledebouria* tepals are faint in *Drimiopsis.* In terms of tepal length, *Resnova* varies from 5–18 mm, *Ledebouria* from 5–22 mm and *Drimiopsis* from 2–10 mm. Due to the overlap in size between the three genera, these characters have not been included in the data matrix (Table 2). Furthermore, only *Drimiopsis* possesses apical tepal margins that are conduplicate.

It is evident that flower and bud colour are not significant taxonomic characters in the Ledebouriinae. A survey of living and herbarium material of *Drimiopsis* demonstrates intraspecific variation in perianth colour. For example, an analysis of *Drimiopsis maculata* Lindl. & Paxton records reveals 63% of specimens possessing white flowers, a further 34% with green flowers and 3% with yellowish or cream flowers. 40% of *D. burkei* Bak. subsp. *burkei* specimens possess white flowers, 17% green and 43% include either cream, pink or purple flowers. Venter (1993: 32), in the context of *Ledebouria*, opines: “Colour is, in most cases, not of taxonomic importance.” Although a thorough analysis of flower colour in the case of *Resnova* has not been done, it is noteworthy that Van der Merwe (1946) delimits *Resnova* from other Hyacinthaceae on the basis of, amongst another, perianth segments “never being blue or purple” (translation ours). Here also, we have refrained from including flower colour in the data matrix.

3.2 Androecium

Drimiopsis, Resnova and *Ledebouria* possess six stamens with dorsifixed anthers. In *Drimiopsis* and *Resnova* the stamens are exclusively epitepalous (fused to the tepals). In *Ledebouria* they may be either epitepalous or free (Venter, 1993). *Drimiopsis* and *Resnova* possess erect stamens, where as they may either be erect, patent or connivent in *Ledebouria.* The stamens of *Drimiopsis* are more or less equal in length and possess deltoid filaments (Fig. 1D). The base is as broad as the tepal in most of the species. Some of the filament bases, like in *D. maculata* and *D. botryoides* Baker subsp. *botryoides,* are valvate. In *Resnova* the lanceolate stamens (Fig. 2D) are of two lengths (biseriate), the one alternating with the other (Fig. 2A). In *Ledebouria* the filiform stamens (Fig. 3D) appear to be either equal or unequal in length (Venter, 1993). In all three genera the filaments are flattened to a greater or lesser degree at the base where the ovary rests. It is well documented that stamen length relative to pistil length can vary depending on the developmental stage of the flower in terms of male and female phases. We suspect that fully matured flowers of all three genera possess stamens that are as long as the pistil.

3.3 Gynoecium

The pistils of all the Ledebouriineae are tricarpellate and conduplicate i.e. they possess a longitudinal groove, to a degree. *Drimiopsis* possesses terete styles, *Resnova*

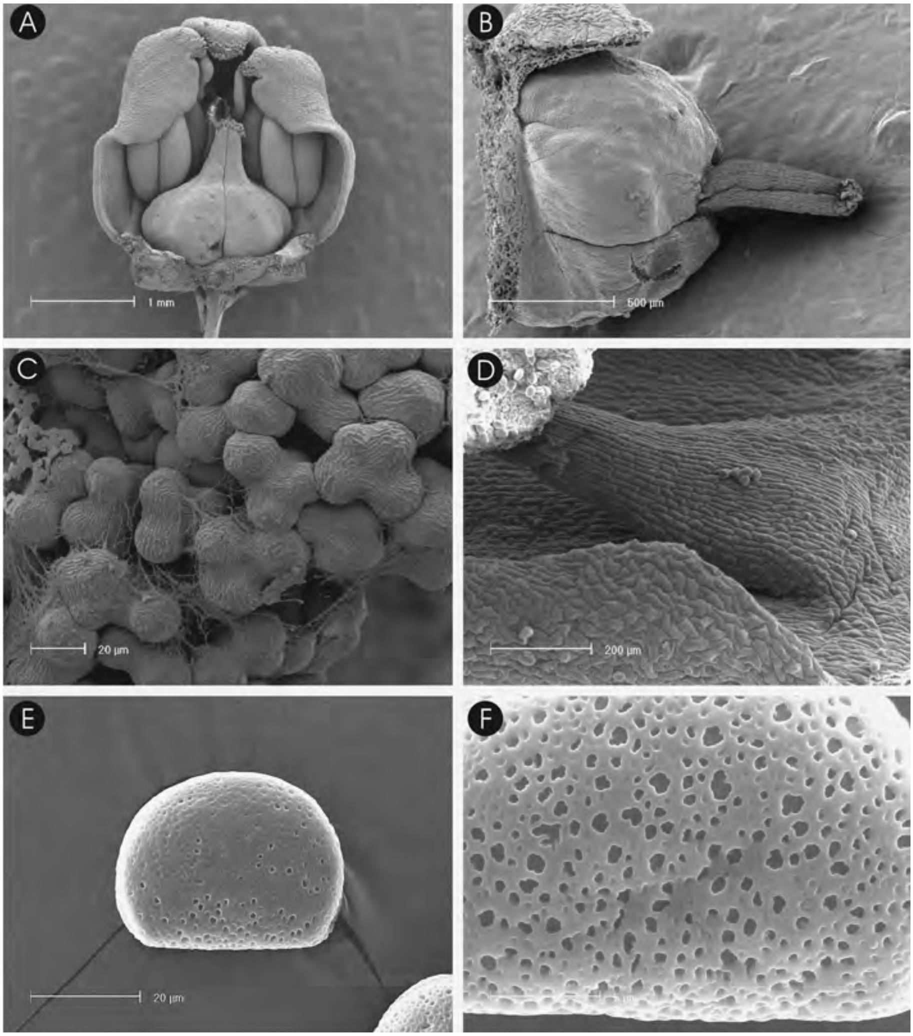

FIG. 1. Flower characters in *Drimiopsis maculata*. A. Sectioned flower illustrating the connivent inner and cucullate outer tepal segments; B. Sessile globose gynoecium, with style as long as the ovary; C. Corrugated, lobed and sessile stigmatic papilla; D. Epitepalous deltoid filaments; E. Equatorial view of pollen, note the flat pole opposite to the sulcus; F. Punctate pollen ornamentation.

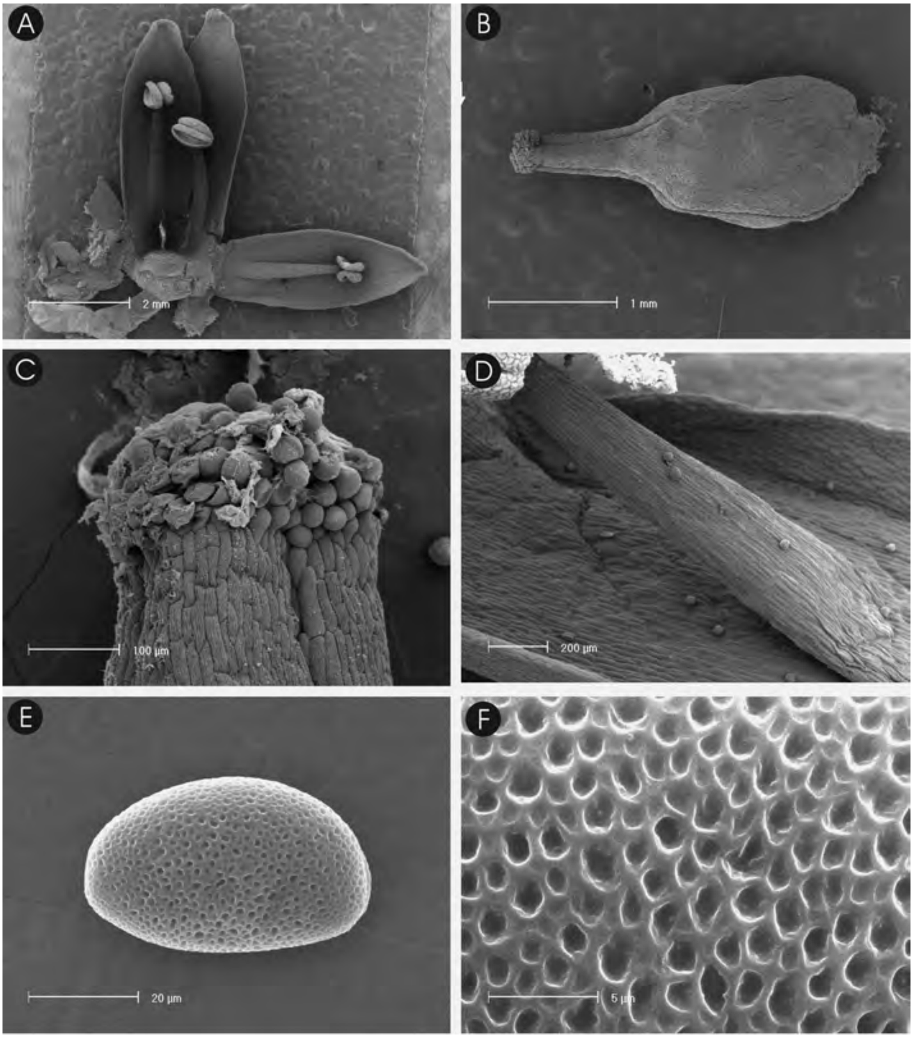

FIG. 2. Flower characters in *Resnova*. A. Sectioned flower of *R. maxima* to illustrate the isomorphic perianth and biseriate androecium; B. Sectioned pistil of *Resnova* sp. illustrating that the ovoid-oblong ovary is longer than the style and the short stipe (arrow); C. The stigma of *Resnova maxima* illustrating the round and shortly stalked papillae; D. Slightly lanceolate filaments in *R. maxima*; E. Equatorial view of pollen in *R. maxima*; F. Reticulate ornamentation in *R. maxima* pollen.

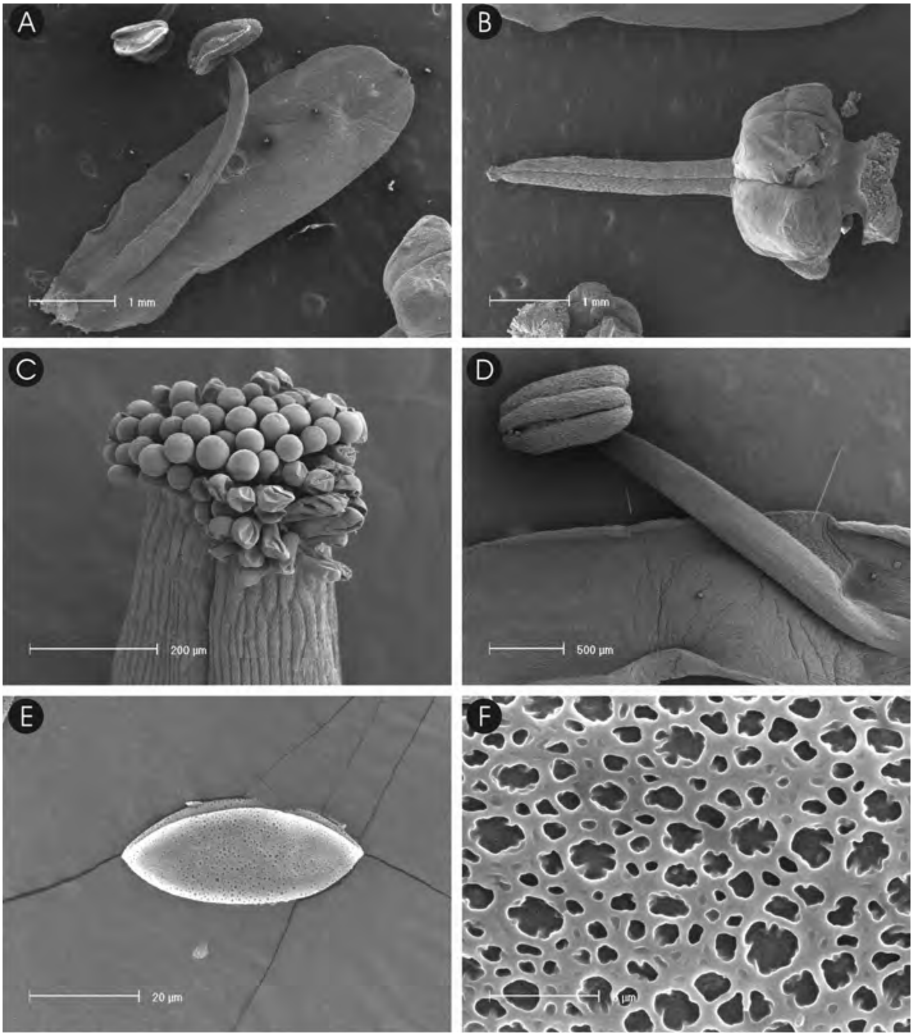

FIG. 3. Flower characters in *Ledebouria*. Sectioned flower of *Ledebouria* sp. illustrating the epitepalous stamen and the flat longitudinal posture tepal apex; B. *L. revoluta* pistil with a conical ovary and a distinct stipe; C. *L. revoluta* stigma with distinctly stalked papillae; D. Filiform filament in *L. ovatifolia*; E. Equatorial view of pollen belonging to *Ledebouria* sp., note the tapered ends; F. Pollen of *Ledebouria* sp. illustrating punctuate-reticulate ornamentation.

triangular, and *Ledebouria* terete or triangular styles. *Drimiopsis* taxa possess globose and sessile ovaries (Fig. 1A & B). All *Resnova* ovaries are ovoid to oblong in shape and possess a short stipe (Fig. 2B). The aforementioned observation of a stipe in *Resnova* is novel (Lebatha & Buys, in prep.). *Ledebouria* in turn possesses conical and conspicuously stipitate ovaries (Fig. 3B). The shoulders of the ovaries (sensu Venter 1993) vary from exclusively tapering into the style in *Drimiopsis* and *Resnova* to either tapering into, or being rectangular to, or raised in relation to the base of the style in *Ledebouria*. We feel it necessary to caution readers here against errors in Venter's work, e.g. in couplet no. 32 of the key Venter (1993: 78) mentions that *L. ensifolia* (Eckl.) Venter does not possess shoulders, whereas in the full description thereof (Venter, 1993: 90) he mentions the presence of rectangular shoulders. It is only *Ledebouria* taxa that possess expanded and basal lobes. It is the basal lobes that possess nectaries, when these are present. *Resnova* in turn, solely possesses ridges on the shoulders (see Müller-Doblies & Müller-Doblies, 1997: 60, Fig. 2g). The style in *Drimiopsis* is as long as the ovary (Figs. 1A & 1B). In *Resnova* (Fig. 2B) they are shorter than, and in *Ledebouria* they are longer than the ovary (Fig. 3B). The stigma of *Drimiopsis* taxa investigated have corrugated, trilobed and sessile papillae (Fig. 1C). The *Resnova* stigmatic papillae are rough, round and shortly stalked and those of *Ledebouria* smooth, round and conspicuously stalked (Figs. 2C & 3C respectively).

3.4 Pollen

The monosulcate Ledebouriinae pollen almost become zonasulcate, i.e. the sulcus almost extends right around the pollen grain. Viewed equatorially, the *Drimiopsis* pollen are depressed ovate (Fig. 1E) and those of *Resnova* and *Ledebouria* ellipsoid (Figs. 2E & 3E). From a polar view, the *Drimiopsis* pollen is elliptic while those of *Resnova* and *Ledebouria* are narrowly elliptic – harmomegathy (change in shape due to hydration) – notwithstanding. *Drimiopsis* pollen is subequiaxe (the polar axis more or less equal to the equatorial diameter). They possess a linear pole opposite to the sulcus (Fig. 1E) as well as blunt lateral sides. The pollen in *Resnova* and *Ledebouria* are breviaxe (polar axis is shorter than the equatorial diameter) and possess a tapered pole opposite to the sulcus as well as tapered lateral sides (Figs. 2E & 3E respectively). Heterospory (in terms of shape) occurs in *Ledebouria* where the pollen sometimes resembles either those of *Drimiopsis* or *Resnova*. The only intra- or interspecific difference in *Drimiopsis* and *Resnova* pollen is size. *Drimiopsis* possesses punctate (pitted) pollen (Fig. 1F), *Resnova* reticulate (Fig. 2F) and *Ledebouria* punctate to reticulate pollen (Fig. 3F).

4 Phenetic analysis

We have refrained from doing a cladistic analysis at this stage primarily due to limited accessibility to adequate material to complete a data matrix. Keeping the shortcomings of phenetics in mind, the analysis, run with the parameters as set out above, clustered *Resnova* to *Ledebouria* (Fig. 4). This result raises questions about views in support of sinking *Resnova* under *Drimiopsis* (Phillips, 1951; Jessop, 1970, 1972; Dyer, 1976; Arnold & De Wet, 1993; Meyer & Williams, 1997). Given the fact that we included for the first time the presence of stipitate ovaries in *Resnova*, we ran an additional analysis excluding this character. The results were the same.

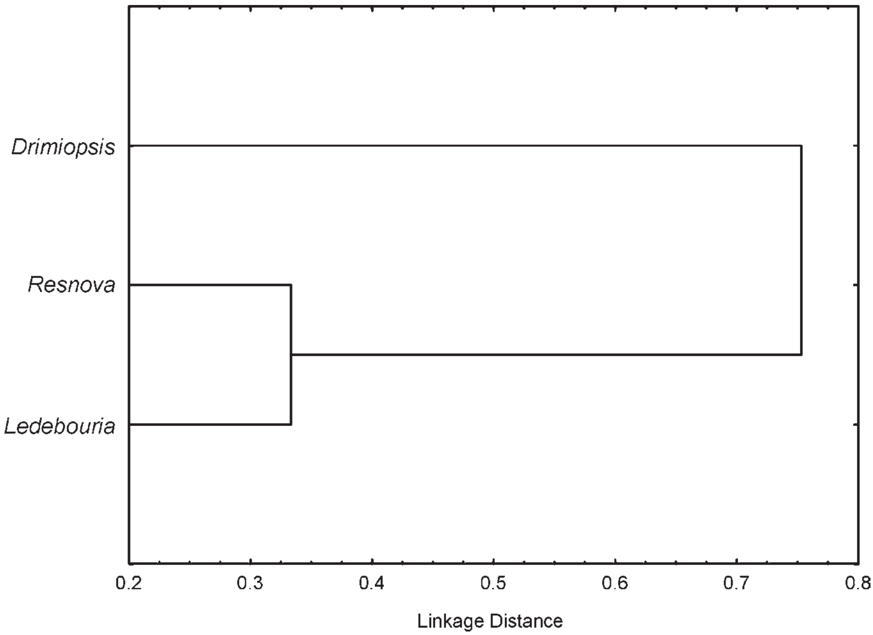

FIG. 4. Phenogram based on an analysis of 27 non-polymorphic characters (Table 2) in *Drimiopsis*, *Resnova* and *Ledebouria* using Ward's Method of minimum-variance clustering and percentage disagreement as a measure of distance.

5 Discussion and conclusion

Our results can be interpreted in one of two ways: 1, for the splitter, *Resnova*, *Ledebouria* and *Drimiopsis* are three separate genera, with *Resnova* having more in common with *Ledebouria* than with *Drimiopsis* or 2, if lumping is preferred, then *Resnova* and *Ledebouria* should be grouped in one taxon.

A phenetic analysis of conventional flower characters in the Ledebouriinae, with the addition of new pollen characters as well as the novel observation that *Resnova* possesses a short stipe, provides sufficient data to demarcate *Resnova*, *Ledebouria* and *Drimiopsis*. In addition, *Resnova* clusters with *Ledebouria*, a result contrary to traditional thinking. Our results, based on morphology, give credence to Wetschnig & Pfosser's (2003) results where a cladistic analysis of the *trnL* intron and the *trnL-F* intergenic spacer also grouped *Resnova* with one of the *Ledebouria* clades.

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LES RUBIACEAE ENDÉMIQUES DU CAMEROUN ET LEUR STATUT DE CONSERVATION

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Résumé

Un inventaire basé sur la bibliographie et les spécimens des Rubiaceae du Cameroun disponibles à BR, BRLU, K et YA est fait. Cet inventaire permet de reconnaître 54 taxons endémiques du Cameroun. 25,9% de ces Rubiaceae sont en danger critique d'extinction (CR) d'après les catégories de l'UICN, 29,6% sont menacées d'extinction (EN), 24% sont vulnérables (VU) et seulement 20% sont sans risque (LR). Des zones prioritaires pour la conservation des Rubiaceae au Cameroun sont également identifiées.

Abstract

A preliminary list of endemic Rubiaceae is presented for Cameroon. This list is based on a study of literature available and Cameroonian herbarium specimens at BR, BRLU, K and YA. 54 species are found to be endemic to Cameroon. Following the IUCN categories, 25.9% of species are critically endangered, 29.6% are endangered (EN), 24% are vulnerable (VU) and 20 are lower risk (LR). The priority regions for the conservation of Rubiaceae in Cameroon are identified.

Key words – Cameroon, endemic, risk categories, Rubiaceae

1 Introduction

Les espèces dans leur distribution spatiale peuvent être confinées à des régions précises et devenir endémiques de ces régions. L'étude de ces espèces endémiques est importante à plus d'un titre. En effet, elle permet d'avoir des informations sur l'évolution des espèces ou tout au moins de certaines espèces (Keener, 1983; Major, 1991). De même, l'étude peut permettre de faire la reconstitution des conditions biogéographiques passées des régions occupées par ces espèces et par-là même déterminer leur Catégorie de l'UICN. Ce statut est lié à l'habitat, la distribution et la taille de la population en question. Ces espèces, qui sont quelquefois liées à des écosystèmes qui sont très menacés, seront très certainement les premières à être victimes des processus d'extinction (Heywood & Watson, 1995); il y a donc un besoin que des mesures urgentes et effectives soient prises en vue de leur protection. Ces espèces endémiques se retrouvent non pas en population homogène mais plutôt dans un cortège d'espèces endémiques vivant dans des habitats particuliers qui constituent des "hotspots" ou zones d'importance pour la conservation de la biodiversité.

La flore et la faune du Cameroun sont exceptionnellement riches et diverses. Ce pays est traversé par de nombreux centres régionaux d'endémisme. Cette position du Cameroun, le place parmi les pays les plus importants en matière de biodiversité. Cette biodiversité, qui est à l'image de celle de tout le Bassin du Congo, est sous la menace constante des activités anthropiques: de vastes étendues de forêts disparaissent et si rien n'est fait de nombreuses espèces vont disparaître avant d'avoir été décrites. A la faveur des dernières glaciations, la végétation de nombreuses régions a changé. Toutefois, quelques régions ont été préservées, ce qui a favorisé le développement d'un certain endémisme.

La famille des Rubiaceae, avec environ 1000 espèces au Cameroun, est l'une des plus importantes des forêts camerounaises. Elle représente près de 12% environ de la flore camerounaise. Cette famille représente une part importante de l'endémicité au Cameroun.

Il est urgent que des mesures de conservation (*in situ* et *ex situ*) soient prises pour ces différentes espèces d'autant plus que certaines sont connues d'un seul site et d'un seul individu.

Le présent travail donne les résultats de l'inventaire des Rubiaceae endémiques du Cameroun et propose pour chaque espèce sa Catégorie au regard des critères de l'UICN. Cet inventaire est principalement basé sur les genres déjà révisés (*Coffea*, *Ixora*, *Oxyanthus*, *Pavetta*, *Psychotria*, *Tricalysia*, etc.).

2 Matériel et méthodes

Une étude bibliographique et un examen du matériel d'herbiers de Rubiaceae disponibles à BR, BRLU, K et YA nous ont permis d'identifier les espèces endémiques du Cameroun. La distribution de ces espèces a été réalisée en utilisant le programme Arc View 3.3®. Une subdivision du Cameroun en carrés de 20 minutes de côté nous a permis de déterminer la richesse spécifique de chaque maille. L'examen des cartes de distribution faites à partir des spécimens disponibles nous permet de déterminer la Catégorie de l'UICN des espèces. Nous avons reconnu les taxons en danger critique d'extinction (CR), les taxons en danger d'extinction (EN), les taxons vulnérables (VU) et les taxons moins menacés (LR). La citation des spécimens d'herbier se fait de l'ouest vers l'est et du nord vers le sud. Il convient cependant de signaler que les cordonnées géographiques n'ont pas été retrouvées pour tous les spécimens cités.

3 Résultats

Au total, 54 taxons (espèce, sous-espèce, variété) ont été reconnus endémiques au Cameroun. Ce nombre représente environ 6% de la flore camerounaise des Rubiaceae qui est estimée à 1000 espèces (Sonké & Simo, 1996). Ces taxons ont été groupés en trois catégories en suivant les critères des Listes Rouges de l'UICN (2001).

TABLEAU 1. Répartition des taxons entre les différentes catégories. CR, EN, en danger d'extinction; LR, moins menacés; VU, vulnérables.

Catégories de l'UICN	CR	EN	LR	VU
Nombre de taxons	14	16	11	13
Proportion (%)	25,9	29,6	20	24

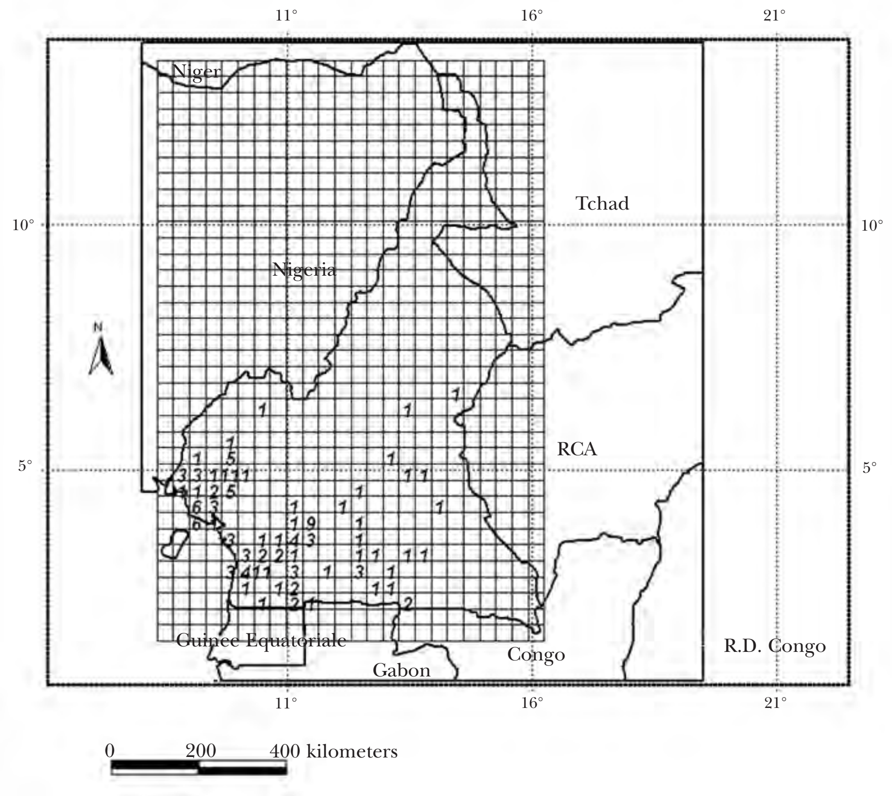

FIG. 1. Richesse spécifique en Rubiaceae endémiques (maille de 20' de côté).

La cartographie de ces espèces (Fig. 1) permet d'observer quatre grandes zones de concentration des Rubiaceae endémiques. La zone de Bipindi-Lolodorf (11), la région de Bakossi et Kupe (11), la région de Yaoundé (9) et la zone du mont Cameroun (6).

Aulacocalyx mapiana Sonké & Bridson in Syst. Geogr. Pl. 71(1): 17 (2001).

Sanctuaire Banyang Mbo, 5 km NW Ebamut, *Sonké* 2109 (BR, BRLU, K, MO, SCA, WAG, YA); ibid., *Sonké* 2117 (BR, BRLU); ibid., *Sonké* 2143 (BR, BRLU, K, SCA, WAG, YA); 2 km NE Ebamut, *Sonké* 2230 (BR, BRLU, K, MO, SCA, WAG, YA); Efoulan, 5 km S Akom II, *Sonké* & *Beina* 33226 (BR, MO, YA).

Catégorie de l'UICN. Compte tenu de son aire géographique très restreinte mais contenue dans deux zones de protection, nous la classons dans la catégorie VU B2a.

Belenophora ongensis S.E.Dawson & Cheek in Kew Bull. 55: 75 (2000).

Onge Reserve, *Sonké* 667 (BR); ibid. *Tchouto* 497 (BR, K); Dikoumé Barondo Forest, *Sonké* 1169, 1178, 1181 (BR, K); Bomana, *Tchouto* 916 (BR, K); Korup National Park, *Harris* 2461 (BR).

Catégorie de l'UICN. Cette espèce est localisée dans une aire protégée et très accidentée. Aucun risque de disparition ne pèse sur elle pour le moment et c'est pour cette raison que nous la plaçons dans la catégorie LR.

Bertiera laxa Benth. var. *bamendae* Hepper in Kew Bull. 13: 405 (1959).

Bui (réserve forestière), *Ujor* FHI30087 (K, P); mont Rumpi (entre Bulu et Lokando), *Letouzey* 14056 (YA); Liwenyi, *Watts* 749 (SCA); Etome, *Nning* 131 (SCA); Ekumbe Mofako, *Acworth* 124 (SCA); petit mont Cameroun, *Ndam* 169 (SCA); Dikulu, *Cable* 538 (SCA); Moliwé, *Lynn* 4 (SCA); près de Sahé (3 km SWW de Nkondjock), *Letouzey* 11161 (P, YA); Djanton, *CNAD* 886 (YA); Engon, (S Efoulan, 5 km S Akom II), *Sonké* & *Beina* 3384 (BR, BRLU, K, MO, WAG, YA).

Catégorie de l'UICN. Cette espèce présente une distribution fragmentée et les localités connues par les récoltes sont en dehors des zones qui bénéficient d'une mesure spéciale de conservation et c'est pour cette raison que nous lui attribuons la catégorie VU D2.

Bertiera laxissima K.Schum. in Engl. Bot. Jahrb. 33: 348 (1904).

Près du village Mbu, *Mambo* & *Thomas* 28 (YA); ibid., *Mambo* & *Thomas* 54 (P, YA); versant N d'Enyandong (5 km WNW de Bamguem – Mamfe), *Villiers* 1285 (YA); mont Bakossi (W de Bangem), *Thomas, Mambo* & *Nemba* 4977 (YA); ibid., *Thomas* & *McLeod* 5290 (P, WAG); NW d'Edumseh (75 km W de Bangem), *Manning* 449 (YA); forêt de Bakaka (km 11 route Nkongsamba – Loum), *Leeuwenberg* 8232 (BR, P, WAG); ibid., *Leeuwenberg* 8731 (BR, P, WAG, YA); Etinde, *Lynn* 65 (SCA); ibid., *Cheek* & *Tchouto* 3615 (SCA); 15 km E de Yingui (35 km de Yabassi), *Letouzey* 11011 (P, YA); réserve forestière de Makak, *Bamps* 1481 (BR, P, YA); mont Ngoyang (8 km E de Ngoyang), *Letouzey* 12758 (P, YA); Bipindi, *Manning* 1340 (YA); 23 km de Yaoundé (route de Douala), *Breteler* 1574 (P, WAG, YA); Akoas, 40 km de Yaoundé, *Sonké* 2725, 2726 (BR, BRLU, K, SCA, WAG, YA); Nkolbison (8 km N de Yaoundé), *de Wilde* & *de Wilde-Duyfjes* 1194 (BR, P, WAG, YA); 9 km de Yaoundé, *Breteler* 1971 (BR, P, WAG, YA); 5 km NNW de Yaoundé, *Breteler* 1952 (BR, P, WAG, YA); mont Elounden, *Lejoly* 586 (BR); près d'Oveng, *Breteler* 2660 (BR, P, WAG, YA); Nkolmayos, *Letouzey* 11407bis (P); Sangmélima, *Essiane* 9 (P, YA); réserve d'Ototomo, *Sonké* 355 (BR); Yaoundé, *Zenker* 1425 (K, P, WAG); mont Meza (Nanga-Eboko), *Letouzey* 1949 (BR, P, YA); Nanga-Eboko, *Jacques-Félix* 4741 (BR, P, WAG); près de Ngoubi (Nanga-Eboko), *Letouzey* 1723 (BR, P, YA); s.l., *Zenker* 4272 (P).

Catégorie de l'UICN. Cette espèce présente par sa distribution une bonne représentativité aussi bien dans des zones protégées que dans des zones sans mesures spéciales de protection. Elle ne court donc aucun risque de disparition pour le moment et nous la mettons dans la catégorie LR.

Coffea bakossii Cheek & Bridson in Kew Bull. 57: 676 (2002).

Nyale, *Etuge* 4172 (BR, K); Mt Kupe, *Etuge* 2675 (BR, K); Kupe, *Lane* 361 (BR, K); Ngomboku, *Gosline* 260 (BR, K).

Catégorie de l'UICN. Cette espèce présente une distribution assez restreinte et très peu de localités sont connues pour cette espèce; ceci la place dans la catégorie VU D2.

Coffea fotsoana P.Stoffelen & Sonké ined.

Akoas, *Sonké 2731* (BR, BRLU, K, P, YA).

Catégorie de l'UICN. Cette espèce est connue d'une seule localité et la place dans la catégorie CR B2a.

Coffea heterocalyx P.Stoffelen in Belg. Journ. Bot. 129(1): 72 (1996).

Divo, *Zadi Koubi* 410 (BR); Colline Bissa, *Dang* 760 (BR); N'Kolbisson, *de Wilde W.J.J.O., de Wilde J.J.F.E.* & *Wilde-Duyfjes B.E.E.* 3725 (BR).

Catégorie de l'UICN. Cette espèce est connue de moins de cinq localités; elle peut être placée dans la catégorie EN B2a.

Coffea leonimontana P.Stoffelen in Belg. Journ. Bot. 129(1): 72 (1996).

Etinde, *Faucher P., Faucher M., Etuge* & *Furneaux* 5 (K); ibid., *Tchouto* 399 (K); Mbu-Bakundu, *Mambo* & *Thomas* 241 (K); Kompina, *Leeuwenberg* 8754 (BR, K).

Catégorie de l'UICN. Cette espèce est connue de moins de cinq localités; elle peut être placée dans la catégorie EN B2a.

Coffea montekupensis P.Stoffelen in Kew Bull. 52(4): 990 (1997).

Nyasoso, *Balding Sivell* 30 (BR, K); ibid., *Cable* 1134, 1148 (BR, K); ibid., *Cable* 700 (BR); ibid., *Lane* 112, 156, 251 (BR, K); ibid., *Sebsebe* 5016 (BR); ibid., *Wheatley* 466 (BR); Kupe, *Sebsebe* 5051 (K); ibid., *Cheek* 7190, 7327 (K); ibid., *Lane* 151 (K); ibid., *Wheatley* 466 (K); ibid., *Cable* 744 (BR); ibid., *Cheek* 7022, 7160, 7681, BR, 7777 (K); Bakossi, *Thomas & Mcleod* 5306 (BR, K).

Catégorie de l'UICN. Cette espèce est connue de moins de dix localités; elle peut être placée dans la catégorie VU B2a.

Coffea sp. 'nkolbison', Sonké & Bridson in Syst. Geogr. Pl. 69: 121 (1999).

Bipindi, *Zenker* 4815, 4878 (BR); Nkolbison, *Breteler, de Wilde* & *Leeuwenberg* 2284 (BR); ibid., *Leeuwenberg* 6039 (BR).

Catégorie de l'UICN. Cette espèce est connue de moins de dix localités; elle peut être placée dans la catégorie VU B2a.

Hymenocoleus glaber Robbr. in Bull. Nat. Plantentuin Belg. 47: 14 (1977).

Mambé, *Letouzey* 12279 (BR, YA); Boando (Etinde), *Cable* 260 (K); Limbe ("Victoria"), *Schlechter* 12366 (BR); Kupe, *Cheek* 6081 (K); Nyasoso, *Lane* 159, 250 (K); ibid., *Cable* & *Epie* 641 (K).

Catégorie de l'UICN. Le nombre de d'individus matures est moins de 250 et nous la mettons pour cette raison dans la catégories EN D1.

Hymenodictyon pachyantha K.Krause in Engl. Bot. Jahrb. 57: 26 (1920).

Entre Song et Gribe 65 km SSW Yokadouma, *Letouzey* 12238 (BR, K); 3 km E Monjeom, route Yokadouma - Mouloudon, *Letouzey* 5204 (BR).

Catégorie de l'UICN. Cette espèce présente une distribution fragmentée et connue de moins de cinq localités; elle se classe alors dans la catégorie EN B2a.

Ixora batesii Wernham in Journ. Bot. 1916: 227 (1916).

Yaoundé, *Breteler* 2148 (K); Bitye, *Bates* 641 (BR); ibid., *Bates* 1845 (K).

Catégorie de l'UICN. Cette espèce présente une distribution fragmentée et connue de moins de cinq localités; elle se classe alors dans la catégorie EN B2a.

Ixora synactica De Block in Opera Bot. Belgica 9: 156 (1998).
Atog Boga, *Letouzey* 12824 (P, YA); Memel II, 22 km N Bipindi, *Sonké* & *Beina* 3260 (BR, BRLU, K, MO, WAG, YA).
Catégorie de l'UICN. Cette espèce présente une distribution fragmentée et connue de moins de cinq localités; elle se classe alors dans la catégorie EN B2a.

Oxyanthus okuensis Cheek & Sonké in Kew Bull. 55: 890 (2000).
Oku, *Cheek* 8583 (K); ibid., *Maisels* 107 (SCA, YA); ibid. *Zapfack* 1665 K (YA); Ajung, *Cheek* 10103 (K).
Catégorie de l'UICN. Cette espèce présente une distribution fragmentée et connue de moins de cinq localités; elle se classe alors dans la catégorie EN B2a.

Oxyanthus oliganthus K.Schum. in Bot. Jahrb. 33: 345 (1903).
Nkolembembe, *Asonganyi* 186 (YA); Nkuanbe, *Zenker* 407 (BR); Mven, *Letouzey* 8140 (YA); Bipindi, *Zenker* 2936 (BR); ibid., *Zenker* 3325 (BR); ibid., *Zenker* 3362 (BR); ibid., *Zenker* 3500 (BR); ibid., *Zenker* 4010 (BR); ibid., *Zenker* 4167 (BR); Etou, *Sonké* 1764 (BR); Bitye, *Sonké* 1935 (BR); Mékas, *Sonké* 1781 (BR); Meka'a, *Sonké* 1546 (BR), ibid., *Sonké* 1554 (BR); Djolimpoum, *Sonké* 1356 (BR); ibid., *Sonké* 1866 (BR); ibid., *Sonké* 1691 (BR); ibid., *Sonké* 1750 (BR), Altat Makay, *Sonké* 1626 (BR); Djaposten, *Sonké, Nguembou* & *Esono* 2667 (BR); ibid., *Sonké, Nguembou* & *Esono* 2627 (BR).
Catégorie de l'UICN. Cette espèce présente par sa distribution une bonne représentativité aussi bien dans des zones protégées que dans des zones sans mesures spéciales de protection. Elle ne court donc aucun risque de disparition pour le moment et nous la mettons dans la catégorie LR.

Pavetta baconiella Bremek. in Repert Spec. Nov. Regni Veg. 37: 73 (1934).
Monjala-Mole, *Mildbraed* 8374 (BR); S. Parc National Korup, *Thomas* 2212 (BR, YA).
Catégorie de l'UICN. Cette espèce présente une distribution fragmentée et connue de moins de cinq localités; elle se classe alors dans la catégorie EN B2a.

Pavetta bidentata Hiern var. *sessilifolia* S.D.Manning in Annals Missouri Bot. Gard. 83(1): 105 (1996).
Kombeng Hill, *Letouzey* 11557 (BR, YA); Kala, *Farron* 7245 (P).
Catégorie de l'UICN. Cette espèce présente une distribution fragmentée et connue de moins de cinq localités; elle se classe alors dans la catégorie EN B2a.

Pavetta brachycalyx Hiern in Fl. Trop. Afr. 3: 169 (1877).
Mont Cameroun, *Mann* 2159 (BR).
Catégorie de l'UICN. Cette espèce est connue d'une seule localité, donc une distribution restreinte. Elle se classe dans la catégorie CR B2a.

Pavetta brachysiphon Bremek. in Repert Spec. Nov. Regni Veg. 37: 74 (1934).
Deng Deng, *Mildbraed* 8536 (K).
Catégorie de l'UICN. Cette espèce est connue d'une seule localité, donc une distribution restreinte. Elle se classe dans la catégorie CR B2a.

Pavetta camerounensis S.D.Manning ssp. *breviana* S.D.Manning in Annals Missouri Bot. Gard. 83(1): 108 (1996).
Kumba, *Manning* 856 (YA); Bakundu, *Manning* 101 (YA).
Catégorie de l'UICN. Cette espèce présente une distribution fragmentée et connue de moins de cinq localités; elle se classe alors dans la catégorie EN B2a.

Pavetta camerounensis S.D.Manning ssp. *camerounensis,* S.D.Manning in Annals Missouri Bot. Gard. 83(1): 108 (1996).

Ngovayang, *Satabié* & *Letouzey* 373 (YA); Bipindi, *Manning* 1408 (YA); colline Mvounodjigi, *Letouzey* 9776 (BR, YA); 30 km Eséka, W of Yaoundé, *de Wilde* & *Wilde-Duyfjes* 1491 (BR); 27 km Kribi–Ebolowa, *Bos* 6173 (BR, K).

Catégorie de l'UICN. Cette espèce présente par sa distribution une bonne représentativité aussi bien dans des zones protégées que dans des zones sans mesures spéciales de protection. Elle ne court donc aucun risque de disparition pour le moment et nous la mettons dans la catégorie LR.

Pavetta grossissima S.D.Manning in Annals Missouri Bot. Gard. 83(1): 114 (1996).

Korup National Park, *Thomas* 449 (BR, K); ibid., *Manning* 1710 (BR, YA); Mundemba, *Manning* 973 (YA); ibid., *Manning* 906 (YA); Fabe, *Manning* 944 (BR, K, YA); Nkolbisson, *Manning* 2128 (YA).

Catégorie de l'UICN. Cette espèce est connue de moins de dix localités et se classe dans la catégorie VU B2a.

Pavetta hookeriana Hiern var. *pubinerva* S.D.Manning in Annals Missouri Bot. Gard. 83(1): 117 (1996).

Limbe, *Kalbreyer* 94 (BR, K).

Catégorie de l'UICN. Cette espèce est connue d'une seule localité, donc une distribution restreinte. Elle se classe dans la catégorie CR B2a.

Pavetta kribiensis S.D.Manning in Annals Missouri Bot. Gard. 83(1): 118 (1996).

Lobe, *Letouzey* 9148 (BR, YA); Mont Koupé, *Letouzey* 450 (BR); ibid., *Thomas* 5481 (BR); Kribi, *Bos* 4638 (BR); ibid., *Bos* 6202 (BR); Zingui, *Letouzey* 9116 (BR).

Catégorie de l'UICN. Cette espèce est connue de moins de dix localités et se range dans la catégorie VU B2a.

Pavetta kupensis S.D.Manning in Annals Missouri Bot. Gard. 83(1): 118 (1996).

Konye, *Thomas* & *Nemba* 5197 (BR); Nyasoso, *Lane* 141 (K); ibid., *Cable* 1201 (K, SCA, YA); Mt Kupe, *Letouzey* 450 (BR); ibid., *Thomas* & *Mcleod* 5481 (BR, K).

Catégorie de l'UICN. Cette espèce est connue de moins de dix localités et se range dans la catégorie VU B2a.

Pavetta laxa S.D.Manning in Annals Missouri Bot. Gard. 83(1): 123 (1996).

Mékomo, *Letouzey* 4581 (BR).

Catégorie de l'UICN. Cette espèce est connue d'une seule localité, donc une distribution restreinte. Elle se classe dans la catégorie CR B2a.

Pavetta longibrachiata Bremek. in Repert Spec. Nov. Regni Veg. 37: 75 (1934).

Guéré (Manjou), *Letouzey* 3428 (YA); Dimako, *Leeuwenberg* 7785 (BR, YA); M'balmayo, *de Wilde* & *de Wilde-Duyfjes* 1807 (BR); Bitye, *Bates* 1520 (BR); Meyos Mela, *Letouzey* 8324 (BR); Mbang-Ndemba, *Breteler* 1451 (BR).

Catégorie de l'UICN. Cette espèce présente par sa distribution une bonne représentativité aussi bien dans des zones protégées que dans des zones sans mesures spéciales de protection. Elle ne court donc aucun risque de disparition pour le moment et nous la mettons dans la catégorie LR.

Pavetta longistyla S.D.Manning in Annals Missouri Bot. Gard. 83(1): 125 (1996).

Route d'Ambos, *Meurillon* 645 (BR).

Catégorie de l'UICN. Cette espèce est connue d'une seule localité, donc une distribution restreinte. Elle se classe dans la catégorie CR B2a.

Pavetta muriana S.D.Manning in Annals Missouri Bot. Gard. 83(1): 128 (1996).

Bakossi Mountains, *Thomas* & *Mcleod* 5303 (BR, K).

Catégorie de l'UICN. Cette espèce est connue d'une seule localité, donc une distribution restreinte. Elle se classe dans la catégorie CR B2a.

Pavetta namatae S.D.Manning in Annals Missouri Bot. Gard. 83(1): 131 (1996).

Njantibda, canton Longe, *Manning* 2097 (BR, YA).

Catégorie de l'UICN. Cette espèce est connue d'une seule localité, donc une distribution restreinte. Elle se classe dans la catégorie CR B2a.

Pavetta owariensis P.Beauv. var. *opaca* S.D.Manning in Annals Missouri Bot. Gard. 83(1): 134 (1996).

60 km S de Edea, S de Mboké, 11 km E de km 58 de la route Edéa–Kribi, *Leeuwenberg* 5555 (BR); Bipindi, *Zenker* 2554 (BR); Song Bong, *Bamps* 1378 (BR, YA); ibid., *Leeuwenberg* 5069 (BR, YA); Badjob, *de Wilde* & *de Wilde-Duyfjes* 1538 (BR, YA); Eséka, *Mpom* 202 (BR, YA); Mabama Plain, *Stone, Walkers, Nzabi* & *Mboumbore* 3280 (BR).

Catégorie de l'UICN. Cette espèce présente par sa distribution une bonne représentativité aussi bien dans des zones protégées que dans des zones sans mesures spéciales de protection. Elle ne court donc aucun risque de disparition pour le moment et nous la mettons dans la catégorie LR.

Pavetta owariensis P.Beauv. var. *satabiei* S.D.Manning in Annals Missouri Bot. Gard. 83(1): 137 (1996).

Butu-Dikome, *Satabié* 252 (BR, YA); route Ndilose–Mejelet, W de Bakossi, *Etuge* & *Thomas* 534 (BR); Bakossi Mountain, *Etuge* & *Thomas* 178 (BR).

Catégorie de l'UICN. Cette espèce est connue de moins de cinq localités et se classe donc dans la catégories EN B2a.

Pavetta rubentifolia S.D.Manning in Annals Missouri Bot. Gard. 83(1): 138 (1996).

Bakossi, *Thomas* & *Mcleod* 5343 (MO, YA).

Catégorie de l'UICN. Cette espèce est connue d'une seule localité, donc une distribution restreinte. Elle se classe dans la catégorie CR B2a.

Pavetta staudtii Hutch. & Dalz., Fl. West Trop. Afr. 2: 91 (1931).

Nganjo, *Thomas* & *Nemba* 5664 (BR); Mejelet, *Etuge* & *Thomas* 474 (BR); Chantier Bakaka, *Leeuwenberg* 8153 (BR); Kribi, *Bos* 5373 (BR); 40 km de Kribi, *Bos* 6259 (BR); Bipindi, *Zenker* 4335 (BR); ibid., *Zenker* 4427 (BR); ibid., *Zenker* 4913 (BR); Song Bong, *Bamps* 1339 (BR); 60 km SW de Eseka, S de la rivière Nyong, 12km de Song Bong, *Leeuwenberg* 1989 (BR); Station du cacaoyer de Nkoemvone, *de Wilde* 7438 (BR); colline Nkolomeyan, *Letouzey* 9839 (BR, YA); Ambam, *de Wilde* & *de Wilde-Duyfjes* 2044 (BR); Nkol Nlong, *Manning* 2145 (BR, YA); Alati, *Biholong* 261 (BR, YA).

Catégorie de l'UICN. Cette espèce présente par sa distribution une bonne représentativité aussi bien dans des zones protégées que dans des zones sans mesures spéciales de protection. Elle ne court donc aucun risque de disparition pour le moment et nous la mettons dans la catégorie LR.

Pavetta tenuissima S.D.Manning in Annals Missouri Bot. Gard. 83(1): 142 (1996).

Kéllé River, *de Wilde* & *de Wilde-Duyfjes* 1293 (BR); Tissongo, *Thomas* 471 (K); Banga, *Brenan* 9280 (YA, K); ibid., *Brenan* 9280 (BR, K); Ma'an, *Letouzey* 15211 (BR); ibid., *Letouzey* 15217 (BR, YA); Mékomengona, *Raynal* & *Raynal* 9897 (BR); Adjou, *Raynal* & *Raynal* 10148 (BR).

Catégorie de l'UICN. Cette espèce présente par sa distribution une bonne représentativité aussi bien dans des zones protégées que dans des zones sans mesures spéciales de protection. Elle ne court donc aucun risque de disparition pour le moment et nous la mettons dans la catégorie LR.

Pavetta urophylla Bremek. ssp. *bossii* S.D.Manning in Annals Missouri Bot. Gard. 83(1): 144 (1996).

Calvary Mountain, *Bos* 6611 (BR).

Catégorie de l'UICN. Cette espèce est connue d'une seule localité, donc une distribution restreinte. Elle se classe dans la catégorie CR B2a.

Pavetta viridiloba K.Krause var. *meurillonii* S.D.Manning in Annals Missouri Bot. Gard. 83(1): 146 (1996).

Fontem, *Meurillon* 617 (BR).

Catégorie de l'UICN. Cette espèce est connue d'une seule localité, donc une distribution restreinte. Elle se classe dans la catégorie CR B2a.

Pavetta viridiloba K.Krause var. *viridiloba* in Bot. Jahrb. Syst. 54: 353 (1917).

7 km SE de Makak, *Manning* 2095 (BR, YA); ibid., *Manning* 2037 (BR, YA); 14 km SW de Yaoundé, *Manning* 1891 (BR); Lomié, *Leeuwenberg* 6688 (BR).

Catégorie de l'UICN. Cette espèce est connue de moins de cinq localités et se classe donc dans la catégorie EN B2a.

Psychotria bimbiensis Bridson & Cheek in Kew Bull. 57: 389 (2002).

Bomana, *Akogo* 94 (K, SCA, YA); Dikulu (Mabeta), *Cable* 593 (BR, K, MO, P, SCA, WAG, YA); ibid., *Cheek* 5709 (K, SCA, YA); ibid., *Cheek* 5761 (K, SCA, WAG); Nguti, *Cheek* 10707 (BR, K, YA); Mabeta, *Gereau* 5602 (K, MO); Bomana, *Ndam* 748 (K, SCA, YA); ibid., *Tchouto* 945 (K, SCA, YA); Bimbia, *Baker* 272 (K, SCA, YA); ibid., *Jaff* 149 (SCA, YA); ibid., *Watts* 127 (K, SCA, WAG, YA); ibid., *Wheatley* 100 (K, SCA, YA).

Catégorie de l'UICN. Cette espèce connaît une distribution dans une aire ne dépasse pas 5000 km^2. Elle appartient à la catégorie EN B1.

Psychotria camerunensis Petit in Bull. Jard. Bot. Etat Brux. 36: 158 (1966).

Mimfia, *Zenker* 327 (BR); Masore, *Thomas* 4840 (BR, P); Bassin du Mungo, *Chevalier* 33288 (BR), Tombel, *Etuge* & *Thomas* 192 (BR, MO); Kwambo, *Manning* 1471 (BR, MO); Bipindi, *Zenker* 4762 (BR); ibid., *Zenker* 4814 (BR); Yaoundé, *Breteler* 895 (BR, WAG).

Catégorie de l'UICN. Cette espèce présente par sa distribution une bonne représentativité aussi bien dans des zones protégées que dans des zones sans mesures spéciales de protection. Elle ne court donc aucun risque de disparition pour le moment et nous la mettons dans la catégorie LR.

Psychotria ingentifolia Petit in Bull. Jard. Bot. Etat Brux. 34: 208 (1964).

Bipindi, *Zenker* 3048 (BR); ibid., *Zenker* 3119 (BR).

Catégorie de l'UICN. Cette espèce est connue d'une seule localité et se range dans la catégorie CR B2a.

Psychotria lanceifolia K.Schum. in Engl. Bot. Jahrb. 33: 367 (1903).

Mimfia, *Zenker* s.n. (BR); Ekona, *Etuge* & *Thomas* 414 (BR, MO); Bipindi, *Annet* 329 (BR); ibid., *Zenker* 1008 (BR, K); ibid., *Zenker* 2672 (BR); ibid., *Zenker* 3162 (BR); ibid., *Zenker* 3227 (BR); ibid., *Zenker* 3575 (BR); ibid., *Zenker* 843 (BM, BR, K); Lolodorf, *Bamps* 1737 (BR); colline Nkol Tsia, *Letouzey* 12721 (BR, YA).

Catégorie de l'UICN. Cette espèce est connue de moins de dix localités et avec une aire d'occupation très restreinte. Elle appartient donc à la catégorie VU D2.

Psychotria microthyrsa Petit in Bull. Jard. Bot. Etat Brux. 36: 178 (1966).

Ngoko, *Schlechter* 12731 (BR, K).

Catégorie de l'UICN. Cette espèce est connue d'une seule localité et se range dans la catégorie CR B2a.

Psychotria moliwensis Bridson & Cheek in Kew Bull. 57: 392 (2002).

Limbe, *Schlechter* 1234 (K); Mabeta, *Watts* 110 (BR, K, MO, SCA, WAG, YA).

Catégorie de l'UICN. Cette espèce est connue de moins de cinq localités. Elle appartient à la catégorie EN B2a.

Psychotria sadebeckiana K.Schum. in Engl. Bot. Jahrb. 28: 99 (1899).

Mission catholique de Mundemba, *Manning* 1700 (BR, MO); Bipindi, *Zenker* 4771 (BR); ibid., *Zenker* 4938 (BR); Batanga, *Dinklage* 904 (BR); Ebolowa, *Mildbraed* 5589 (BR); Nkolbewa, *Letouzey* 8996 (BR).

Catégorie de l'UICN. Cette espèce présente par sa distribution une bonne représentativité aussi bien dans des zones protégées que dans des zones sans mesures spéciales de protection. Elle ne court donc aucun risque de disparition pour le moment et nous la mettons dans la catégorie LR.

Psychotria sycophylla (K.Schum.) Petit in Bull. Jard. Bot. Etat Brux. 34: 213 (1964). *Grumilea sycophylla* K.Schum. in Engl. Bot. Jahrb. 33: 370 (1903).

Yaoundé, *Zenker* & *Staudt* 660 (BM, BR, K).

Catégorie de l'UICN. Cette espèce est connue d'une seule localité et se range dans la catégorie CR B2a.

Rothmannia ebamutensis Sonké in Syst. Geogr. Pl. 70(1): 149 (2000).

Sanctuaire Banyang Mbo, 5 km NW Ebamut, *Sonké* 2110 (BR, K, SCA, WAG, YA); 6 km NW Ebamut, *Sonké* 2145 (BRLU, K, MO, YA); 3 km NE Ebamut, *Sonké* 2155 (BR, BRLU, SCA, YA); 5 km NE Ebamut, *Sonké* 2156 (BR, K, MO, YA); ibid., *Sonké* 2157 (BR, BRLU, K, MO, SCA, WAG, YA); ibid., *Sonké* 2178 (BR, BRLU, K, MO, YA); ibid., *Sonké* 2233 (BR, BRLU, K, YA); 6 km NE Ebamut, *Sonké* 2255 (SCA, YA); Kodmin, *Biye, Etuge, Godon, Hutt & Clement* 50 (K).

Catégorie de l'UICN. Cette espèce présente une distribution fragmentée et avec des populations de taille réduite. Elle appartient à la catégorie VU D2.

Sericanthe raynaliorum (N.Hallé) Robbr. in Bull. Jard. Bot. Nat. Belg. 48: 58 (1978). *Neorosea raynaliorum* N.Hallé, Adansonia, ser. 2, 12: 199 (1972).

Kribi, *Bos* 4498, 5571 (BR,WAG); Nta Ali, *Achoundong* 1182 (BR); Bidou, *Bos* 6082 (BR,WAG); Song Bong, *Bamps* 1342 (BR); Reserve forestière de Makak, *Bamps* 1467 (BR); Mont Kala, *Mezili* 158 (BR); Sadolko, *Raynal* 12230 (BR, WAG); 46 km E de Ngaoundéré, *de Wilde J.J.O., de Wilde J.J.F.E. & de Wilde-Duyfjes* 4281 (BR); Bagodo, *Letouzey* 7564 (BR, YA); Meiganga, *Jacques-Felix* 8138 (BR).

Catégorie de l'UICN. Cette espèce présente une distribution fragmentée et avec des populations de taille réduite. Elle appartient à la catégorie VU D2.

Tricalysia amplexicaulis Robbr. in Bull. Jard. Bot. Nat. Belg. 57(1/2): 156 (1987).

Kribi, *Bos* 4498, 5571 (BR, WAG, YA); Bidou, *Bos* 6082 (BR,WAG); Song Bong, *Bamps* 1342 (BR, YA); Makak, *Bamps* 1467 (BR, YA); Mont Kala, *Mezili* 158 (BR).

Catégorie de l'UICN. Cette espèce est connue de moins de dix localités et se range donc dans la catégorie VU B2a.

Tricalysia ferorum Robbr. in Bull. Nat. Plantentuin Belg. 53: 318 (1983).

Korup, *Thomas* & *McLeod* 5878 (K); 50 km NW Eska, *de Wilde J.J.O.,de Wilde J.J.F.E. & de Wilde-Duyfjes* 1242, 1502C (BR, K, YA); Eseka, *de Wilde J.J.O., de Wilde J.J.F.E. & de Wilde-Duyfjes* 3883 (BR, K, WAG, HBG, MO); Bidjouka, *Letouzey* 12920 (BR, K, YA).

Catégorie de l'UICN. Cette espèce est connue de moins de dix localités et se range donc dans la catégorie VU B2a.

Tricalysia lasiodelphys (K.Schum. & Krause) A.Chev. ssp. *lasiodelphys*. *Coffea lasiodelphys* K.Schum. & Krause in Engl. Bot. Jahrb. 39: 545 (1907).

Lep Mbikeno, *Letouzey* 12376 (BR, YA); Douala-Edea Reserve, lake Tissongo, *Thomas* 1012 (BR, K); Bella, *Letouzey* 4171 (BR, YA); Bipindi, *Zenker* 232 (BR); ibid., *Zenker* 3843, 4742 (K); ibid., *Zenker* 2303, 4014, 4857 (BR, K); Song Bong, *Bamps* 1430 (BR, K, YA); N'Koemvone, *de Wilde* 7750 (BR, K, WAG); Alati, *Letouzey* 11838 (BR, YA); Nkol Tsia, *Letouzey* 12700 (K, YA); Munyenge, *Letouzey* 15028 (K).

Catégorie de l'UICN. Cette espèce présente par sa distribution une bonne représentativité aussi bien dans des zones protégées que dans des zones sans mesures spéciales de protection. Elle ne court donc aucun risque de disparition pour le moment et nous la mettons dans la catégorie LR.

Tricalysia lejolyana Sonké & Cheek in Kew Bull. 57: 682 (2002).

E of Nguti, Banyang Mbo Wildlife Sanctuary, *Sonké* 2402 (BR, BRLU, K, MO, SCA, WAG, YA); ibid., *Sonké* 2403 (K, BR, BRLU, K, MO, SCA, WAG, YA).

Catégorie de l'UICN. Cette espèce est connue de moins de cinq localités et se classe donc dans la catégorie EN B2a.

Vangueriella zenkeri Verdc. in Kew Bull. 42(1): 192 (1987).

Mt Eléphant, *Bos* 5654 (K); Bipindi, *Zenker* 1114 (K).

Catégorie de l'UICN. Cette espèce est connue de moins de cinq localités et se classe donc dans la catégorie EN B2a.

4 Discussion & conclusions

L'objectif du présent travail était de faire un inventaire des Rubiaceae endémiques du Cameroun et déterminer pour chaque taxon, sa catégorie au regard des critères de l'UICN. Le fait le plus remarquable du présent travail est l'observation de plusieurs hotspots de Rubiaceae endémiques au Cameroun. Les zones que nous avons identifiées comme très riches en taxons endémiques se superposent aisément aux zones déjà signalées par Sosef (1994, 1996) et Robbrecht (1996). Toutefois, il apparaît ici que Yaoundé et ses environs forme une zone qui est également riche en Rubiaceae endémiques, phénomène que Sosef (1996) n'a pas observé avec la distribution des taxa du genre *Begonia*. Bien que la région du mont Cameroun soit souvent citée comme la plus riche et la plus diversifiée, il apparaît ici que c'est la région de Bipindi-Lolodorf qui connaît une grande concentration en Rubiaceae endémiques. La Fig. 1 montre certaines mailles où aucune espèce endémique n'est signalée. Il ne s'agit pas des zones sans importance mais plutôt elles indiquent que des prospections doivent s'intensifier dans ces zones afin de clarifier leur situation.

La présence d'un grand nombre d'espèces endémiques dans une région serait en relation avec l'hétérogénéité spatiale et climatique et combinée aux variations périodiques de la stabilité écologique (Goldblatt, 1997; Linder, 1985). D'autres par contre pensent qu'une longue stabilité environnementale justifierait la présence à un endroit d'un grand nombre de taxons endémiques (Lovett & Friis, 1996). Nous pensons pour notre part que différents processus pourraient être à l'origine du phénomène de forte endémicité dans une région. Ces processus pourraient être des faits historiques ou contemporains. Les propriétés biologiques des taxons endémiques et leur combinaison, le bas niveau de perturbation et les grandes précipitations pourraient également contribués à justifier l'endémicité d'une région.

Il est intéressant de noter que plus de la moitié des taxons signalés sont dans les catégories d'espèces menacées (CR et EN) de l'UICN et si on y ajoute les espèces vulnérables (VU), cette proportion passe à 80%. Il est souhaitable qu'à la lumière des ces zones de forte endémicité, que des mesures spéciales de protection soient prises en vue de la sauvegarde de ces zones qui sont pour la plupart devenues fragiles du fait de l'explosion démographique et des activités anthropiques. Il est presque certain que d'autres groupes taxonomiques endémiques pourraient exister en ces lieux en plus des Rubiaceae et des *Begonia* déjà signalées. Il est donc important que d'autres inventaires similaires se fassent pour d'autres groupes comme les Orchidaceae, les Euphorbiaceae, les Caesalpiniaceae, etc.

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TOWARDS A NEW NATIONAL FOREST CLASSIFICATION FOR SOUTH AFRICA

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Abstract

The indigenous mixed evergreen forests of South Africa were classified to define forest types at the national level as a basis for policy development and to conserve biodiversity. The forests are generally small and occur in a fragmented zone along the eastern side of the country, mainly along the eastern escarpment and mountain ranges, but also along the Indian Ocean coast. About 4500 relevés from many different published and unpublished vegetation studies were used. Most data used are based on stems by species and stem diameter on 400 m^2 plots. Some data sets included all higher plant species, some of which were recorded by cover-abundance values. The vegetation data were subject to computer-assisted formalized classification and ordination procedures to delimit the major forest types and to define their position along major environmental gradients. A series of iterative steps involving global TWINSPAN analyses (including all relevés), and local analyses (limited to part of the handled table) were performed. A total of eight Forest Groups and 24 Forest Types were identified and described.

Key words: biogeography, classification, forest, evergreen, South Africa

Résumé

Vers une nouvelle classification nationale des forêts en Afrique du Sud –Les forêts sempervirentes mixtes indigènes d'Afrique du Sud furent classifiées afin de définir les différents types forestiers au niveau national et ainsi créer une base pour la politique de développement et de conservation de la biodiversité. Les forêts sont généralement petites et se concentrent dans une zone fragmentée le long de la côte Est, principalement le long de l'escarpement oriental et dans les zones montagneuses, mais aussi le long des côtes bordant l'Océan Indien. Approximativement 4500 relevés provenant de nombreuses études de la végétation (études publiées et non publiées) furent utilisés.

La plupart des données utilisées sont basées sur le nombre de troncs pour chaque espèce et sur le diamètre de ceux-ci dans des lots de 400 m^2. Quelques études comprennent toutes les espèces de plantes supérieures, certaines données furent enregistrées avec des valeurs de type surface couverte-densité. Les données de végétation furent soumises a un logiciel de classification et, numération afin de délimiter les types forestiers majeurs et pour définir leur position par rapport à un gradient environnemental.

Une série de pas itératifs mettant en œuvre une analyse TWINSPAN (contenant tous les relevés) et des analyses locales (limitées a une partie des données) furent testés. Un total de huit groupes forestiers et vingt-quatre types forestiers furent identifiés et décrits.

1 Background

Mixed evergreen forests form the smallest, but widely distributed and most fragmented vegetation formation in South Africa. An indigenous forest was defined as a generally multilayered vegetation unit dominated by trees (largely evergreen or semi-deciduous) whose combined strata have overlapping crowns (crown cover >75%), and where graminoids in the herbaceous stratum (if present) are generally rare. Fire does not normally play a major role in forest function and dynamics except at the fringes (Shackleton *et al.* 1999). At least 7% of the country is potentially suitable for forest growth on the basis of climate and substrate, but forest covers just more than 3,000 km^2 (or 0,1%) of the land area of South Africa (Cooper, 1985; Anonymous, 1987; Geldenhuys, 2000a). This area varies depending on the reliability of the methods used (mapping down to minimum forest size of 50 ha, 30 ha or 1 ha, or using satellite imagery and/or aerial photographs).

Forests occur as a series of scattered patches along the eastern and southern margins (escarpment, mountain ranges and coastal lowlands) of South Africa, from the Soutpansberg (inland, 22°40'S) and Maputaland (along the coast, 27°S) to the Cape Peninsula (34°S) (Cooper, 1985; Anonymous, 1987). High forest (10 to 35 m tall) and scrub forest (3 to 10 m tall) persist in areas with mean annual rainfall >525 mm with strong winter rain and >725 mm with strong summer rain (Rutherford & Westfall, 1986; Geldenhuys, 1991). Mist precipitation along the escarpment and some mountain ranges supplements the rainfall. Forests may, however, also be found along rivers and in protected gorges in lower rainfall areas (Von Maltitz *et al.*, 2003). Inland mountain ranges, surrounded by seasonally dry regions, provide important refugia for these forests. Such is the case of the south-facing slopes of the Soutpansberg (Geldenhuys & Murray, 1993) and the sheltered valleys of the southwestern Cape (McKenzie, 1978; Masson, 1990; Geldenhuys, 1997a). The substrates supporting the forests include a wide range of rocks, such as quartzitic sandstones, mudstones, shales, schists, aeolian sands, Enon conglomerates, dolerites and granite-gneiss (Geldenhuys, 2000a). The soils derived from these rocks vary in depth, water-holding capacity and nutrient status.

The forests typically occur as (very) small patches (<10 ha) (Cooper, 1985; Geldenhuys, 1991). Few large, but widely separated, forest complexes occur. The largest single forest (25,706 ha) occurs around Knysna in the Southern Cape Region and belongs to a forest complex of 60,560 ha at 34°S and between 22°E and 24°30'E (Geldenhuys, 1991). Most forests are characterized by a large ratio of forest margin to forest area. This accentuates the importance of forest margins in forest survival. The forests are naturally surrounded by fire-adapted vegetation, such as sclerophyllous shrublands (fynbos) in the south and grasslands and deciduous woodland in the summer-rainfall areas in the north of the country. Today, commercial timber plantations and cultivated land surround extant forest in many areas.

Until recently, there has not been any national, generally accepted classification for indigenous forests. Without an objective classification, the government would neither be able to report on the state of the forest resources within the country (as required by the National Forests Act [Act No 84 of 1998] and the White Paper on Sustainable Forest Management in South Africa of 1996), nor would it be able to set conservation priorities. To effectively monitor, evaluate and protect forests, the types of forests must be clearly defined and their distribution accurately mapped. Understanding the floristics of the forest types and linking this knowledge to an understanding of their ecology, is also important for the setting of wise management targets. A forest type cannot be adequately protected without knowing its key characteristics, general location, and common and endemic species.

This paper reports on the process, methods and partial results employed in the production of a new, formalized biogeographic-floristic classification of the South African indigenous forests (National Forest Classification). The focus of this classification was on floristic data, however faunal data and site characteristics were also considered.

2 Methods

Construction of the National Forest Classification involved the following steps:

2.1

As the first step, the distribution of the extent of forest patches was identified. All available candidate maps showed some deficiencies, either in precision or coverage. The maps of Cooper (1985) and Anonymous (1987), at a scale of 1:1,000,000, were only available in hard copy. The Van der Zel (1988) map, at a scale of 1:250,000 and derived from a combination of LANDSAT and field data, was of questionable spatial accuracy. The National Land Cover (NLC) map (Thompson, 1999), which is spatially accurate, showed some inaccuracy with identification of forest patches. In the end a combined map based on the Van der Zel (1988) and the NLC maps were used.

2.2

As much data (floral, faunal and physical) as possible were gathered from published and unpublished sources.

Vegetation data available in the form of vegetation samples (relevés) were identified. The samples varied in quality as they differ in a number of features (taxonomic reliability and nomenclature; mostly restricted to tree data with varied minimum diameter limits, often excluding other woody species or the herbaceous layer and epiphytes; intensity of sampling). In order to assure compatibility of the data, various data transformations were performed prior to capture into a database (TvWin 2.0; Hennekens & Schaminée, 2001). The relevés usually contained data on woody species of stems ≥10 cm DBH, collected in plots of 400 m^2 (e.g. Geldenhuys & Murray, 1993, Geldenhuys & Pieterse 1993). Some data came from long-term growth study plots where stems were measured down to 5 cm DBH (Geldenhuys, 1998). Other data sets came from sampling along environmental gradients, and often included a combination of tree stems down to 5 cm DBH. Considerable number of relevés were made using Braun-Blanquet cover-abundance scales for total floristic composition (e.g. Everard & Hardy, 1993, Geldenhuys, 1993a), or only for all woody species (MacDevette *et al.*, 1989). The entire data set featured 4500 vegetation relevés. The DBH values were converted to basal area (m^2) per species per plot, and expressed as percent of the total basal area per plot. For presentation purposes, the percentage values were then converted into Braun-Blanquet cover-abundance values as follows: + = <1%; 1 = 1–5%; 2a = 5–12%; 2b = 12–25%; 3 = 25–50%; 4 = 50–75%; 5 = 75–100%.

For animal data, large forest patches throughout the geographic range of forests and incorporating the diversity of known forest types (Cooper, 1985) were selected. The selected forests were then intersected with the quarter-degree of grid cells for

South Africa and binary data (species presence or absence) for certain animal taxa (birds, mammals, reptiles and frogs) compiled for the selected quarter degree cells. Only forest-dependent (only breeding within the forest habitat) and forest-associated (inhabiting other habitats besides forest and not necessarily breeding in forests) animal taxa were considered (for details of the analytical procedures and results, see Von Maltitz *et al.*, 2003).

Modelled national climatic surfaces (Computer Center for Water Research, University of KwaZulu-Natal, Pietermaritzburg), based on long-term rainfall and temperature records and altitude, formed the basis for the climatic analyses of the forest distribution areas. These data are given in a one-minute by one-minute (of arc) grid for the entire country in a GIS format. This climatic data must be interpreted with caution: mountainous areas with steep altitudinal gradients, poorly serviced by weather stations, tend to have localised microclimates. Furthermore, forest patches are often very small and located within micro-habitats such as protected kloofs. A crude approximation of soil fertility (two categories: high and low), was derived from the 1:1,000,000 geological coverage. It does show large-scale fertility as related to forest types.

2.3

The data were entered into digital format suitable for the classification and ordination software. The vegetation samples containing cover-abundance estimates were captured into a number of databases using the database software package TvWin 2.0 (Turboveg). This software was developed for the purposes of storage, transformation, retrieval, and numerical data handling of vegetation plot-based data (Hennekens & Schaminée, 2001). Turboveg allows storage of data originally collected using different estimation (and counting) scales. Translation between various cover-abundance scales is allowed through code-replacement (each cover-abundance category is assigned a representative % cover). This feature assures compatibility of the data. The data have become part of the National Vegetation Database (Mucina *et al.,* 2000).

2.4

At the data analysis stage, the vegetation relevé data were handled by the program Megatab 2.0 (Hennekens, 1996), incorporating basic informal and formal table-sorting procedures. A series of global and local TWINSPAN (Hill, 1973) analyses (also executed by the Megatab 2.0) were performed to identify pools (clusters) of relevés to be interpreted as forest types. The resulting sorted matrix (relevé table) was transformed into a synoptic table (using routine SHAKE also executed by Megatab 2.0), in which each woody species was represented by combined weighted cover-abundance values (range: 0–9). Non-woody species were discarded at this stage of the analysis because of their lack in most of the relevés.

2.5

The synoptic table was subjected to numerical classification and ordination analyses with the aim of formulating a high-level hierarchy of the identified forest types. The following techniques were used and analyses executed using the program package SYN-TAX 2000 (Podani, 1994):

- Average linkage clustering was selected as the clustering technique for its space-conserving properties. The resemblance used in our analyses was Chord Distance for quantitative data and the Jaccard coefficient for qualitative (presence/absence) data.

- Principal Coordinate Analysis was selected as the ordination technique, with Chord Distance as the resemblance index allowing for direct comparison of the clusterings and ordinations.
- Minimum spanning tree (using Chord Distance) was used to visualize the reticular resemblance patterns on ordination planes.

2.6

The initial classification was discussed at a workshop to which most key forest ecologists, all provincial conservation departments and national and provincial representatives of the National Department of Water Affairs and Forestry (DWAF) were invited. The objective was to gain consensus on the classification as well as to gather initial data for the profile descriptions of the forest types. After the workshop, individual forest type descriptions were circulated back to the workshop participants, and to a larger selection of forest ecologists for additions and review.

2.7

After the workshop, additional forest data were collected to fill important identified gaps in the available data. The forest classification was then re-run based on the additional data gathered.

2.8

The draft descriptions of the forest types were refined and finalized, for external review, before submission to the DWAF.

3 Results

3.1 Major vegetation patterns

The series of computer-assisted analyses yielded the following hierarchical system of 7 Forest Groups (1st level of system: coded by Roman numerals) comprising 20 zonal and intrazonal Forest Types (2nd level of system: coded by combined Roman/Arabic numerals). In addition, 4 azonal forests types were recognized (Table 1). Classification of Forest Types into Forest Groups (or their qualification as Azonal) was primarily based upon floristic resemblance patterns. In some cases, however, some biogeographically motivated adjustments were introduced as well. Hence, the forests of South Africa have been classified into 24 floristic-biogeographic Forest Types based on their woody species composition.

The azonal forest types separated out as outliers in quantitative clustering analyses. Mangrove and Swamp Forest formed a single cluster on the basis of a single shared taxon. A quantitative ordination showed the same pattern, with the remaining forest types spanning a horseshoe shaped coenocline ranging from subtropical coastal forests at one end to the Western Cape Talus Forest at the other. In a qualitative clustering the group of outliers was enlarged by addition of Western Cape Milkwood Forest and Western Cape Talus Forest.

An ordination of the zonal forests showed that the Southern Afrotemperate Forest Group and the Northern Afrotemperate Forest Group separated from the other indigenous forests along Axis 1 and became clearly separated on Axis 2. All forests of the south-western regions of the country, including the Western Cape Milkwood Forests, appeared as a compact cluster. All these forest types, except for the Milkwood forests, were placed in the Southern Afrotemperate Group.

TABLE 1. Forest Groups and associated Forest Types of the South African natural evergreen forests (Von Maltitz *et al.*, 2003).

Forest Group	**Forest Type**	**Key References**
I: Southern Afrotemperate Group	I1: Western Cape Talus Forests	Campbell & Moll (1977), Taylor (1996).
	I2: Western Cape Afrotemperate Forests	Taylor (1955), Campbell & Moll (1977), McKenzie *et al.* (1977), McKenzie (1978), Knight (1989), Masson & McKenzie (1989), Masson (1990), Geldenhuys (1997a)
	I3: Southern Cape Afrotemperate Forests	Phillips (1931), Von Breitenbach (1974), Geldenhuys (1989, 1991, 1992b, 1993a, b, 1994), Vermeulen (1995), Van der Merwe (1998)
II: Northern Afrotemperate Group	II1: Marekele Afromontane Forests	Coetzee (1974, 1975), Van Vuuren & Van der Schijff (1970), Westfall *et al.* (1985), Van Staden (2002)
	II2: Northern Highveld Forests	Behr & Bredenkamp (1988), Bredenkamp & Theron (1978, 1980), Van der Meulen (1979), Siebert (2001), Ellery *et al.* (2001)
	II3: Drakensberg Montane Forests	Schelpe (1943), Roberts (1961), Killick (1963), Everard (1986), Du Preez & Bredenkamp (1991), Du Preez *et al.* (1991), Eckhardt *et al.* (1993), Hill (1996)
	II4: Northern KwaZulu-Natal Mistbelt Forests	Cooper (1985), Smit *et al.* (1993), Robesson (1998)
III: Northern Mistbelt Group	III1: Limpopo Mistbelt Forests	Scheepers (1978), Von Breitenbach (1990), Geldenhuys & Murray (1993), Geldenhuys & Pieterse (1993), Geldenhuys (1997b), Geldenhuys (2000b), Geldenhuys & Venter (2002)
	III2: Mpumalanga Mistbelt Forests	Van der Schijff & Schoonraad (1971), Deall *et al.* (1989), Von Breitenbach (1990), Matthews *et al.* (1992), Morgenthal & Cilliers (1999), Stalmans *et al.* (1999)
IV: Southern Mistbelt Group	IV1: Eastern Mistbelt Forests	Edwards (1967), Moll (1972), Cooper (1985), Everard (1992), Everard *et al.* (1995), Cawe (1996), Geldenhuys (1999), Geldenhuys *et al.* (2001)

TABLE 1. continued

Forest Group	**Forest Type**	**Key References**
	IV2: Transkei Mistbelt Forests	Cawe & McKenzie (1989), Cawe (1996), Cooper & Swart (1992)
	IV3: Amatole Mistbelt Forests	Story (1952), Phillipson (1987), Everard & Hardy (1993), Geldenhuys (1993c), Geldenhuys & Rathogwa (1995)
V: Scarp Group	V1: Eastern Scarp Forests	Huntley (1965), Whateley & Porter (1983), Cooper (1985), MacDevette *et al.* (1989), Lawes (1990), Everard (1992), Everard *et al.* (1995)
	V2: Pondoland Scarp Forests	Nicholson (1982), Cawe (1990, 1996), Van Wyk (1989), Van Wyk & Smith (2001)
	V3: Transkei Coastal Forests	Cawe (1990, 1996), Cooper & Swart (1992), Geldenhuys (1993c)
VI: Northern Coastal Group	VI1: KwaZulu-Natal Coastal Forests	Bews (1920), Edwards (1967), Venter (1976), Ward (1983), Bartholomew (1989), MacDevette *et al.* (1989), Lubbe (1996), Van Wyk *et al.* (1996)
	VI2: KwaZulu-Natal Dune Forests	Bews (1920), Breen (1971), Weisser (1978, 1980, 1987), MacDevette (1993), MacDevette *et al.* (1989), Weisser *et al.* (1992), Weisser & Cooper (1993), Von Maltitz *et al.* (1996)
VII: Southern Coastal Group	VII1: Eastern Cape Dune Forests	Comins (1962); Burns & Raal (1993); Lubke & Strong (1988), Lubke & de Villiers (1991)
	VII2: Albany Coastal Forests	Acocks (1988), Phillipson & Russell (1988)
	VII3: Western Cape Milkwood Forests	Taylor (1961), Van der Merwe (1976), Knight (1989)
Azonal Forest Types	A1: Lowveld Riverine Forests	Van Rooyen *et al.* 1981, Whateley & Porter (1983)
	A2: Swamp Forests	Weisser & Ward (1982), Wessels (1991)
	A3: Mangrove Forests	Ward & Steinke (1982), Ward *et al.* (1986)
	A4: Licuati Sand Forests	Kirkwood & Midgley (1999), Matthews *et al.* (1999, 2001); Gaugris *et al.* 2004

Clustering of Western Cape Milkwood Forest with the rest of the Southern Afrotemperate Group can be ascribed to a mass effect (Shmida & Ellner, 1984), since they share a suite of taxa encroaching from the surrounding vegetation (Fynbos and Strandveld). Biogeographically, however, their species-poor composition places them as the westernmost impoverished form of the subtropical coastal group of forests, dominated by *Sideroxylon inerme* (rarely also *Celtis africana*). They were therefore placed into the Southern Coastal Forest Group.

The patches of afrotemperate forests surrounded by grasslands at high altitudes in the Drakensberg, and those straddling the tension zones between the Grassland and Savanna Biomes in northern Highveld, form another comparatively species-poor group of afrotemperate forest types – the Northern Afrotemperate Forest Group.

For a distribution map of the identified Forest types in South Africa, see http://academic.sun.ac.za/botzoo/mucina

The forests of the Soutpansberg Mountains and the Northern (Mpumalanga) Escarpment have been classified within two forest types, such as the Limpopo Mistbelt Forests (comprising Soutpansberg and part of the Magoebaskloof area of the Escarpment; and the Mpumalanga Mistbelt Forests). These two types show high floristic similarity and therefore consistently clustered together in all quantitative and qualitative analyses. They form the well-defined Northern Mistbelt Forest Group.

Two traditional Scarp forest types (Eastern Scarp Forests and Pondoland Scarp Forests) link well in both the clusterings and ordinations. Two other forest types (Transkei Coastal Forest and Eastern Mistbelt Forest) were highly similar to the scarp forest types, and formed a group in the clusterings and ordinations. On the other hand, the Amatole Mistbelt Forest and Transkei Mistbelt Forest together formed a separate group in quantitative clustering as well as in ordinations. In qualitative analyses the Amatole Mistbelt Forest grouped with forests of the Southern Afrotemperate Forest Group. This group displays an intricate similarity pattern involving three traditional mistbelt forest types (Eastern Mistbelt, Transkei Mistbelt, Amatole Mistbelt), traditional scarp forests (Eastern Scarp, Pondoland Scarp), and one traditional coastal type (Transkei Coastal Forest) that is located topographically between the Eastern Cape and KwaZulu-Natal coastal and montane forests. Although the Transkei Coastal Forest is situated along the southern subtropical Transkei coast, it shows clear floristic links to Scarp Forest rather than to subtropical coastal groups. Therefore, the Eastern Scarp Forest, Pondoland Scarp Forest and Transkei Coastal Forest were grouped into the Scarp Forest Group.

The pair-wise similarity patterns of the Amatole Mistbelt Forest with other regionally close forest types precludes clear-cut resolution of similarity patterns within the discussed group of forest types. The Amatole Mistbelt Forest includes large patches of forest deep inland (along the Escarpment), as well as a number of patches on low-altitude inland ridges in the Albany region. In the vicinity of East London this type comes into contact with forests of scarp character (Transkei Coastal Forest) or those of clearly subtropical coastal character (Eastern Cape Dune Forest). The forest patches along the low inland ridges (from Zuurberg to as far as East London) are undersampled and therefore their relationship with the Albany Coastal Forest as well as to Transkei Mistbelt Forest remains, pending further research. The position of the Eastern Mistbelt Forest is another problem, as it is floristically closer to the Transkei Coastal Forest than to the Amatole Mistbelt Forest. Further data, especially from regions linking the Amatole Mistbelt Forest and the coastal areas of the Eastern Cape, may shed more light on this problem in the future. After separating the Scarp Forest Group, the pragmatic biogeographic approach was taken of linking the remaining traditional mistbelt forests to form the Southern Mistbelt Group.

The coastal forests are represented by a series of forest types of which KwaZulu-Natal Coastal Forest and KwaZulu-Natal Dune Forest form a consistent cluster in all the numerical analyses. The cluster is identified as the Northern Coastal Forest Group and is limited to a narrow, geologically young coastal strip along the Maputaland and Zululand coasts of KwaZulu-Natal (and to a small extent also Eastern Cape) Province.

In quantitative clusterings the Eastern Cape Dune Forest was most closely linked to the cluster comprising the Northern Coastal Forest Group. Albany Coastal Forest joined a major cluster composed of species-rich forest groups (Northern and Southern Mistbelt Forest Groups, Scarp Forest Group and Northern Coastal Forest Group) as a local outlier. However, in ordinations, Albany Coastal Forest and Eastern Cape Dune Forest appear to be very close in floristic terms. Therefore, both forest types were combined in the Southern Coastal Forest Group. The use of the minimum spanning tree technique brings a new and interesting insight into resemblance patterns of the coastal forest types of the Eastern and Western Cape Province. The Eastern Cape Dune Forest was linked to Transkei Coastal Forest (both co-occur along the Transkei coast). Albany Coastal Forest was linked to Amatole Mistbelt Forest (they co-occur in the Albany region). Western Cape Milkwood Forest, as discussed above, is the most impoverished type of coastal forest, and closely linked to the Southern Afrotemperate Forest. Indeed, the coastal-bound subtypes of this afrotemperate forest do contain some flora elements of prevalently subtropical provenance (Geldenhuys, 1989).

There are three clearly hydrologico-edaphic azonal forest types typical of habitats controlled by specific hydrological regimes. These include:

1. Lowveld Riverine Forests (gallery forest fringing rivers and water-filled pans in subtropical regions of South Africa and neighbouring countries),
2. Swamp Forests (forest showing evolutionary and ecological links to tropical swamp forests of Central Africa),
3. Mangrove Forest (specific intertidal forests of subtropical and tropical coasts, reaching their southernmost distribution along South African coast of Indian Ocean).

The Licuati Sand Forests are not an edaphic (or hydrologico-edaphic) azonal phenomenon, but a case of “relictual azonality”. They form mosaics with woodland and are considered as late Holocene relicts on old, Neogene (10–3 Myr) dune sands that have been mainly degradational land-surfaces for much of the Pleistocene. Red sand is constantly eroding from these areas and most of the surface is devoid of dune structures. The substrate on which the Sand Forest grows is very irregular and dune remobilization and accretion has been patchy in time and space over the past 40,000 years with the last recorded accretion of the upper 3 m during the early Holocene (Botha *et al.,* 2002). The dunes in the areas of much of the Sand Forest have not been sufficiently stable over the last 12,000 years for forest to have persisted for longer than 2000–3000 years at any one site. Nevertheless, this would make these forests amongst the oldest of the tropical coastal forest types.

4 Discussion

South African indigenous forests show an interesting distribution pattern. They form an archipelago of scattered forest patches that vary in size and are arranged in several longitudinal belts running either parallel to the coast or following the main escarpment or some of its lower-lying steps, or arching mountain ranges. It is an archipelago of isolated pieces of a formerly more continuous distribution of forest. Although this extensive archipelago was probably fairly fragmented even at the height of its distribution in the past (c. 40,000 years BP; Eeley *et al.,* 1999), it has been subjected to a further series of fragmentation events in more recent times (i.e. since 40,000 years BP) such as climate changes (Deacon *et al.*, 1983; Scholtz, 1986; Lawes, 1990; Scott *et al.,* 1997), large-scale fires (Geldenhuys, 1994), or lately through destructive exploitation by Man (Cooper, 1985; Feely, 1980, 1986). Man has played an important role in the fragmentation of Indian Ocean Coastal Belt forests (Scott & Steenkamp, 1996; Mazus, 2000).

The patchy distribution of some forest types reflect natural features of isolated (and ecologically very specialized) habitat complexes such as mangroves, swamps, screes and river alluvia.

The vegetation units recognized in the study are of floristic nature in the first instance and biogeographic in the second. Naturally, both biogeography and floristics reflect two sides of the same phenomenon. Therefore, and unsurprisingly, the floristic similarity (measured in terms of shared occurrence of taxa and their relative cover values) is greater between forests that are topographic neighbours.

The low woody species diversity of the high-latitude Southern Afrotemperate Forests reflects the general north-south decrease in species richness possibly resulting from plant migration patterns (Geldenhuys, 1992a; Midgley *et al.,* 1997) or significant climatic filtering (extinction associated with Pleistocene climate changes) at high latitudes.

The Highveld forests are probably the most “biogeographically eroded” type, as they contain a very small portion of the typical afrotemperate elements. They were probably originally linked (floristically and also physically) to species-rich afrotemperate forest, still found in remnants today along the Mpumalanga Escarpment (and possibly also to those of the Soutpansberg Mountains). This link is suggested by the anomalous occurrence of a number of afrotemperate elements (both woody species and herbaceous flora), a phenomenon that White (1978) singled out as the “Magaliesburg Extension”. After the (hypothetically nearly-continuous) afrotemperate belt underwent fragmentation, these forests retreated either into deep gorges where they lost much of their afrotemperate character through encroaching woodland (savanna) flora (Northern Highveld Forest), or found refugia in relictual scarp situations on elevated ranges such as Waterberg Mountains (Marekele Afromontane Forest).

Biogeographically the Northern Mistbelt Forest Group is afrotemperate in nature with considerable local levels of woody endemism and a number of relict species that reach their southern distributional limit in this group. Three centres of endemism form the geographic backdrop of this Forest Group: Soutpansberg, Wolkberg and Barberton Centres of Endemism (Van Wyk & Smith, 2001). Dry facies of these forests are enriched by a subtropical woodland element.

The relationships between the Scarp Forests and the Southern Mistbelt Forests still remain to be clearly determined, with further data from this region required.

Forests of the Scarp Forest Group form a discontinuous belt of patches along low-lying scarps extending from southern Kruger National Park and northern Swaziland (a considerable distance from the coast), to more proximal to the coast in southern KwaZulu-Natal, to coastal positions along the Eastern Cape coast. The Scarp Forests are often called “transitional” (i.e. falling between Afrotemperate and subtropical coastal forests) in character. This may have led some forest ecologists to interpret the distributional patterns of South African indigenous forests in terms of a continuum (see

Midgley *et al.,* 1997). However, the Scarp Forests are not composed of merely a mixture of elements of the two above-mentioned major forest groups – they possess their own ecological character and their own species combinations. These forests are a valuable biodiversity asset to South Africa and are comparatively rich in woody endemics, at both the species and genus level. Pondoland Scarp Forest, arguably the most unique forest in Africa, supports an endemic family, Rhynchocalycaceae.

Both forest types of the Northern Coastal Group are of subtropical character and limited strictly to the Indian Ocean Coastal Belt.

Albany Coastal Forest and Eastern Cape Dune Forest are, from a biogeographic point of view, impoverished forms of the Northern Coastal forests. They are found outside the Indian Ocean Coastal Belt (or Subtropical Coastal Forest Biome) and are surrounded either by subtropical Albany Thickets or (at the westernmost limits of distribution) by a complex of grassy fynbos and coastal thickets.

Due to the fragmented distribution of forests, the concept of zonality (as defined by Walter, 1976) can be applied only to a limited extent. The notion of a "zone" relates (by definition) to biome (see Mucina *et al.,* 2000 for a definition). In the past the indigenous forests of South Africa were classified broadly into either two biomes (Afromontane Forest Biome and Subtropical Coastal Forest Biome) or just one biome (Forest Biome) as in Low & Rebelo (1998). The classification of forests within biomes is complicated by the definition of a biome (see Walter & Breckle, 1991; Mucina, 2000) and the fragmented distribution of the forests in South Africa.

In the case of the so-called Afromontane (better "Afrotemperate"; see Meadows & Linder, 1993) forests only a few forest types would qualify as a piece of a biome in their own right. An example is the Southern Cape Afrotemperate Forests, which is a representative of the evolutionarily old Warm-Temperate Forest Biome, descending to sea level at 34°S latitude. It sets a mirror image to the distribution pattern of warm-temperate forests of the Northern Hemisphere (Kloetzli, 1988) in Eastern Asia (e.g. Ohsawa, 1993) and southwestern United States (Christensen, 1988; Fujiwara & Box 1994; Haeupler, 1994) in particular. The rest of the Afrotemperate "forest archipelago" should be seen as "wreckage" of a warm-temperate biome occupying an albeit narrow, but probably formerly continuous belt along the steps of the Escarpment. These forests are embedded in various temperate biomes such as Fynbos and Grassland or straddle ecotones between the Grassland and Savanna Biomes.

The evolutionary young Subtropical Coastal Forest Biome, also recognized under different names in the past (see Bews, 1920; Moll & White, 1978; Huntley, 1984; White, 1983) was most probably dominated by a subtropical forest, of which only fragments classified as KwaZulu-Natal Coastal Forest Group remain. The other forest types rich in subtropical elements (the remainder of the Northern and Southern Coastal Forest Groups) are basically intrazonal – hence forming specific vegetation units embedded within (and unique to) well-defined vegetation zones (biomes).

5 Conclusions

1. Most of the South African indigenous forests are afrotemperate in character, hence linking these forests with the global Warm-Temperate Forest Biome.
2. The evolutionary young subtropical coastal forests (supported by geologically young substrates) can be interpreted as remnants of a previously more extensive Subtropical Coastal Forest Biome (today considerably decimated by human disturbance).

3. There are two distinct groups of impoverished afrotemperate forests and two mistbelt groups. The latter are more species-rich and contain a number of endemics, relic species, and species linking these afrotemperate forests with those of subtropical character.

4. There are a number of plausible ways to group the Forest Groups into high-level units, but neither the traditional two-group model (Model 1: "Afromontane" versus "Coastal"), nor the recent three-group model (Model 2: "Afromontane", "Scarp", Coastal") is entirely supported by the numerical classification analyses presented here. We rather prefer to view the Forest Groups as members of a multi-group reticular continuum model. The essence of this model is that each of the Forest Groups shows a number of floristic and biogeographically plausible links to other groups and the amalgamation of the forest groups into higher units should follow a reticular rather than linear pattern.

5. The Scarp forests are clearly of intermediate character linking the afrotemperate forests with the coastal (subtropical) groups. The systematic position and origin of the Scarp Forest Group remains unclear. The numerical analyses (based purely on floristic information) have not confirmed the status of the Scarp Forest Group as a forest classification unit of level equal to traditional afrotemperate and coastal (subtropical) forests. In fact, the intricate pattern of pairwise resemblances suggests that the Scarp Forests are more closely linked to the Southern Mistbelt Group than to any other forests. Climatically as well as from their apparently ancient relic (endemic) component, they show both subtropical as well as afrotemperate links.

6. This is the first formalized and comprehensive analysis of floristic data from indigenous forests of South Africa. Despite an impressive number of samples involved in these analyses (over 4500), there are major gaps in our knowledge. Regions such as Albany, the northern Highveld, and the northern regions of Western Cape Province remain undersampled. Lack of data on herbaceous understorey flora in vegetation samples is a major drawback in drawing clear patterns of floristic and biogeographic relationships between South African indigenous forests. We submit that well-targeted molecular-phylogenetic and phylographic studies may shed more light on the ways South African forests experienced assembly and dis-assembly processes leading to the patterns of today.

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A FIRST CHECKLIST OF TREES AND LIANAS OF THE RÉSERVE DE FAUNE DU PETIT LOANGO*, GABON

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Abstract

This is the first inventory for trees and lianas in the Réserve de Faune du Petit Loango on the coast of Gabon, a complex mosaic of closed- and open-canopy forest, secondary forest, swamps, savannahs, coastal scrub and *Sacoglottis gabonensis*-dominated forest. Six transects of varying length were cut. Habitat type was ascertained at internals along all transects. Species composition along the total 19.85 km transect length was evaluated by tagging, identifying, and measuring dbh (diameter at breast height) of all individual trees and lianas 10 cm dbh within a 5 m strip, 2.5 m either side of the transect line (total area 9.825 ha). Positive identifications to taxonomic level of family or above were made for 3907 of the total 3943 stems. The 3907 identified stems represent 115 species, 95 genera and 40 families.

Despite the limits of this short-term evaluation, several new species have probably been collected, and the need or further collections is obvious. The nature of the vegetation changes with distance from the sea and the quantity of distinctive habitats suggests that legal protection for the Reserve could and should be argued for on botanical terms as well as on zoological grounds.

Résumé

Un premier inventaire des arbres et lianes de la Réserve de Faune du Petit Loango, Gabon. Cette étude constitue le premier inventaire des arbres et lianes de la Réserve de Faune du Petit Loango sur la côte gabonaise, une mosaïque complexe de forêt dense et ouverte, de forêt secondaire, de marais, de savanes, de buissons côtiers et de forêt dominée par *Sacoglottis gabonensis.* Six transects de longueur variable ont été établis. Le type d'habitat a été vérifié à plusieurs endroits le long des transects. La composition spécifique le long des 19,85 km de transect a été évaluée par marquage, identification et mesure du dhp (diamètre à hauteur de poitrine) de tous les arbres et lianes de plus de 10 cm de dhp, ceci à l'intérieur d'un couloir de 5 m (2,5 m de part et d'autre de la ligne de transect, soit une superficie totale de 9,825 ha). Les identifications jusqu'au niveau de la famille, ou au-delà, ont été réalisées pour 3907 des 3943 pieds. Les 3907 pieds identifiés représentent 115 espèces, 95 genres et 40 familles. Malgré les limites de cette évaluation à court terme, plusieurs nouvelles espèces ont probablement été récoltées et la nécessité de récolter des échantillons supplémentaires est évidente. La

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* now Loango National Park

nature de la végétation change en fonction de la distance à la mer et la quantité d'habitats distincts suggère que la protection légale de la Réserve pourrait et devrait être appuyée par des facteurs botaniques autant que sur base d'arguments zoologiques.

Key words: coastal, forest trees, Gabon, inventory, lianas

1 Introduction

The vegetation of Gabon has classically been divided into three zones, based for the main part on forestry inventories and geomorphological factors (Caballé, 1978; EDICEF, 1983). According to this view, the Réserve de Faune du Petit Loango is situated in type 1, the coastal sedimentary basin, and is described as being of 'Guineo-Congolian' phytogeographical type. Subdivisions based on characteristic tree species put it in phytogeographical cline zone 1a, dominated by species such as *Aucoumea klaineana* (Burseraceae), *Sacoglottis gabonensis* (Humiriaceae) and *Erismadelphus exsul* (Vochysiaceae) which White (1983) describes as 'hygrophilous coastal evergreen Guineo-Congolian rainforest'.

No substantial vegetation inventories have been conducted for Petit Loango, and few studies on the fauna have been published (Yamagiwa *et al.*, 1995; Furuichi *et al.*, 1997; Morgan & Lee, 2003). Tutin *et al.* (1994) note that a comparison of ape diets in different areas of Africa can only advance if floristic inventories for each study site are compiled and published. This is the first, albeit limited, inventory for trees and lianas in the Reserve de Faune du Petit Loango, Gabon. The study was conducted during a one-year period, from January to December 1998.

2 Study area and methods

The 500 km^2 Réserve de Faune du Petit Loango is situated on the southwest coast of Gabon 200 km south of Libreville, within the 12,000 km^2 Complexe d'Aires Protegées de Gamba (Fig. 1). The 20 km^2 study area has high habitat diversity despite its small size – a complex mosaic of closed- and open-canopy forest, secondary forest, swamp areas, savannahs, coastal scrub and *Sacoglottis gabonensis*-dominated forest (Morgan, 2001).

The climate at Petit Loango is described in detail in Morgan (2001). Total annual rainfall in 1998 was 2363 mm, and was strongly seasonal with six consecutive months with less than 70 mm rain (April to September). Data from Gamba, a coastal site approximately 60 km south of the study site, noted 2107 mm mean annual rainfall between 1986 and 1998, with June–September receiving less than 40 mm mean monthly rainfall (Shell Gabon, unpublished data). There was a very minor dry season in January to February, which varies in intensity and duration inter-annually.

In the reconnaissance period of the present study, in late 1997, a marked change in vegetation structure and species composition was noted with perpendicular distance from the sea. Therefore, to sample within each major habitat type, five transects were cut at carrying distances parallel to the coastline, and one transect was cut perpendicular to the sea to ascertain the relative proportions of each of the habitat types. Specifically, the parallel transect closest to the sea (the coastal transect) crossed a combination of coastal scrub and small grassy areas exposed to the strong onshore winds. The savannah transect crossed a series of three savannahs, each separated from each other by gallery forest and small waterways to the sea. The three inland transects

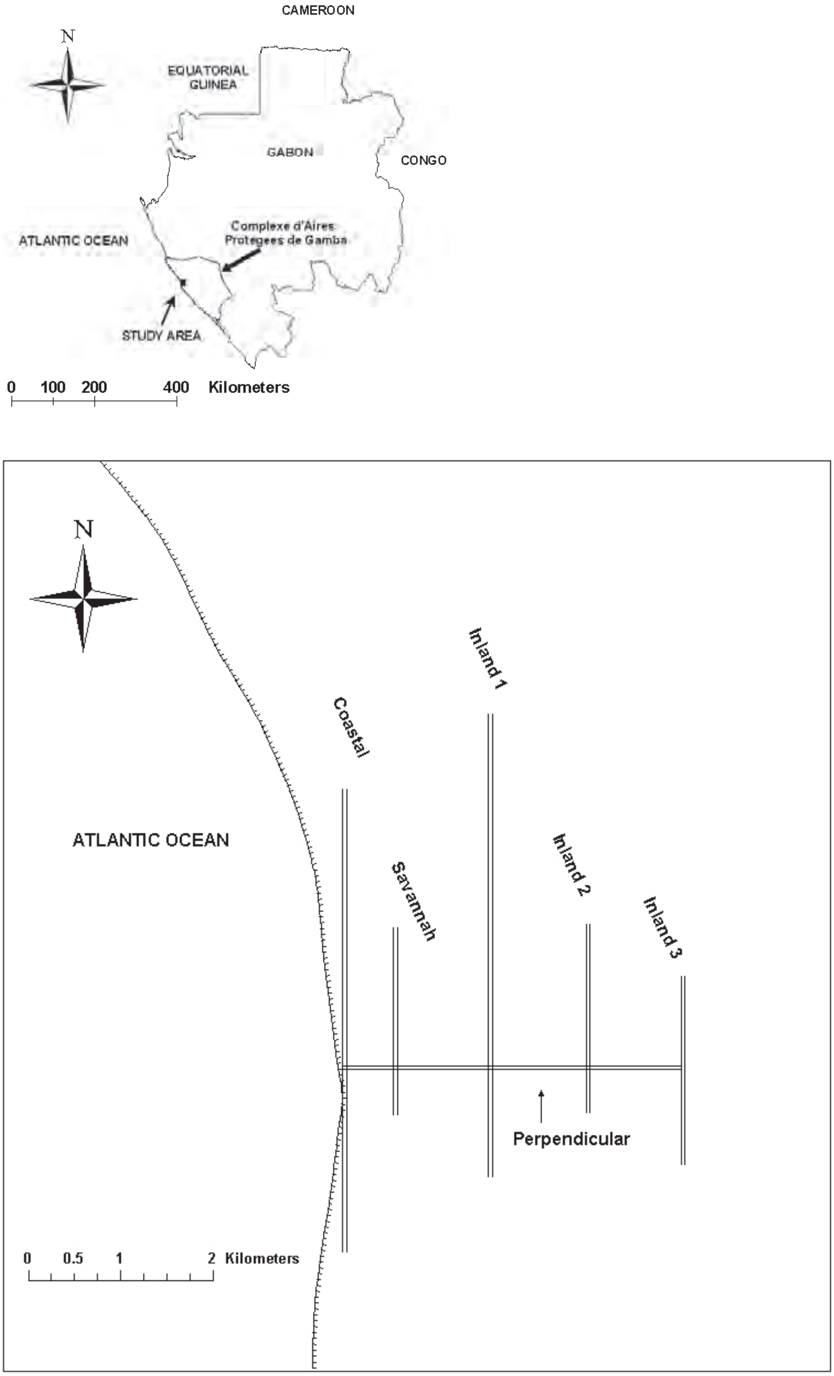

FIG. 1. Study area.

each ran through a mosaic of closed- and open-canopy forest, small areas of secondary forest as swampy 'marecage' areas. Mono-dominant *Sacoglottis* forest spanned approximately 1 km along inland transect 1.

It is not assumed that the vegetation of the coastal study site is representative of the vegetation within the Reserve as a whole. However, the Gamba Complex vegetation map (Ministère des Eaux et Forêts et du Reboisement, 1998) indicates a similar diversity of habitat types throughout the Reserve.

In order to determine habitat types within the study area and along each transect, habitat category was subjectively assigned to each 50 m point along all transects to best represent the immediate environment of the point. Some habitats are obviously distinctive (e.g. sandy beach as compared to closed canopy forest), others were more difficult to assign to category (e.g. closed canopy versus open canopy forest). This is inevitable since any zonal classification is by its very nature continuous, not discrete. However, categorising the environment is essential where, for example, differential use of habitat types by animals is the major emphasis of a study, as was the case in this work. Most of the categories are based on vegetation structure and in some cases a distinctive flora. None of the sample points were situated on the sandy beach.

The ten categories used were:

Treeless coastal scrub: predominantly grassy coastal scrub with low, scattered bushes of *Phoenix reclinata*, *Eugenia fernandopoana* and *Barteria sp.*

Tree covered coastal scrub: cover present (although not necessarily continuous) and a high density of shrubs and small trees to approximately 3 m in height.

Savannah: dominated by low grasses, rarely more than 25 cm in height. Some savannahs seem to be in the process of recolonisation by *Sacoglottis gabonensis*, having swathes of young trees up to around 3 m in height.

Open canopy forest: the height of the canopy is usually between 12 m and 18 m, and light reaches the forest floor as a result of an incomplete foliage cover (judged to be less than 70%). This usually results in lower visibility at the ground level due to the vigour of fast-growing ground shrubs and saplings within the understorey.

Closed canopy forest: here there is a high degree of visibility at the ground level, the canopy tends to be high (over 20 m) and less light falls directly onto the forest floor as a result of canopy cover assessed as more than 80%.

Single-species forest: in the study area the species was *Sacoglottis gabonensis*, a fast-growing species thought to be a pioneer species of reclaimed savannah (e.g. White, 1992), dominating forest along approximately 1 km of the inland 1 transect.

Disturbed forest: the canopy is rarely more than 8 m high, and consists of a tangle of small trees, shrubs and lianas. It may occupy the site of an ancient or recent tree-fall area.

Secondary forest: this vegetation type is distinctive since it is the product of a large-scale destructive event (clearance for a helicopter landing pad) during the mid 1960s and has developed uniformly since. This has led to fairly homogeneous regrowth throughout the area, characterised by a number of distinct species such as *Psydrax subcordata*. Only 118 m of the inland 1 transect is dominated by this vegetation type (corresponding to a surveyed vegetation area of 590 m^2).

Marecage: this is defined as a 'marshy area' and varies from a seasonally flooded area to a constantly wet habitat where certain species thrive, such as *Anthostema aubryanum* and *Mitragyna ciliata*. As such, although the classification 'marecage' does not directly indicate a distinctive flora, the adaptations required by plants in order to exist under such extreme environmental conditions often render it a distinct vegetative category. A few of the coastal marecage areas were occasionally brackish, but the majority throughout the site were fresh water.

Water: permanent flowing or standing water, most often in the form of a permanent brackish lagoon. No rooted plants were present.

To sample species composition along the total of 19.85 km transect length, all individual trees and lianas ≥ 10cm dbh (diameter at breast height)) within a five metre strip, 2.5m either side of the transect line (an area of 9.825 ha) were tagged, identified, and dbh measured (White, 1992; Williamson, 1993; Powell, 1999). The lower limit cut-off allowed for the inclusion of large saplings and some rooted lianas, while excluding younger saplings. Dbh was measured at approximately 1.3 m from the ground. If stilt roots (e.g. *Uapaca* species) or buttresses (e.g. *Pterocarpus soyauxii*) were present, measurements were taken above root level. For trees with multiple large trunks, each was considered separately and the basal area for each stem summed.

All trees and lianas of uncertain identity (the vast majority) within the 9.825 ha sampling area were tagged at the start of data collection to allow reference collections to be made if and when the plant came into flower or fruit. Identifications were made *in situ* from various documented characteristics, such as the overall tree form, bark characteristics, the presence, consistency odour and colour of latex, as well as vegetative and reproductive parts. Leaves, flowers and fruits of each species were collected where possible and lodged with the National Herbarium in Libreville. Identifications were made at the Royal Botanic Gardens, Kew.

3 Results

The most similar transects in terms of perceived vegetation type were the inland 2 and inland 3 transects. The coastal and savannah transects were the most different, despite their proximity, suggesting increasing habitat homogeneity with distance from the sea.

Of the 3943 stems of ≥ 10 cm dbh enumerated, 24 individual lianas and 12 individual trees were not named since no specimens were obtained and other characteristics were not definitive. These were allocated an identification number. These 36 individuals (representing 0.91 % of the total sample) comprise a total basal area of 1.752 $m^2 ha^{-1}$ (trees 1.371 $m^2 ha^{-1}$; lianas 0.38 $m^2 ha^{-1}$). Of the remaining 3907 individuals, positive identifications to taxonomic level of family or above were made for 3831. Thus 76 individuals (23 species) remain to be identified to family or higher level, and account for 1.93% of the total sample size. The 3907 identified stems represent 115 species, 95 genera and 40 families (Table 2).

4 Discussion

There are several directly comparable plant community studies throughout the tropics that have furnished data using methods similar to these. Within central Africa, data are available from Gabon (the Lopé Reserve – e.g. Makokou – Hladik, 1978; Reitsma, 1988; Williamson, 1988; White, 1992; and several localised sites), from Cameroon (Powell 1999) and from the Central African Republic (Carroll, 1996). Since

TABLE 1. Stem density, basal area and species richness at tropical forest sites for stems ≥ 10 cm dbh.

Study	Site	Plot size sampled (ha)	N individuals		N spp		Basal area
			plot^{-1}	ha^{-1}	plot^{-1}	ha^{-1}	(m^2 ha^{-1})
This study	Coastal transect	2.5	634	385 ‡	41	29	24.0
	Savannah transect	1	291	291	36	36	27.3
	Inland 1 transect	2.5	1032	411 ‡	83	53	32.8
	Inland 2 transect	1	623	623	57	57	41.3
	Inland 3 transect	1	552	552	56	56	46.0
	Perpendicular transect	1.825	811		70		
White 1992	Lopé, Gabon	2.5 × 5		304–468	84–163	33.6–65.2	29.6–40.0
Williamson 1993	Lopé, Gabon	1				56	39.4
Reitsma 1988	Lopé	1	396	396	69	69	35.8
	Oveng	1	497	497	131	131	36.4
	Doussala	1	425	425	109	109	35.7
	Ekobakoba (all Gabon)	1	438	438	85	85	42.9
Hladik 1978; 1982; 1986	Makokou, Gabon	427	92	35			
Powell 1999	Douala-Edéa, Cameroon	2.5 × 5	1046–1707	418–683	131–204	52.4–81.6	26.7–180.3
Gartlan *et al.* 1986 **a**	Korup Forest Reserve, Cameroon	0.64		471	75		
Carroll 1996	Dzanga-Sangha (logged), C.A.R.	5.0	669.4	61.5	46.6		
	(unlogged)	2.5		738.5		33.2	49.8
Bernhard-Reversat *et al.* 1975	Côte d'Ivoire						32
Struhsaker 1975; 1997 **b**	Kibale, Uganda					36	
Eggeling 1947	Budongo, Uganda					39	
Gentry 1982	Neotropics			167–1947			
Korning & Balslev 1994	Cuyabeno Reserve, Ecuador	1.0	697	697	313	313	
Proctor *et al.* 1983	Malaysia			678			
Brunig 1983	Pantropical mean						33

‡ for standard 1 ha sections (see Chapter 2)
a Mean of 135 plots (40,668 trees, 411 spp.)
b Greater than 9 m tall (≈ ≥ 13 cm dbh)

no significant botanical collections have ever been made at the Petit Loango Reserve, evaluation is still in the preliminary stages. Several new species have probably been collected during this study (Cheek, pers. comm.), e.g. the largest-fruited *Magnistipula* species (Chrysobalanaceae) which appears to be dispersed by elephants. The need for further collections and study is obvious. The nature of the vegetation changes with distance from the sea and the number of distinctive habitats, together with the fresh-, salt- and brackish- water habitats not discussed here, suggests that permanent legal protection for the Reserve could and should be argued for on botanical terms as well as on zoological grounds.

The most important ecological characteristic of tropical rain forests is their wealth of plant and animal species (Richards, 1996). While inland areas may be comparable to other Central African sites in terms of species richness per hectare in the size class studied (Table 1), it is evident that the coastal and savannah transects have a relatively poor floral composition. In comparison to the Neotropical regions and Asia, all of the African sites have low species diversity, although individual sites may show comparable species richness. It has been suggested (Richards, 1973) that the relative species poverty of some parts of the African rainforest compared to those forests of the Americas and the eastern tropics result from a relatively recent origin of the African forest, which has spread from the refugia to which it was confined during the dry periods of the late Pleistocene. The relative aridity of the continent (e.g. Axelrod & Raven, 1978) and recent human influences may also contribute to this lower species richness in the size class studied. However, although overall floristic diversity in African forests appears to be lower than that on other continents, the number of species in small sample plots may be comparable (e.g. White, 1992), perhaps reflecting differences in local site characteristics rather than the species diversity of the region as a whole. In primary lowland rainforest, the number of species in the size class studied can vary between 60 and 150 species ha^{-1}, though in certain parts of South America and Malaysia it can exceed 300 species ha^{-1} (Table 1).

Of four 1 ha plots assessed by Reitsma (1988), that with greatest species richness was situated in the Monts de Crystal, east of Petit Loango, believed to be a Pleistocene forest refuge (Bourlière, 1973). All five of Powell's (1999) transects in south Cameroon were situated in a postulated Pleistocene forest refuge and he cites this as the major reason for the high diversity encountered. Rainfall is also thought to explain differences in species richness (Wright *et al.*, 1993), with Swaine and Hall (1986) identifying low rainfall as the single most important environmental variable determining floristic composition in Ghana. They found that species richness was highest in the wetter forests, although tree heights were maximal at intermediate rainfall levels (between 1250 and 1750 mm per annum), suggesting that the decline in canopy height in higher rainfall areas was due to poor soil quality due to leaching. The lowest species richness encountered by Reitsma was at Lopé, and he suggested that a combination of unfavourable soil conditions and rainfall reduced species diversity. At Petit Loango, there is extreme seasonality of rainfall (Morgan, 2001) and very sandy, porous soil. The main cause of low tree species richness at this site may lie in the relatively recent geological origin of this area coupled with poor soil conditions and extreme environmental conditions near to the coast.

Interestingly, although the Gabonese coastal forest is supposed to be characterised by *Aucoumea klaineana*, (e.g. Caballé, 1978) this species was not present in the study site, and no young saplings were evident. This may have been due to the high level of logging activities in the past, which has affected around 80% of the Reserve (Ministère des Eaux et Forêts et du Reboisement, 1998; Walsh & White, 1999). This species,

TABLE 2. Tree and liana checklist and density of species ≥ 10 cm dbh in the 9.83 ha sample area.

Family	Life form	ID number	Total # trees	Total	Density (stems ha-1) Coastal transect	Savannah transect	Inland 1 transect	Inland 2 transect	Inland 3 transect	Perpendicular transect
Acanthaceae										
Thomandersia laurifolia (T.Anders) Baill.	T	221	11	1.12	4.4	0	0	0	0	0
Agavaceae										
Dracaena cf. congoensis Hua.	T	326	1	0.10	0	0	0	0	1	0
Anacardiaceae										
Fegimanra africana Pierre	T	241	11	1.12	4	0	0	0	0	0.55
Trichoscypha acuminata Engl.	T	305	5	0.51	0	1	0.8	1	1	0
Annonaceae										
Hexalobus crispiflorus A.Rich.	T	251	22	2.24	0	0	5.2	3	2	2.19
Uvaria baumannii Engl. & Diels	L	163	34	3.46	2.8	0	2.8	7	4	4.93
Uvariastrum pierreanum Engl. & Diels	L	48	80	8.14	0	2	12	7	12	15.89
Xylopia aethiopica A.Rich.	T	180	3	0.31	0	2	0.4	0	0	0
Xylopia quintasii Engl. & Diels	T	277	60	6.11	2	3	12	10	7	2.74
Apocynaceae										
Landolphia pyramidata (Pierre) Persoon	L	236	2	0.2	0	0	0	1	1	0
Rauvolfia vomitoria Afzel.	T	301	2	0.20	0	0	0.4	1	0	0
Burseraceae										
Canarium schweinfurthii Engl.	T	90	1	0.10	0	0	0	1	0	0
Dacryodes sp.	T	257	25	2.54	0	0	10	0	0	0
Celastraceae										
Salacia sp. L	146	4	0.41	1.2	0	0	0	0	0.55	
Chrysobalanaceae										
Chrysobalanus icaco L.	T	35	40	4.07	2.4	28	2	0	0	0.55
Ebenaceae										
Diospyros abyssinica (Hiern) F.White	T	9	16	1.63	0	0	2.4	5	3	1.10
Diospyros cf. deltoidea F.White	T	152	20	2.04	0	0	0.4	1	13	2.74
Diospyros dendo Welw. ex. Hiern	T	109	47	4.78	1.2	3	12.4	4	0	3.29
Diospyros polystemon Gürke	T	230	145	14.76	2	29	25.2	12	18	9.86
Diospyros zenkeri (Gürke) F.White	T	231	1053	107.18	0.4	1	81.2	298	191	196.71
Erythroxylaceae										
Erythroxylum mannii Oliver	T	21	20	2.04	0	0	4.4	2	0	3.84

TABLE 2. continued.

				Density (stems ha-1)						
Family	**Life form**	**ID number**	**Total # trees**	**Total**	**Coastal transect**	**Savannah transect**	**Inland 1 transect**	**Inland 2 transect**	**Inland 3 transect**	**Perpendicular transect**
Euphorbiaceae										
Anthostema aubryanum Baill.	T	270	226	23	19.6	55	13.6	19	29	21.92
Elaeophorbia cf. drupifera (Thonn.) Stapf	T	32	7	0.71	2.4	0	0	1	0	0
Erythrococca welwitschiana (Muell.Arg.) Prain	S	223	3	0.31	1.2	0	0	0	0	0
Macaranga monandra Muell.Arg	T	269	10	1.02	0	0	1.2	2	4	0.55
Manniophyton sp.	T	338	4	0.41	0	0	0	0	4	0
Phyllanthus cf. delpyanus Hutch.	T	117	20	2.04	0	0	2.4	3	8	1.64
Ricinodendron heudelotii Baill.	T	286	4	0.41	0	0	0.8	1	0	0.55
Sapium ellipticum (Hochst.) Pax.	T	156	16	1.63	0	0	4.4	0	3	1.10
Spondianthus preussii Engl.	T	141	5	0.51	0.4	1	0	0	0	1.64
Uapaca guineensis Muell.Arg.	T	271	10	1.02	0.8	1	0.4	1	5	0
Flacourtiaceae										
Calancoba glauca (P.Beauv.) Gilg.	T	188	1	0.10	0	0	0	0	0	0.55
Casearia barteri Mast.	T	200	3	0.31	0	0	1.2	0	0	0
Homalium cf. letestui Pellegrin	T	233	29	2.95	0	0	4	11	4	2.19
Scottelia coriacea A.Chev.	T	151	50	5.09	0	0	3.6	12	15	7.67
Guttiferae										
Garcinia sp.	T	114	207	21.07	0	0	3.6	88	70	21.92
Harungana madagascariensis Choisy	T	274	1	0.10	0	0	0	0	1	0
Symphonia globulifera L.	T	325	1	0.10	0	1	0	0	0	0
Humiriaceae										
Sacoglottis gabonensis (Baill.) Urb.	T	309	132	13.44	3.6	35	28.4	2	2	7.12
Irvingiaceae										
Irvingia gabonensis Baill.	T	302	102	10.38	0	0	18	19	14	13.15
Irvingia grandifolia Engl.	T	203	1	0.10	0	0	0	0	0	0.55
Klainedoxa gabonensis Pierre	T	308	20	2.04	0	1	2.8	4	3	2.74
Leguminosae										
Afzelia bella Harms	T	254	1	0.10	0	0	0.4	0	0	0
Anthonotha macrophylla P.Beauv.	T	243	76	7.74	0	2	14.8	3	4	16.44
Baikiaea insignis Benth.	T	172	17	1.73	0	0	6.8	0	0	0
Baphia cf. buettneri Harms	T	142	42	4.27	3.6	19	2	3	0	3.29

TABLE 2. continued.

					Density (stems ha-1)					
Family	**Life form**	**ID number**	**Total # trees**	**Total**	**Coastal transect**	**Savannah transect**	**Inland 1 transect**	**Inland 2 transect**	**Inland 3 transect**	**Perpendicular transect**
Baphia sp.	T	298	10	1.02	4	0	0	0	0	0
Berlinia bracteosa Benth.	T	248	45	4.58	0	0	10.8	1	7	5.48
Craibia sp. 1	T	137	1	0.10	0	1	0	0	0	0
Craibia sp. 2	T	185	4	0.41	1.6	0	0	0	0	0
Dialium sp.	T	321	2	0.20	0	0	0	0	2	0
Didelotia cf. africana Baill.	T	171	11	1.12	0	0	4.4	0	0	0
Erythrophleum ivorense A.Chev.	T	115	1	0.10	0	0	0	0	0	0.55
Gilbertiodendron demonstrans (Baill.) J.Léonard	T	184	64	6.51	0	2	3.2	5	37	6.58
Guibourtia tessmannii J.Léonard	T	318	2	0.20	0.4	0	0	0	0	0.55
Librevillea klainei Hoyle	T	267	1	0.10	0	0	0.4	0	0	0
Lonchocarpus sericeus (Poir.) Kunth	T	199	1	0.10	0.4	0	0	0	0	0
Millettia sp.	T	158	37	3.77	0	0	8	1	6	5.48
Parkia bicolor A.Chev.	T	173	1	0.10	0	0	0.4	0	0	0
Pentaclethra macrophylla Benth.	T	119	1	0.10	0	0	0.4	0	0	0
Pterocarpus soyauxii Taub.	T	175	2	0.20	0	0	0.8	0	0	0
Loganiaceae										
Anthocleista nobilis G.Don.	T	324	2	0.20	0	2	0	0	0	0
Malvaceae										
Hibiscus tiliaceus L.	S	93	7	0.71	0.8	4	0	0	0	0.55
Melastomataceae										
Memecylon memecyloides Exell.	T	139	6	0.61	0	6	0	0	0	0
Meliaceae										
Entandophragma angolense (Welw.) C.DC.	T	27	7	0.71	0	0	0	4	2	0.55
Khaya ivorensis A.Chev.	T	303	5	0.51	0	0	0	4	0	0.55
Trichilia sp. 1	T	280	1	0.10	0	0	0	1	0	0
Trichilia sp. 2	T	246	131	13.33	0	0	34.4	16	9	10.96
Trichilia sp. 3	T	283	13	1.32	0	0	4.4	0	0	1.10
Moraceae										
Ficus sp.	L	268	2	0.20	0	0	0.4	0	1	0
Myrianthus arboreus Beauv.	T	336	1	0.10	0	0	0	0	1	0

TABLE 2. continued.

Family	Life form	ID number	Total # trees	Density (stems ha-1)						
				Total	Coastal transect	Savannah transect	Inland 1 transect	Inland 2 transect	Inland 3 transect	Perpendicular transect
Myristicaceae										
Coelocaryon cf. preussii Warb.	T	340	1	0.10	0	1	0	0	0	0
Pycnanthus angolensis (Welw.) Exell.	T	310	9	0.92	0	1	2	1	1	0.55
Staudtia gabonensis Warb. (var. 1)	T	304	11	1.12	0.8	0	1.6	1	0	2.19
Staudtia gabonensis Warb. (var. 2)	T	242	7	0.71	0	0	0.8	1	0	2.19
Myrtaceae										
Eugenia cf. staudtii Engl. & V.Brehm	T	105	371	37.76	128.4	36	0.4	0	0	7.12
Syzygium guineense (Willd.) DC.	T	36	49	4.99	12.4	10	0	0	0	4.38
Olacaceae										
Coula edulis Baill.	T	311	7	0.71	0	0	0.8	2	1	1.10
Diogoa zenkeri (Engl.) Exell & Mendonça	T	255	4	0.41	0	0	0.8	0	2	0
Ongokea gore (Hua) Pierre	T	313	1	0.10	0.4	0	0	0	0	0
Strombosia grandifolia Hook.f.	T	96	53	5.39	0	0	4.4	9	12	11.51
Palmae										
Hyphaene guineensis Thonn.	T	317	7	0.71	2	0	0	0	0	1.10
Pandaceae										
Panda oleosa Pierre	T	306	8	0.81	0	1	0.4	3	3	0
Passifloraceae										
Barteria sp.	T	104	57	5.80	16.4	11	0.8	0	0	1.64
Barteria fistulosa Mast.	T	328	9	0.92	0	0	2.4	0	2	0.55
Rhamnaceae										
Maesopsis eminii Engl.	T	167	1	0.10	0	0	0	0	0	0.55
Rhizophoraceae										
Rhizophora racemosa G.Mey.	T	315	2	0.20	0.4	1	0	0	0	0
Rubiaceae										
Coffea canephora Pierre	T	19	31	3.16	0	0	3.2	3	7	7.12
Dictyandra cf. *involucrata* (Hook.) Hiern	T	292	3	0.31	0	0	1.2	0	0	0
Heinsia crinita (Afz.) G.Tayl.	T	290	17	1.73	5.2	0	0.8	2	0	0
Massularia acuminata (G.Don) Bullock	T	334	1	0.10	0	0	0	1	0	0
Mitragyna ciliata Aubr. & Pellegr.	T	312	12	1.22	1.2	2	0.8	0	4	0.55
Psydrax moendensis Bridson	T	138	6	0.61	0.4	5	0	0	0	0

TABLE 2. continued.

Family	Life form	ID number	Total # trees	Total	Density (stems ha-1)					
					Coastal transect	Savannah transect	Inland 1 transect	Inland 2 transect	Inland 3 transect	Perpendicular transect
Psydrax subcordata Bridson	T	145	32	3.26	0	0	12.8	0	0	0
Rothmannia macrocarpa De Wild.	T	34	7	0.71	0	0	2	0	0	1.10
Tarenna cf. pavettoides Gaertn.	T	291	3	0.31	0	0	1.2	0	0	0
Unknown	T	247	1	0.10	0	0	0	1	0	0
Unknown	T	249	1	0.10	0	0	0.4	0	0	0
Sapindaceae										
Eriocoelum macrocarpum Gilg	T	177	31	3.16	0	0	6.8	6	3	2.74
Placodiscus cf. caudatus Pierre	T	359	3	0.31	0	0	0	0	3	0
Unknown	T	322	1	0.10	0	0	0	0	0	0.55
Sapotaceae										
Chrysophyllum sp.	T	323	1	0.10	0	1	0	0	0	0
Manilkara cf. obovata Sabine & G.Don	T	197	1	0.10	0	1	0	0	0	0
Manilkara lacera (Baker) Dubard	T	39	24	2.44	8.8	0	0	0	0	1.10
Manilkara sp. 1	T	314	21	2.14	8	0	0.4	0	0	0
Manilkara sp. 2	T	133	1	0.10	0	0	0.4	0	0	0
Tieghemella africana Pierre	T	179	1	0.10	0	0	0	0	0	0.55
Scytopetalaceae										
Scytopetalum pierreanum Pierre	T	192	2	0.20	0	0	0	1	1	0
Simaroubaceae										
Hannoa klaineana Pierre	T	237	3	0.31	0	0	0	3	0	0
Sterculiaceae										
Cola cf. ballayi Cornu	T	319	14	1.42	0	0	2	1	4	2.19
Unknown	T	320	11	1.12	0	0	2	3	1	1.10
Tiliaceae										
Grewia coriacea Mast.	T	281	11	1.12	0	0	0	9	1	0.55
Ulmaceae										
Celtis tessmannii Rendh.	T	50	1	0.10	0	0	0.4	0	0	0
Verbenaceae										
Avicennia nitida Jacq.	T	316	2	0.20	0.8	0	0	0	0	0
Vitex doniana Sweet	T	71	25	2.54	4.4	10	0.4	0	0	1.64

TABLE 2. continued.

					Density (stems ha-1)					
Family	**Life form**	**ID number**	**Total # trees**	**Total**	**Coastal transect**	**Savannah transect**	**Inland 1 transect**	**Inland 2 transect**	**Inland 3 transect**	**Perpendicular transect**
Violaceae										
Rinorea sp.	T	273	16	1.63	0	0	2	5	3	1.64
Vitaceae										
Cissus cf. dinklagei Gilg. & Brandt	L	82	6	0.61	0	0	0	0	4	1.10
Unknown										
Unknown	L	159	1	0.10	0	0	0.4	0	0	0
Unknown	T	160	1	0.10	0	0	0.4	0	0	0
Unknown	T	162	1	0.10	0	0	0	0	0	0.55
Unknown	T	165	1	0.10	0	0	0	0	0	0.55
Unknown	T	166	25	2.54	0	0	4.8	4	1	4.38
Unknown	T	235	1	0.10	0	0	0	1	0	0
Unknown	T	239	2	0.20	0	0	0.8	0	0	0
Unknown	T	250	1	0.10	0	0	0.4	0	0	0
Unknown	T	252	1	0.10	0	0	0.4	0	0	0
Unknown	T	258	1	0.10	0	0	0.4	0	0	0
Unknown	T	288	11	1.12	0.8	0	2	1	2	0.55
Unknown	L	294	2	0.20	0.8	0	0	0	0	0
Unknown	T	295	2	0.20	0	0	0.4	0	1	0
Unknown	T	335	1	0.10	0	0	0	1	0	0
Unknown	L	350	1	0.10	0	0	0	0	0	0.55
Unknown	T	351	1	0.10	0	0	0	0	0	0.55
Unknown	L	352	4	0.41	0	1	0.8	0	1	0
Unknown	L	354	5	0.51	0.4	1	0	1	2	0
Unknown	L	355	4	0.41	1.6	0	0	0	0	0
Unknown	L	356	4	0.41	0	0	0.8	0	2	0
Unknown	L	357	2	0.20	0	0	0	0	2	0
Unknown	T	358	1	0.10	0	0	0	0	1	0
Unknown lianas	L		24							
Unknown trees	T		12							

Life form: T – tree; L – liana; S – shrub.

however, was frequently seen in the Sounga area, approx. 15 km inland (pers. obs.), despite large-scale selective logging in that area in the past (T. Mbouga, pers. comm.). It may be that *Aucoumea klaineana* (and several other species that were not present in the coastal study area) are poor competitors at distances close to the sea due to environmental stresses or possible ecological competition with other species better adapted to the extreme conditions.

Petit Loango is rich in lianas: 3.4% of individual stems throughout the study site were lianas, composing 0.6% of the total basal area and included a minimum of 15 species (10.3% of the total stem species). Lianas have been categorised as an early successional guild of pioneer species (e.g. Hegarty, 1989; Dewalt *et al.*, 2000). Gentry (1982) noted that liana diversity increased directly with species diversity in the Neotropics, at approximately 20% of the trees species diversity, although liana stem density was relatively constant for all communities that he sampled. At Oveng, in the species-rich Monts de Crystal, Reitsma (1988) calculated 2.4% of individual stems ≥ 10 cm dbh were lianas (approximately 6% of species). The importance of lianas may be better estimated in terms of leaf weight; at Lopé, lianas contribute less than 5% to the total forest leaf biomass (Harrison, 1984, cited in Williamson, 1993), and at Makokou, Hladik (1974) calculated it as 36% of the total forest leaf biomass.

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THE IMPORTANCE OF CLOSED AREAS FOR THE NATURAL REGENERATION OF *BOSWELLIA PAPYRIFERA* (DEL.) HOCHST. IN ETHIOPIA

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Abstract

The population of *Boswellia papyrifera* (Burseraceae), a dryland tree species known for the production of frankincense, is declining. This paper attempts to evaluate the effectiveness of closed areas on the natural regeneration of the species in northern Ethiopia. The distribution of seedlings with respect to mature trees at four sites is analysed. Two of the sites were closed for livestock grazing since 1994 whereas open grazing is practiced at the other two sites. Cutting down trees is not allowed at any of the four sites. Data were collected from sixteen plots (each 20 m × 20 m) at the four sites. The results show that there is a significant improvement of natural regeneration in closed sites and that regeneration is mainly concentrated within a radius of two metres from mature trees. Higher mortality rate (>90%) of seedlings was recorded in the sites where open grazing is practiced. The study shows that protection from livestock grazing is essential for the growth and survival of seedlings of *B. papyrifera*. The use of closed areas is an effective way of promoting natural regeneration of this important but declining species.

Résumé

La population de *B. papyrifera*, un arbre de zones sèches, connue pour la production d'Oliban erythrée est en diminution. Cet article évalue l'effet des enclos sur la régénération naturelle de cette espèce au nord de l'Ethiopie. La distribution des plantules et plantes adultes fut analysée dans quatre sites. Deux des sites furent clôtures éliminant le bétail depuis 1994, pendant que les deux autres sites contiennent du bétail. La coupe des arbres n'est pas autorisée sur les quatre sites. Les données furent collectées a 16 différentes locations (chacune 20 m sur 20 m) dans chaque site. Les résultats montrent une amélioration significative de la régénération naturelle dans les sites clos, et celle-ci est principalement concentrée dans un rayon de deux mètres autour des arbres adultes. Des taux de mortalité des plantules plus élevés (>90%) furent enregistrés dans les sites avec bétail. Cette étude démontre que l'exclusion du pâturage est essentielle à la croissance des jeunes plants de *B. papyrifera*. La création de zones clôturées est une manière d'augmenter la régénération naturelle de cette importante espèce en déclin.

Key words: *Boswellia papyrifera*, closed area, Ethiopia, natural regeneration, Tigray

1 Introduction

Boswellia papyrifera (Del.) Hochst. (Burseraceae) is the main source of Ethiopian frankincense in the world market. Frankincense has great value since ancient times in religious worship and for medicinal purposes. It is burnt in many churches throughout the world, and is also used as raw material in the perfume, pharmaceutical, paint and paper industries. In addition, *B. papyrifera* in Ethiopia provides various products and services including fuelwood, construction material, livestock fodder, bee keeping, medicinals and the rehabilitation of degraded lands (MUC, 1996; Tilahun, 1997). However, *B. papyrifera* is reported to be in critical condition and needs priority in the conservation of wildlife resources of Africa (Marshall, 1998). The natural stock of this species throughout this area is decreasing due to extensive farming, overgrazing, fire, poor incense harvesting practices, shifting cultivation, termites and other insect infestations (MUC, 1996; Tilahun, 1997; Ogbazghi, 2001; Wubalem *et al.*, 2002). Some efforts are now underway to rehabilitate degraded forests in northern Ethiopia including the closure of degraded sites to protect them from livestock grazing and human encroachment. This paper attempts to evaluate the effectiveness of closed areas[1] on the natural regeneration of the species in northern Ethiopia.

2 Materials and methods

The study was conducted in Tigray, northern Ethiopia (13°14'–13°42'N, and 38°38'–39°02'E). The altitude varies from 1400 to 1650 m a.s.l. The dominant soil types are Cambic Arenosols and Chromic Cambisols; Leptosols are also found. The land is flat but hemmed in by surrounding mountains from which rivers descend. Limestone, schist and mixtures of these are the dominant parent materials found at the study sites. The study area has a mean annual rainfall of 657 mm and a mean annual temperature of 22.3°C. It has a tropical climate with a long dry season of 9 months. The natural vegetation, generally classified as ''Ethiopian undifferentiated woodland'' under the Sudanian regional centre of endemism (White, 1983), is dominated by the following tree species: *Anogeissus leiocarpa*, *Balanites aegyptiaca*, *Boswellia papyrifera, Combretum collinum*, *Lannea schimperi* and *Lonchocarpus laxiflorus.*

The study was undertaken at four sites. The first two sites are closed for livestock while open grazing is practiced at the other two sites. Cutting down trees is not allowed in any of the four sites. In terms of trees $\geq$ 10 cm dbh, Site I has a basal area of 7.52 m^2/ha and density of 311 per ha, Site II has a basal area of 8.22 m^2/ha and tree density of 383 per ha, Site III has a basal area of 6.93 m^2/ha and density of 280 per ha and the Site IV has a basal area of 4.58m^2/ha and 139 per ha. Sixteen plots with a size of 20 m × 20 m (0.25 ha) were randomly selected in each of the sites. In all plots, seedlings were

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[1] The use of the term "closed areas" throughout this study refers to the management intervention of setting degraded lands aside with the exclusion of human and livestock interference in order to promote natural regeneration (Kindeya, 2003).

counted three times: in July 2001 (wet season), October 2001 and January 2002 (dry season). Counted saplings were subdivided into two size classes, i.e. newly emerging seedlings with a height of less than 30 cm ('*juvenile*') and established seedlings between 30 cm and 130 cm height and less than 10 cm diameter ('*saplings*'). Distances of each seedling to the nearest mature tree was measured and grouped into three classes, within 2 m, 2–5 m and 5–10 m. Differences in terms of seedling density and mortality in the three distance classes among the four were determined using analysis of variance (Anon., 1995).

3 Results and discussion

3.1 The natural regeneration of *Boswellia papyrifera*

The results in this study (Figs. 1 & 2) showed that *B. papyrifera* was producing sufficient juveniles to sustain its population in the natural environment and had no problems of seed germination despite some worries in earlier reports (e.g. TFAP, 1996; MUC, 1996). Seed dormancy of the species has been investigated in the laboratory (Tilahun & Legesse, 1999), which showed that there is little or no seed dormancy in *B. papyrifera*. Hence, probably due to immediate germination after dispersal, *B. papyrifera* does not accumulate long-lived seeds in the soil (Wubalem *et al.*, 2002). In this regard, the major regeneration route will be the formation of a seedling-sapling bank under the forest canopy. Dispersed seeds would immediately germinate followed by establishment and growth of seedlings into saplings, and eventually grow into mature trees. Therefore, the rehabilitation of *B. papyrifera* forests through natural regeneration depends greatly on conditions after germination. Itoh *et al.* (1997) underlined the fact that the conditions just after germination are generally critical for seedling survival in tropical forests. Any factor that interferes in any of the development phases after germination, such as fire, grazing, trampling or clearing, could hamper or completely eliminate the chances of natural regeneration (Wubalem *et al.*, 2002).

Significant improvement of natural regeneration of *B. papyrifera* was obtained in closed areas (Sites I and II) as compared to freely grazed areas (Sites III and IV) (Figs. 1 & 2). Cattle grazing can change the floristic composition of a vegetation type, therefore, protection from various biotic disturbances such as from livestock grazing has clearly contributed to the higher number of seedlings in closed areas. The stems of the seedlings of *B. papyrifera* are succulent, and hence preferred by browsing and grazing animals. The germination of *Boswellia* is epigeal (Ogbazghi, 2001), which makes it vulnerable to grazing and trampling. Grazing on *B. papyrifera* seedlings results in the total removal of all above-ground vegetative parts, which makes survival difficult. The higher survival rate in saplings as compared to juveniles indicates that the effect of livestock is generally more deleterious on juveniles.

Improvement of natural regeneration through closed areas is also observed in other regions. A study in eastern China has recommended closed areas as an effective measure for developing forest cover on the Qilian mountains because of a remarkable improvement of regeneration (Yaoshan *et al.,* 1999). Namdeo *et al.* (1989) reported a higher number of plant seedlings and recruitment rate over 2–3 years in closed areas as compared to adjacent open forest areas in Madhya Pradesh, India. Ogbazghi (2001) also showed that seedling establishment of *B. papyrifera* is better in protected areas and those inaccessible to livestock in Eritrea. However, this does not mean that there are no other factors influencing the regeneration of *B. papyrifera.* Even if there is the need to address other factors that influence natural regeneration of *B. papyrifera,* the

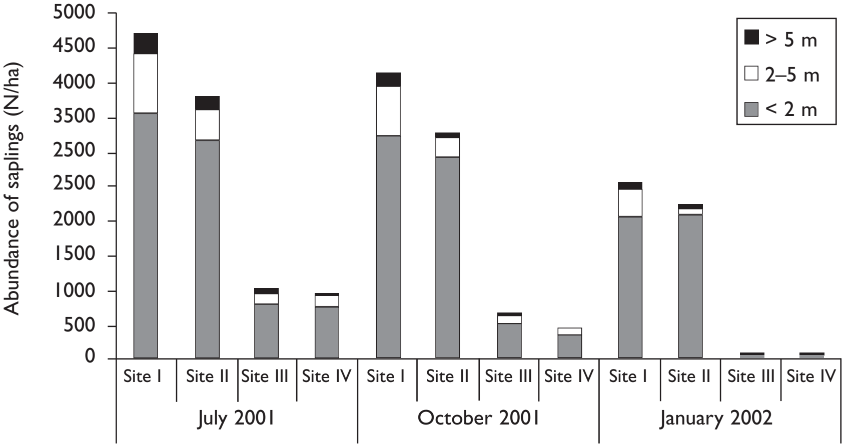

FIG. 1. The density and distribution of juveniles (< 30 cm height) at different distance classes at each site in July 2001, October 2001 and January 2002 in northern Ethiopia.

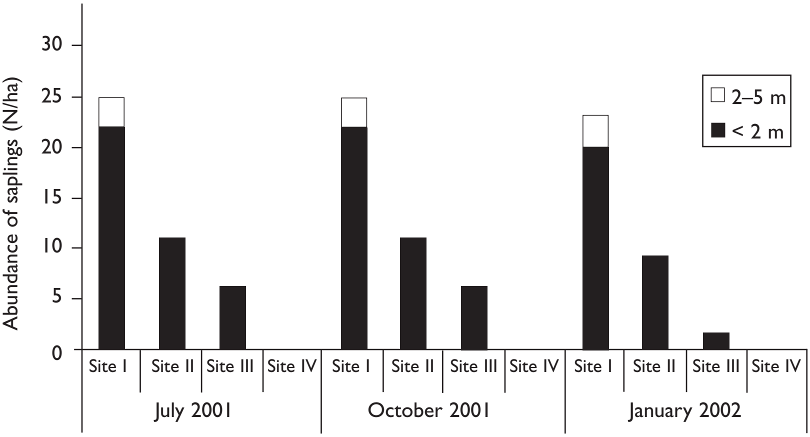

FIG. 2. The density and distribution of saplings (30–130 cm height) at different distance classes at each site in July 2001, October 2001 and January 2002 in northern Ethiopia.

advantages of promoting natural regeneration through closed areas are well recognized. A study revealed that local people were more willing to participate in closed areas for natural regeneration than in community plantation programmes due to the lower labour requirement and visible positive changes in the former and lower seedling survival in the latter (MUC, 1996).

3.2 The spatial distribution of natural regeneration

According to the ANOVA ($P<0.05$) and subsequent mean separation using the Tukey HSD test (Anon., 1995), a significantly higher number of juveniles (at $P<0.05$) are concentrated within 2 m distance from the mother trees as compared to those juveniles counted in the other two distance classes. The distribution of juveniles in each of the distance categories was also analyzed in terms of their percentage of the total number of juveniles in each plot. In all the three counts, the same trend was revealed. There was a significant difference in the percentages of juveniles as a proportion to the total of juveniles in each plot among the distances from adult tree. In July 2001, 77%, 17% and 6% of the juveniles were distributed within 2 m, 2–5 m and 5–10 m of the adult tree respectively. In October 2001 the corresponding figures were 80%, 17% and 3%. In January 2002 these were 77%, 15% and 3% (Fig. 1).

Similarly, there was a significant difference in terms of density of saplings among distance classes. There were no saplings recorded in any distance categories of the 16 plots at Site IV and no saplings were recorded at the 5–10 m distance class at Site I. Saplings were found only within 2 m distance at Sites II and III. (Fig. 2). In terms of proportion, 92.6% and 7.4% (in July 2001), 92.3% and 7.7% (in October 2001), 90.9% and 9.1% (in January 2002) of seedlings were found within 2 m, and between 2 m and 5 m, respectively (Fig. 2).

The occurrence of seedlings is a pre-requisite for the formation of a seedling bank in natural regeneration of forests. Such knowledge can provide insight into processes affecting the distribution of plants (Hamill & Wright, 1986). Moreover, their spatial distribution is important for the design of management strategies, optimisation of stock, and site utilisation. Among juveniles, more than 77% were concentrated within a 2 m distance of adult trees, whereas the remaining 17% and 16% were found at 2–5 m and 5–10 m distances respectively. The same pattern was also observed in saplings. The results of this work are consistent with other similar studies. Condit *et al.* (1992) found that the number of sapling recruits was greatest near the adult trees on Barro Colorado Island, Panama. The same results were also reported by Burkey (1994) in Mexico. In 15 out of the 30 common species in the dry forest of Costa Rica, the highest mean juvenile density occurred in the immediate vicinity of adult trees (Hubbell, 1979), who also observed that juvenile density decreased approximately exponentially away from adults. Condit *et al.* (2000) reported on the spatial patterns in the distribution of tropical species and also reached a similar conclusion. Lieberman & Li (1992) found higher seedling density under crowns than in “exposed open sites” in an African dry tropical forest.

There could be a number of possible causes, acting alone and/or simultaneously, that determine the spatial distribution of *B. papyrifera*. Seeds could be too heavy to be dispersed widely or the dispersing agents may not be active for some reason. *B. papyrifera* has a dehiscent fruit, which is a pseudocapsule (about 2 cm long) dividing into three valves with 3 hard seeds inside and an apical extension (Vollesen, 1989). Tilahun (1997) estimated that there are about 45,000 seeds of *B. papyrifera* per kg. Hamill & Wright (1986) indicated that poor seed dispersal and specialisation for particular habitats generally result in clumped distribution of adults and juveniles.

B. papyrifera trees are known to clump together. Patterns of seed dispersal result in initial distribution of juveniles, which are unlikely to be random. When seeds tend to fall near, rather than far, from their parents, the expected result is clumping of juveniles relative to both other juveniles and adults (Hamill & Wright, 1986). This might have a negative effect on the future growth of the seedlings. For a population with a low abundance like *B. papyrifera*, the rate of population increase may depend directly on the successful dispersal of seeds. Seeds that are not carried away from their source may later suffer high mortality from predation or intraspecific competition (Clark & Clark, 1981).

Shading does not seem to have a great impact on seed survival, germination and seedling establishment in *B. papyrifera.* It has been indicated that if seedlings need open conditions to survive and grow into saplings, growth could be concentrated in less shaded sites, which are not under the mother trees (Hamill & Wright, 1986). However, *B. papyrifera* seedlings have access to light at all distances as the canopy is not closed in the study area. The soil conditions around the mother trees could be improved due to litter input, and can have an influence on the germination. Hubbell (1979) has pointed out the fact that the distance at which the density of juveniles is the maximum is not necessarily the distance with the highest probability of eventually producing an adult. Condit *et al.* (2000) have reported that aggregation becomes weaker in large diameter classes in dry forests of India and Thailand. This supports the notion that herbivores and plant diseases play a key role in reducing aggregation around the adult tree. The results of seedling distribution in the present study should further be supplemented with soil seed bank studies in order to pinpoint the major causes for such spatial distribution.

3.3 The mortality of seedlings

The analysis of variance on the mortality of juveniles between July 2001 and January 2002 showed a significant difference among sites and distance classes. Site I had significantly (at $P<0.05$) lower mortality statistically (50.1%), followed by Site II (63%), whereas Site III and Site IV had high juvenile mortality rates of 94% and 91.2%, respectively. The difference between mortalities in Sites III and IV was not statistically significant. These results showed that mortality is significantly reduced in closed sites while there was high mortality in the open grazing sites. Based on reduced mortality, it can be stated that closure was more effectively implemented in Site I as compared to Site II. This was also observed during fieldwork. In terms of spatial distribution, there was significantly (at $P<0.05$) higher mortality of juveniles found between 5 and 10 m away (85%), followed by those between 2 m and 5 m away (76%) and those within 2 m distance from adult trees of *B. papyrifera* (64%).

The results of analysis of variance for the mortality rate of saplings between July 2001 and January 2001 indicate that there was no difference in terms of mortality rate among sites (Site I = 6.25%, Site II = 6.25%, Site III = 18.75%). Mortality rate was generally low in saplings as compared to juveniles. Site IV had no recorded saplings at all in July 2001, and, therefore, mortality could not be calculated for it.

The present results do not agree with the Janzen-Connell model of density and/or distance-dependent mortality of seedlings (Janzen, 1970; Connell, 1971). Janzen (1970) predicted higher juvenile mortality in close proximity to adult crowns because of host specific seed predators, pathogens, or herbivores, which normally feed on adults. Other studies (e.g. Hubbell & Foster, 1990; Condit *et al.*, 1992; Burkey, 1994; Condit *et al.,* 1994; Okuda *et al.*, 1997), however, reveal that such relationships depend on the species, canopy position, the condition at the site and the existence of

TABLE 1. Mean and SE of mortality of seedlings and saplings of *Boswellia papyrifera* between July 2001 (rainy season) and January 2002 (dry season) in northern Ethiopia.

Sites	**Distance from nearest mature tree (m)**	**Mortality (%)**	
		Juveniles (≤30 cm height)	**Saplings (30–130 cm height)**
I	≤ 2m	36.6 ± 3.4	6.3 ± 6.3
	2–5 m	48.0 ± 4.2	0
	5–10 m	65.6 ± 8.5	0
II	≤ 2m	32.2 ± 3.0	6.3 ± 6.3
	2–5 m	72.2 ± 4.0	0
	5–10 m	84.8 ± 4.4	0
III	≤ 2m	93.8 ± 1.2	18.8 ± 10.1
	2–5 m	91.4 ± 3.0	0
	5–10 m	96.7 ± 2.4	0
IV	≤ 2m	92.5 ± 1.1	No observation
	2–5 m	93.53 ± 2.0	No observation
	5–10 m	87.50 ± 8.5	No observation

herbivores or pathogens that cause mortality. Hubbell (1980) argues that distance-dependent mortality requires very good seed dispersal and/or a very efficient predator. Hence, depending on the circumstances of each species, regeneration may take place through clumping close to, over-dispersing or perhaps clumping away from adult trees (Hamill & Wright, 1986). Clark & Clark (1984) found that interactions between adults and juveniles were unimportant in early mortality of *Dipteryx panamensis* in Costa Rica. Seedling abundance in nature depends on the availability of viable seeds. A large proportion of seeds reaching the ground are usually destroyed by insects or become infected by fungi. About 18–25% of the bulk seeds of *B. papyrifera* collected in Ethiopia and Eritrea were found to be affected by insects (Tilahun & Legesse, 1999; Ogbazghi, 2001). However, abundant seedling proliferation (up to 4500 seedlings/ha) indicated that there is no notable influence of such insect attack on the overall germination. The challenge for natural regeneration is on providing better growing conditions for seedlings into saplings and then into mature trees. Mortality among germinants is high and the growth rates of seedlings can be extremely low. In this regard, the seedling density in different months provides an insight into the development of seedlings into saplings. Significant variation in the mortality rate of the seedlings in open grazing and closed sites demonstrates the fact that the lack of growth into saplings is highly influenced by external factors such as grazing.

There was high mortality even in closed sites (>50%), highlighting the existence of other factors in addition to livestock grazing. Bendz (1990) has suggested that severe defoliation coupled with drought may also lead to retarded growth, or ultimate death of young seedlings in Ethiopia. There might also be pests or other organisms, which could increase mortality of seedlings. Tilahun & Legesse (1999) reported that all transplanted seedlings of *B. papyrifera*, after a germination experiment in the laboratory, were eaten up by mice. This suggests that newly emerging germinants could also face the same fate in the field. Moreover, recruitment of seedlings into saplings can be limited due to interspecific competition. Such competition is likely to be intensified in environments with low water availability such as the present study area (Davis *et al.*, 1998). Hence, a high emergence of juveniles does not necessarily mean that natural regeneration is assured; the seedlings might be short lived. The overall low density in saplings warns us that the effort at ensuring *B. papyrifera* regeneration is far from sufficient.

4 Conclusions

The high level of natural regeneration is a good indicator of the effectiveness of closed areas. To this effect, not only was seedling density enhanced but mortality of naturally regenerated seedlings of *Boswellia papyrifera* was also significantly reduced. This shows that *B. papyrifera* can easily regenerate in its natural environment when livestock grazing, which is detrimental to the growth and survival of its seedlings, is excluded. Hence, providing protection for regenerated seedlings is an immediate task for rehabilitating the species in northern Ethiopia. However, this does not presuppose the absence of other factors interfering with natural regeneration. Long term demographic studies on seedling growth and survival are necessary in order to fully analyse other factors of seedling mortality. More studies are also equally important on the relative distribution of other species, mature-juveniles relationships, relationship between spatial patterns and light condition, soil seed bank and reproductive properties such as fecundity and seed dispersal patterns.

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INDIGENOUS TAXONOMY IN THE MOUNT CAMEROON REGION, CAMEROON

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Abstract

Scientific training on the naming of plants is based on the interpretation and analysis of information on plants that can be verified either through simple observation or by the use of some scientific laboratory devices. Scientists and tourists have realized that local people have a system of naming and grouping plants found in their locality while on the other hand, local people have recognised the essential role they play as information/service providers to the former. However, there has been a problem of communication between the two groups, which makes it imperative to look for ways to bridge this gap. This paper looks at some methods that have been used to understand and describe the processes that some local communities within the Mount Cameroon region use to identify and classify plants. As a result of this a local plant list is being developed to include local names alongside their scientific names with descriptions that can be used by both scientists/tourists and local people for a common understanding.

Resumé

Taxonomie indigène dans la région du Mont Cameroun, Cameroun. La formation scientifique à l'identification des plantes est basée sur l'interprétation et l'analyse des l'informations qui peuvent être vérifiées par la simple observation ou par l'utilisation de certains procédés scientifiques de laboratoire. Les scientifiques et les touristes se sont rendus compte que les communautés locales ont un système propre d'identification et de classification des plantes alors que d'un autre côté, les communautés locales ont reconnu le rôle essentiel que les communautés ruraux jouent en tant que fournisseurs d'information/de service aux premiers. Cependant, le problème de communication qui se pose entre les deux groupes rend impératif la recherche de moyens pour briser cette barrière. Cet article s'intéresse à des méthodes qui ont été utilisées pour comprendre et décrire le processus que certaines communautés locales de la région du Mont Cameroun utilisent pour identifier et classer les plantes. Le résultat repose également sur le processus de développement d'une liste locale de plantes qui regroupe les noms vernaculaires, les noms scientifiques ainsi que des descriptions qui peuvent être utilisées tant par les scientifiques/touristes que par les communautés locales.

Key words: Cameroon, indigenous taxonomy, local knowledge, Mount Cameroon, local names

1 Introduction

The interest of the Environmental Research Programme (ERP) project discussed in this paper was to find ways to facilitate communication. The project looked at scientific knowledge and indigenous knowledge and examined ways to bridge the gap between the two.

Scientific knowledge

In the past there was a tendency for conservation and environment authorities to be concerned only with scientific information – this applies as much to plant information as to anything else. Based on this, most resource management and policy decisions were for a very long time been made by scientists and politicians based on their knowledge and needs. However, there has been increased concern regarding global environment protection after the holding of the biggest ever environment conference in Rio de Janeiro in Brazil in 1992. The adoption of Agenda 21 on the development and implementation of ways to manage and develop mountain environments sustainably is particularly relevant to our study area, Mt Cameroon. This conference was attended by governments, scientists and policy-makers world-wide who emphasized the need for the involvement and participation of the local populations in forest conservation and management.

A lot of scientific training is based on the interpretation and analysis of information, relating one thing to another in order to solve problems and also to study similar situations in other parts of the world.

Local knowledge

Local people base local knowledge on direct experience over time through involvement, reflection and discussion. In typical local settings, this knowledge is embedded in people's cultural value system and affects their beliefs and attitudes towards forest management practices. Whether we like it or not, it has come to a point that we must recognise that local or culture based systems are valuable and important especially in addressing the problems of development and involvement. This is because local knowledge has built over time, shaping tradition, on the basis of people's everyday experiences over generations. They have in their own way been observing and adapting, developing ways of interacting to enable them to maintain a livelihood in their environment.

Linking knowledge paths

In contemporary times, people have come to realise that knowledge is not just information and ideas originating in Western science and academic sources. They are now starting to appreciate that indigenous cultures around the world have their own sciences and that we need to find ways to bridge the gap between the two.

The objective of the exercise on which the presentation is based is to "develop methods to produce plant identification manuals that are easy to use and understand, and to be used by local communities to support participatory resource conservation in countries like Cameroon". It was not intended to produce manuals but to find out the best ways to produce them.

2 Background

This paper is based on the DFID (R7112 Environmental Research Programme) – ERP Bangor funded project that was run by the University of Wales, under the management of Dr. John Healey and Dr. John Hall with Dr. Jenny Wong as field co-ordinator. The work here reflects the work of output one of the project, which was, "Improved methods for the development and extension of tools for indigenous identification of plants, particularly to support participatory approaches". Those directly concerned with this phase were Bianca Ambrose (Research assistant, Wye College at the time); Penny Fraser (Research assistant, Bangor at the time); Dr. Anna Lawrence (Lecturer, University of Reading at the time). Other collaborators included Dr. William Hawthorne of the University of Oxford.

The Limbe Botanic Garden, Cameroon was the overseas partner and had Dr. Nouhou Ndam (Conservator & Research Co-ordinator at the time) as direct supervisor of trainees (Rita Lysinge, Stella Asaha, Joyce Atemacha, Princewill Tamon and Ndive Elias) for field work. Other Cameroon Partners included Dr. Manfred Bissong of IRAD Ekona, Dr. Foucho Derek of Dchang University and Dr. Caleb Nebane of the University of Buea. The work was done in close collaboration with the Mount Cameroon Project (MCP), Limbe and four local communities: Bakingili, Bwassa, Ekona Lelu and Boa Balondo, located on Mount Cameroon.

The following sections will look at the methods that were used in output one, some observations and results. We did not know the best way to find out how people perceive their environment, nor how to work how these compare or relate to the scientific idea of biodiversity. Therefore we wanted to explore the best ways to explain things, and to compare and relate the information that different stakeholders use. It was hoped that by doing so, we would be able to understand and communicate local perceptions of biodiversity, and ways to combine these perceptions with those of scientists, in order that local communities will have a stronger voice in the negotiation of natural resource management plans and conservation interventions.

3 Methods

3.1 Sampling of communities

The selection of villages for the research was done in collaboration with the staff of the former Mount Cameroon Project (MCP)/The Limbe Botanic Garden who had been working in the area for several years. It took into consideration the following criteria

- The duration of the project, such that the number of communities selected will just be enough to fit into the timeframe.
- The location of communities in relation to project objectives, in such a way that they reflect the characteristics of the projects' interest.
- Exposure of communities to research activities; that they are willing to collaborate with strangers.
- Present activities in communities, to avoid conflicting interest with other institutions presently working in the area, and that they are not saturated with research.
- Climate, to include communities with high altitude/dry; low altitude/wet regions so we have a fair representation of the all habitat and landscape characteristics of the region.

Based on the above criteria, the following villages were selected: Bwassa, Ekona Lelu, Bakingili, Boa Balondo.

3.2 Selection of user groups

The project considered the variation of the different activities that are going on in the forest environment within the region. It was obvious that people had particular interest in the use of their environment so it was therefore important to group participants according to their specific interest. Based on this we came up with the following user group categories: hunters, herbalists, farmers, timber exploiters, and wrapping leaf/NTFP (non timber forest product) collectors.

3.3 Participant selection

In each of the four communities we worked with 25 participants. Selection of these participants was drawn from a household map done a few days earlier by trainees selected for the project execution. The following criteria were used in the selection:

- Age, to make sure that the views of the old and young were represented
- Sex, to include both men and women
- Wealth status, to include both the rich and the poor
- User group. It was important to get a fair representation of all the different local forest actors (hunters, herbalists, farmers, timber exploiters, and wrapping leaf collectors) so participants selected had to belong to one of these.

3.4 Use of different techniques

Penny Fraser and Bianca Ambrose developed four different methods for the study, known to us as: the Forest walk (also known as the student-teacher exercise), the Venn diagram, the Recognition test, and the Triadic test.

3.5 Methodology refinement workshop

We saw a need to organise a methodology refinement workshop prior to the field activities. During the workshop, the exercises to be done were presented and a list of suitable plants suggested and village representatives were asked to comment or add to it. This was held at the Limbe Botanic Garden with two participants each from the selected communities. A pilot study was conducted for all the exercises to be conducted after which the whole team discussed the practicalities and adopted the best ways of going about the research proper.

3.6 Village workshops

Village workshops were then organised as the first step of the study to serve as a sensitisation exercise. Books were displayed - manuals for the identification of plants, animals, birds etc. This was done two weeks prior to the start of field activities to create awareness and to get participants prepared.

The field work began with community meetings involving selected participants and some village notables to present a reminder of the project objectives based on the sensitisation exercise held earlier. During the briefing, a fair description of what the work would entail was presented to the participants following by a question and answer session. A work programme was then adopted by the whole team and respected by all.

Method 1: Forest walk

On the day of the activity, a short briefing session was held. This was meant to remind participants of what we planned to do. At the end of the discussions, participants were asked to discuss amongst themselves and identify a route to be taken by the group to walk through such that each participant will be able to select a plant of their choice and describe it to the rest of the group.

The route started off from the closest point to the village to the furthest that the group could reach after dividing into two separate groups taking different directions. We called this the student/teacher exercise and in the process, the participants were expected to say those characters and/or other factors that they would use to identify the plant. As we walked along the path, participants looked around and stopped others as soon as they found a plant they felt comfortable enough to describe to the group. We asked participants to pretend as if they were describing the plant to someone or assume that they were sending a child, or anyone, to go and find the plant. During this activity, participants were encouraged to describe the differences between similar plants e.g. a plantain and banana. This they did well, with emphasis on the distinguishing factors.

As they went on with their description, the rest of the group listened attentively and asked questions at the end based either on points for clarification, or to add characters not mentioned that they themselves found to be important.

At the end of the exercise, the staff wrote out on flip charts the characters that participants used and asked them to rank the list according to the most important characters when identifying plants. This was done as a group exercise by each user group in order to come up with the most important characters used as well as the number of characters used by the different groups.

Method 2: Venn diagram

This was a village-based exercise. The botanic team went out early in the morning to collect a variety of plant specimens from the forest and from around the village for the activity. Each specimen had duplicates for herbarium collection.

The specimens were put together and participants were asked to group the plants according to how they thought they should be classified together. They gave their reasons for the different groups that they came up with after arranging them into as many groups as they were able to come up with.

Like the Forest walk exercise, a discussion session was held at the end to identify the most important characters used as well as the number of characters used by the different groups.

Method 3: Recognition test

Plant specimens were placed in groups of three and participants asked to group them in twos and ones based on similarities and differences, and also to state their reasons; these were then recorded by the staff. Unlike the Venn diagram exercise that had a lot of leaf specimens, the specimens in this case were mostly of seeds/fruits, bark and stem.

Like the Venn diagram method, ranking was done at the end during a discussion session per user group, to extract the characters used and also to obtain the number of characters used by each of the different user groups.

Method 4: Triadic test

As in the Venn diagram method, botanists collected duplicates of 20 plant specimens from within the village and forest. Unlike the Venn diagram method, these plants were put into groups of three. With an explanation from the research team, each participant was asked to separate each group into two and one. The two were expected to be similar and different from the one. The reasons for each separation was recorded for each by the research team.

Participants worked in groups of threes and had to agree amongst themselves as to which specimens were similar and which different from the third.

As in the previous exercises, ranking was done per user group to get the most characters used and also the number of characters used by the different user groups.

FIG. 1. Participants during the triadic test with a staff member (R.L.) recording their discussion.

4 Results and discussions

We shall in this section look at the characters that participants came up with during the various exercises, some observations and interesting results.

We were interested in developing methods for collecting this kind of information, methods that could be used here and in other places. In the process of testing the methods, we learned about how plant experts on Mount Cameroon (local people) identify plants. To some extent, this was secondary information, information collected "en route" to our main objective. But it is valuable information, and helps in the global objective of increasing the understanding between knowledge domains.

The results showed that the most useful exercise in all communities was the Forest walk – the teacher/student role-playing exercise. It is therefore the most recommended of the methods developed. It gives participants the opportunity to freely describe their views as much as they can, and also helps the staff to appreciate those descriptions that local people find difficult to do using appropriate words.

For exercises that need to be done in the village and involve the collection of plant specimens from the forest, the specimens should be collected so as to avoid withering, as the specimens when withered are difficult to identify. It should also be kept brief as participants easily become bored when it takes a long time to complete the exercise.

4.1 Forest walk

The following are characters that were used by participants during the forest walk:

- Leaf – leaf shape was a very striking feature to most participants, especially for those plants that had very distinctive shapes. However, they were also very particular on the following factors; leaf colour, smell, taste, texture, and special characters like the presence of hairs and the size of the leaf
- Stem – stem colour was frequently used. They also used the shape, texture, smell, and the presence of special characters like spines/thorns
- Latex – although the colour of the latex was important to them, they said this was common to a group of plants and therefore it was necessary to examine the texture of the latex and see if it was viscous or not, whether the colour changes after a while, and the taste as well
- Roots – some plants were selected because of their conspicuous root shapes.

4.2 Venn diagram

Reasons given for grouping by participants in this exercise were:

- Utility – it was common to see participants group plants because of the use they have for it. Amongst this was the following; that it is used as food/fruit, medicine to cure sickness, spiritual/cultural occasions, fuelwood species, timber used for construction etc.
- Habitat – it was important to some participants to classify plants together because they grow in similar habitats. Therefore plants growing e.g. in primary forest, secondary forest, swamp, farmland or savannah were grouped together.
- Habit – what it looks like. They grouped them together as shrubs, herbs, big trees, climbers etc.

4.3 Recognition test

Reasons given for grouping by participants in the recognition tests were:

- Shape – they considered whether it was round, pointed, rough etc.
- Texture – soft, hard, flaky
- Utility – fruits, medicine etc.

4.4 Triadic test

Reasons given by participants for separating the specimens in the triadic test were:

- Utility – what is it used for: food/fruit, medicine, cultural significance etc.
- Leaves – shape, colour, taste, smell
- Stalk – shape, colour, length
- Slash – colour, texture
- Habitat.

4.5 Results in terms of local identification knowledge

A hundred and eleven different characters were used in total. Surprisingly only 21% were used in all of the four villages. Timber exploiters used the most characters and herbalists the fewest.

We found that user groups have more in common than members of the communities, i.e. timber exploiters in Boa Balondo have more in common with timber exploiters in Bakingili than they do with herbalists or hunters from the same village. This means that it may be better to make separate identification manuals to meet the needs of the timber exploiters as opposed to the herbalists, for example.

Habit and utility were the most important characters, but it varied between user groups. Habit was most important for timber exploiters, utility for hunters. Other groups used both, but less often. Herbalists used leaf characters a lot. Flowers were only important for spice collectors and herbalists. Timber exploiters look at the stem most often, hunters rarely use stems for identifying plants.

Timber exploiters frequently use the active characters that can only be detected – seen or smelled – after action, e.g. cutting of the stem to see latex or wood. Other groups also use such characters – herbalists 27% of the time, as a second character, and hunters 64% of the time, as the third character.

Tactile characters – detected by touch, e.g. softness, were used by all except timber exploiters.

Herbalists had most in common with formal taxonomists.

The grouping exercise provided information on how people classify or group plants. There were differences between user groups. The major grouping criteria were things that could be seen. Utility was used 20% of the time. The results suggest that guidebooks arranged according to plant use may be useful.

We have described, and now have a better understanding of, the processes that indigenous people use to identify and classify plants. We have identified differences between user groups, which appear to be based on utility, or the relationship that users have with the plants that they know. The process of the plant identification employed by indigenous plant identification experts makes frequent use of methods analogous to mnemonics, used for remembering (mnemonics are rhymes or little systems we use to help ourselves remember).

The learning process used by indigenous experts is different to that of the formal taxonomist. That of the first is based on direct experience of the plants in their environment.

4.6 Results in terms of methods developed

The sensitisation materials (posters and leaflets) used in this project were useful in preparing people's minds for the village exercises. The period between distribution of sensitisation material and the activity should be between two days and one week for the greatest impact.

When books were displayed for the identification of plants, animals, birds etc. during the village workshops, sometimes the local experts did not recognise the plants being described in the books, when in fact they were species that they knew very well. When we discussed this everyone realised that the pictures in the books were of parts of the plants that taxonomists use when they identify that plant, but that local people do not pay attention to. Local people use and notice other characteristics of the plant. This emphasised the point that we all know the same plants, but we look at them differently, and use different names for them – that if we want to communicate about the plants that we know, we need a way to bridge the gaps between our language and perceptual differences.

During the methodology refinement workshop, the species participants suggested were familiar to everyone present, but we had to discuss, debate and draw pictures before understanding that the participants all were referring to the same plant. For example, the plant called "lisengi" in Bakweri, was called "wokumbo" in Balondo, "*Musanga cecropioides*" by taxonomists, "weed" by foresters and "umbrella stick" in Pidgin.

The use of the methodology refinement workshop prior to the activity was particularly successful. It provided a forum for dialogue and exchange between project participants from different backgrounds, enabling the research team and community participants to contribute to the testing and refinement of ideas, methods and ways of interpretation.

The sensitisation and refinement workshops could therefore be used in other places, to illustrate the value of participatory identification manuals to people not used to books.

Venn diagram, Recognition test, Triadic test: sometimes participants found it difficult to group the plants because they were not sure of their identification of the plant. This was common with cases of similar plants as they needed other parts of the plant to differentiate the plants from each other.

Conclusions

Various problems were recognised during the course of the ERP fieldwork. For some of these solutions were developed and tested during the course of the research, other problems were not resolved at the time, but warnings have been included in reports and guidelines for other workers and recommendations made for ways to address these issues.

For example, problems were encountered in recording and translating local languages. It was realised that this task is not straightforward and requires linguistic skills not available to conservation project staff. It may therefore be advisable to consider using a linguistic expert in the future.

We found that participants most appreciated certain exercises not because they were interested in the exercise itself but, because it gave them an opportunity to discuss and share plant knowledge. The exercises provided a realization that they, the participants, knew a lot, and that their knowledge was valuable and interesting. It is important to promote this appreciation and respect for local knowledge, to encourage young people to absorb this knowledge, and for communities to insist that it is incorporated into environmental management planning.

A feedback workshop was organized in all participating communities and it became clear that participants wanted feedback on projects they contribute to; but this feedback must be well prepared, with key themes and topics well differentiated. It should be clearly presented. People find graphs easier to understand than text, graphs should be clear, and handouts brief. On the other hand, photographs are useful and well received. What we are trying to say here is that people appreciate explanation of how information from workshops is turned into graphs. The research team realized that a lot of information generated with little transformation can be used for community development, such as village maps, and can also be developed into teaching materials for schools. Such resources were appreciated especially when they contained local knowledge and information.

To conclude, many of the exercises were useful in the way they were applied on Mount Cameroon, i.e. as components of the workshop. The results show that the individual exercise in some cases confirmed the findings of other exercises, and in some cases provided unique information. They could therefore be used either on their own, or together, depending on the objectives of the work to be undertaken. Secondly, we realized that the learning process used by indigenous experts is different from that used by formal taxonomists. That of the latter is based on the theory that they use (plant systematics), for the former it is based on direct experience of the plants in their environment. The ideas generated by the ERP project are already being used and accepted as guidelines and recommendations for organizations producing participatory field identification manuals world-wide.

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THE IMPORTANCE OF EARLY SUCCESSIONAL SHRUBS FOR RECRUITMENT OF AFRICAN WILD OLIVE (*OLEA EUROPAEA* SUBSP. *CUSPIDATA*) IN CENTRAL TIGRAY, ETHIOPIA

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Abstract

Recruitment of a late successional tree species, African wild olive (*Olea europaea* subsp. *cuspidata*; Oleaceae), was examined in protected and grazed areas in the Geba river catchment of central Tigray, northern Ethiopia, using T-square plotless sampling. The following hypothesis was tested: recruitment of *O. europaea* is higher under certain early colonizing shrubs compared to within gaps and under other shrubs. Both in grazing land and protected areas, recruits were exclusively found under shrubs, predominantly under *Euclea racemosa*, although *Acacia etbaica* was dominant by far in all sampled land uses. Structural traits of shrubs explain this disparity. However, early results of further research suggest that *E. racemosa* shrubs probably act as preferential perching sites for frugivorous birds and that dispersal of *Olea* propagules is directed to dense *E. racemosa* shrubs with a high number of stems at ground level. The application of appropriate protection of early successional shrubs combined with simple silvicultural measures can therefore significantly enhance natural regeneration of indigenous woodlands in the region without having to rely on expensive plantation activities.

Résumé

Importance des arbustes pionniers pour le recrutement de l'olivier sauvage africain (*Olea europaea* subsp. *cuspidata*) dans le Central Tigray, Ethiopie. L'olivier sauvage africain (*Olea europaea* subsp. *cuspidata*; Oleaceae), qui apparaît tardivement dans la succession, a été examiné dans des zones protégées et pâturées du bassin de la rivière Geba dans le Central Tigray au nord de l'Ethiopie, sur base d'un échantillon T-square plotless. L'hypothèse suivante a été testée: le recrutement de *O. europaea* est plus important sous certains arbustes colonisateurs précoces que dans des clairières et sous d'autres arbustes. Tant en zone pâturée que dans des régions protégées, les recrûs ont été exclusivement trouvés sous des arbustes, principalement sous *Euclea racemosa*, alors que *Acacia etbaica* était de loin l'arbuste dominant dans tous les placeaux échantillonnés. Les différences de structure des arbustes expliquent cette disparité. Néanmoins, les premiers résultats des recherches suggèrent que *E. racemosa* agit préférentiellement comme perchoir pour les oiseaux frugivores et que la dispersion des diaspores de *Olea* est dirigée vers les peuplements denses de *E. racemosa*. Une protection appropriée des arbustes pionniers combinée à des mesures sylvicoles simples pourrait par conséquent accroître la régénération naturelle des forêts claires indigènes sans avoir à recourir à de coûteuses plantations.

Key words: Ethiopia, *Olea*, recruitment, shrubs, succession, wild olive

1 Introduction

The ability of rehabilitation areas to recruit and sustain new life forms is a true measure of their contribution to biodiversity and forest resource conservation (Tucker & Murphy, 1997). In Africa, relatively few studies have evaluated the effect of early colonizing shrubs on woody seedling establishment. Shrubs might facilitate, tolerate or inhibit different stages of tree establishment in abandoned pastures or croplands (Holl, 2002). Moreover, little is known about the specific consequences of avian seed-disperser activity and their interaction with perch and non-perch sites for plant demography (Rey & Alcántara, 2000).

Most research on the ability of trees and shrubs to promote recruitment of woody plants by attracting seed dispersers has been conducted in the temperate zones of the northern hemisphere, in the neotropics and in southeast Asia and tropical Australia (see McDonnell & Stiles, 1983; Guevara *et al.,* 1986; McClanahan & Wolfe, 1987; Guevara & Laborde, 1993; Parrotta, 1993; Debussche & Isenmann, 1994; Vieira *et al.,* 1994; Kollman & Pirl, 1995; Nepstad *et al.,* 1996; Tucker & Murphy, 1997; Holl, 1998; Ferguson & Drake, 1999; Toh *et al.,* 1999; Alcántara *et al.,* 2000; Galindo-Gonzalez *et al.,* 2000; Slocum & Horvitz, 2000; Holl, 2002), but Africa, and the Ethiopian highlands in particular, have received little or no attention so far (but see Duncan & Chapman, 1999).

It has been observed that seed rain of animal-dispersed trees was higher below shrub patches (Holl, 2002), scattered, isolated trees and saplings (Debussche & Isenmann, 1994; Duncan & Chapman, 1999; Toh *et al.,* 1999; Slocum & Horvitz, 2000), logs and fern patches (Slocum, 2000) and artificial perches (McClanahan & Wolfe, 1987; Holl, 1998) than below grass or in open pasture. On the other hand, predation of animal-dispersed seeds was found to be significantly higher below shrub patches compared with grass but then again, seedling survival was found to be higher under shrubs (Holl, 2002). The identity of trees or shrubs and whether or not they offer a fruit reward appears to matter less than their structure and suitability as a bird perch. The characteristics that make some trees or other structures better recruitment foci than others, however, are poorly understood (Slocum & Horvitz, 2000).

In Tigray, the northernmost, highly degraded region of Ethiopia, regrowth of woody vegetation in areas recently closed off to cattle (protected areas or grazing exclosures) is often striking. The recovery process of the vegetation usually starts with the increase in number and cover of grassy species. After some years shrubs and small trees develop and depress the grass component. These shrubs and trees are considered as a key element in forest rehabilitation since it has been shown that grasses present a competitive barrier against the establishment of woody species (Aide *et al.,* 1995). Moreover, grasses tend to attract cattle that may trample and consume recruits

(Slocum, 2000), even in protected areas where grazing is officially prohibited. The woody regrowth in Tigray, however, is often composed of early successional species, mainly from the genera *Acacia*, *Carissa*, *Dodonaea*, *Euclea*, *Maytenus* and *Rhus*. These shrubs are well known in the area for their valuable fuel wood, but not at all for their ability to promote natural forest regeneration.

In many tropical regions seed dispersal by animals is the predominant form of distribution of propagules and has the potential to facilitate recolonisation of native vegetation on degraded sites (Wunderle, 1997). Therefore, one approach to forest rehabilitation could be the plantation or protection of already established indigenous tree or shrub species that attract seed dispersing animals such as birds, which are still abundant in the Tigray highlands, and thus promote the dispersal of seeds from remnant forest patches into the forest rehabilitation areas. This paper discusses the importance of species and structure of early successional indigenous shrubs for recruitment of African wild olive (*Olea europaea* subsp. *cuspidata* (Wall. ex G.Don) Cif., Oleaceae) in protected and non-protected areas.

2 Materials and methods

Site description

The study was conducted in 250 ha of grazing land and protected area on south-west and north-east oriented slopes adjacent to the Dagaber Mheni and the Giorgis Sesemat church forests in central Tigray, northern Ethiopia (13°37'N, 39°21'E, 1980 m elevation). The site is located in the east of the Doga-Tembien district and has an annual rainfall between 550 and 600 mm.

Strips and larger areas of degraded natural vegetation between the various cropland patches are grazed and consist predominantly of grasses and the early successional shrubs typical of the area. In the protected area where logging and grazing is forbidden, larger saplings of *O. europaea* are sporadically present, but were not sufficiently mature to fruit during the study. The forest remnants around the churches of Mheni and Sesemat are respectively mixed *Acacia-Olea* (21 ha) and *Combretum-Olea* (12 ha) associations and serve as seed sources for the area under study.

Data collection

The following hypothesis was tested: recruitment of *O. europaea* is higher under certain early colonizing shrubs compared to within gaps and under other shrubs. Despite the expected higher seed predation and competition under these natural structures, some shrubs are believed to create microhabitats that enhance seedling survival by decreasing the risk of desiccation and predation by livestock and wild animals.

Recruitment of *O. europaea* was assessed in a four-month period (August – November 2002). Eight transects were randomly laid out over four different land use types (degraded grazing land [Gde], bushy grazing land [Gbu], spare grazing land, where grazing is allowed only after all other grazing resources are depleted [Gsp] and protected area, where cutting and grazing is prohibited [Fpa]). At equal intervals (50 m), modified T-square plotless sampling was applied to determine recent *Olea* recruitment densities. At each transect point, the distances from the transect point to the nearest recruit (sample point O), and from that sample to the nearest neighbour recruit (sample point N), were measured. Plotless sampling is typically applied to record sessile organisms that are so sparsely distributed that conventional sample plots are unsuitable (Sutherland, 1996). The technique combines the nearest-individual method with the nearest-neighbour method to limit under- and overestimation of densities in the case of regular or clustered distributions. In total, 44 transect points were sampled. Additionally, 10 × 10 m^2 sample plots were laid out around two randomly selected points in each transect to assess shrub layer species composition independently of presence or absence of *Olea* recruits.

The modification of the T-square method consisted of adding a third sample point S, the shrub nearest to the transect point, to the dataset. For all sample points (S, O and N), 23 shrub and environmental variables were assessed: dominant species of the structure (MainSp), secondary species (OtherSp), shrub height (Hperch), number of stems (Nstem), lower crown height (CHlow), height of largest crown diameter (CHbroa), shrub diameter at ground level (Dbase), mean crown diameter (Dcrown), crown density in lower (CDlow), middle (CDmid) and upper (CDup) part of the shrub, presence of raptor perches (RP), presence of human (DisturH) and animal (DisturC) disturbance, density of surrounding shrubs with spherical (PDb), open (PDo) and thorny (PDs) structure and density of *Aloe* spp. (PDa), shrub height relative to surrounding shrubs (PP), mean soil depth around the perch (Mdepth), presence of soil (Mound) and mulch (Mulch) accumulation, rockiness of the soil (Rock) and slope (Slope).

Statistical analysis

The relation between *Olea* recruit presence, shrub type and land use was analysed by means of categorical regression and one-way analysis of variance. Dominance-diversity curves were constructed and one-way analysis of variance was applied to compare the woody species composition between the different land use types. *Olea* recruit densities were derived from the T-square distance measurements (see Sutherland, 1996). One-way analysis of variance and Tukey's LSD were used to estimate the effect of land use on recruit density. Structural differences between perch types were evaluated by means of principal component analysis (PCA) to determine why some shrubs are better recruitment foci than others. Spearman's rank correlations (r_s) were used to correlate original variables with the principal components. PCA axis interpretation was based on the rotated component matrix (varimax with Kaiser normalisation) and eigenvector scores and was verified by means of Spearman's rank correlation.

3 Results and discussion

Olea recruitment

Within the chosen sampling strategy, not a single *Olea* recruit was found in the open field. The majority of recent *Olea* recruits was found under *Euclea racemosa* subsp. *schimperi* (A.DC.) White (Ebenaceae).

Recruit position was estimated by means of two categorical predictor variables: land use type and shrub species. Only shrub species affects the position of olive recruits significantly (F=9.175; P< 0.01).

These results imply that microhabitat or, in other words, the shrub or perch type defines the spatial distribution of recent *Olea* recruits on a micro-scale irrespective of land use. Multiple comparison of means after one-way analysis of variance showed that *E. racemosa* shrubs support three-quarters of all new *Olea* recruits (77.6%), and that the remaining fraction is found under *Acacia etbaica* Schweinf. (Leguminosae: Mimosoideae) (20.0%) and *Aloe* sp. (2.4%) (Table 1). Mean differences are significant at the 0.05 level. No *Olea* recruits were detected under the other shrub species in the study area (see list of genera in introduction). Estimated recruit densities were 15.27 ha^{-1} for bushy grazing land, 9.83 ha^{-1} for degraded grazing land, 4.82 ha^{-1} for protected area and 2.28 ha^{-1} for spare grazing land. These low densities justify the use of the plotless sampling method.

TABLE 1. Relative frequencies (%) of shrubs supporting recent *O. europaea* recruits per land use type and means over all land uses, based on T^2 plotless sampling in Mheni and Sesemat, Tigray, Ethiopia.

	Shrub species				
Land use[1]	No shrub	*Aloe*	*Acacia*	*Euclea*	Other shrubs
Gde	0.0	4.6	31.8	63.6	0.0
Gbu	0.0	5.0	15.0	80.0	0.0
Gsp	0.0	0.0	0.0	100	0.0
Fpa	0.0	0.0	33.3	66.7	0.0
All	0.0	2.4	20.0	77.6	0.0

[1] Land use types: **Gde**: degraded grazing land; **Gbu**: bushy grazing land; **Gsp**: spare grazing land; **Fpa**: protected area

The overall ratio of *Euclea* to *Acacia* shrubs supporting recent *Olea* recruits reaches more than three to one (3.25). Within individual land use types, the *Euclea/Acacia* ratio with new *Olea* recruits is 2.17 for degraded grazing land and 2.00 for protected area. In the bushy grazing land, this ratio rises to 4.00 (Table 2). For the spare grazing land this ratio could not be calculated since *Olea* recruits were exclusively detected under *Euclea*. If *Olea* recruits are randomly distributed over the shrub or perch pool, overall *Euclea* and *Acacia* shrub densities should have proportions similar to the above-mentioned 3.25 to 1 ratio. Alternatively, if *Olea* recruitment preferentially occurs under *Euclea* perches, the overall *Euclea/Acacia* ratio of the shrub pool should be less than the observed 3.25 to 1 fraction. In that case, recruits are not randomly distributed, and not dominance, but attractiveness or suitability of shrubs will cause *Euclea* to be a preferential recruitment focus.

Dominance-diversity curves of all land use types (Fig. 1) follow geometric series (*sensu* Gray, 1987) indicating strong dominance of one or few species. Pairwise comparison of shrub densities ($\alpha = 0.05$) confirms that *A. etbaica* shrubs are more numerous and dominate all land uses. Overall relative density of *A. etbaica* amounts to 45% as compared to 11% for *E. schimperi.* The general *Euclea/Acacia* ratio is 0.24 or almost 1 to 4 (Table 2).

These findings support the alternative hypothesis that *Olea* recruits are not randomly positioned under the available shrubs, but preferentially under the less dominant *E. racemosa* shrubs. The shrub ratio *Euclea* to *Acacia* harbouring *Olea* recruits divided by the overall *Euclea/Acacia* availability is proposed as a measure for the relative attractiveness of *Euclea* compared to *Acacia* for *Olea* recruitment. A value of 1 would indicate that *Olea* recruits are proportionally located over the available perches. Higher values indicate a preference for *Euclea*; values lower than 1 a preference for *Acacia.* The relative attractiveness of *Euclea* versus *Acacia* ranges from 14.8 in bushy grazing land to

TABLE 2. *Euclea/Acacia* ratios in different land use types and relative attractiveness of *Euclea* versus *Acacia* for *Olea* recruitment in Mheni and Sesemat, Tigray, Ethiopia.

		Land use				
		Gde	Gbu	Gsp	Fpa	Overall
Euclea/Acacia ratio	overall	0.10	0.27	0.45	0.13	0.24
	with *Olea*[1]	2.17	4.00	∞	2.00	3.25
		(n = 19)	(n = 20)	(n = 13)	(n = 15)	(n = 67)
Relative attractiveness		21.7	14.8	∞	15.4	13.5

[1] with *Olea* recruits under the shrubs

21.7 in degraded grazing land. The mean relative attractiveness of *Euclea* is 13.5 (Table 2). Contrary to the findings of e.g. Slocum & Horvitz (2000), the identity of the shrubs therefore appears to determine *Olea* recruitment.

Spearman's rank correlation (r_s) showed a high degree of autocorrelation among the shrub variables, which can be explained by the many mutual interactions between the various size parameters of the shrubs (size relationships). Fig. 2 shows the ordination of the sampled shrubs along the first two principal axes of the PCA; the first two principal components explain 41% of the initial variance in the dataset. The selected variables have the highest eigenvector scores (factor loading) and are significantly correlated to the principal axes at the 0.01 level.

The first (horizontal) axis represents a set of intercorrelated variables that distinguishes shrubs based on their number of stems, diameter at ground level, crown density, thorns and mulch characteristics under the perch. It clearly separates *Euclea* type shrubs (positive side) from *Acacia* types (negative side) (32% of the total variance). The second (vertical) axis can be interpreted as the shrub height component. Small shrubs that are lower than the surrounding vegetation are found on the negative side of the axis. Larger shrubs are found in the mid-range and tree-forms (high shrubs with crowns starting relatively high above ground level) at the upper positive side of the axis. This immediately explains the empty upper-right-hand side of the ordination diagram: multi-stemmed *Euclea* shrubs with a large diameter at ground level are restricted to the mid-range. *Euclea* shrubs that are developing to a tree form will lose some of the multi-stemmed character and become less broad at ground level – this implies a shift to the left over the first axis, which can also clearly be seen in Fig. 2.

Shrubs of the *Euclea* type are more suitable for *Olea* recruitment. Both in the small and mid-ranged types, *Olea* recruitment is present, whereas for the *Acacia* type, *Olea* recruitment is restricted to the mid-range. If shrub characteristics shift to the negative side of the second PCA axis (lower shrubs with crown starting near to ground level), *Acacia* type shrubs lose their suitability for *Olea* recruitment compared to *Euclea* types. This suggests that some characteristics of the latter type can compensate for the less

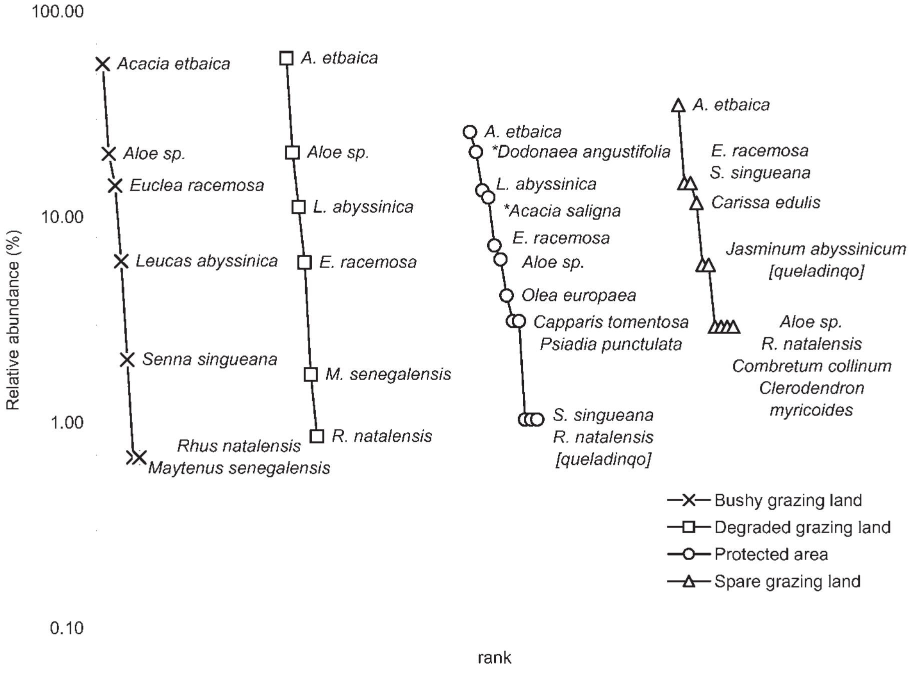

FIG. 1. Dominance-diversity curves for bushy grazing land (×), degraded grazing land (□), protected area (○) and spare grazing land (△). Asterisks (*) indicate shrubs planted in enrichment programs.

suitable characteristics of small shrubs. Although both mid-range size shrubs of the *Acacia* and *Euclea* type seem suitable, higher densities of recruits on the positive side of the first PCA axis suggest that here also, the characteristics of the *Euclea* type facilitate natural regeneration of *Olea.*

The accumulation of soil and organic matter under most of the *E. racemosa* shrubs could create favorable circumstances for olive germination and growth. Moreover, *E. racemosa* shrubs could offer more adequate seedling protection through numerous branches at ground level. However, early results of further research indicate that secondary dispersal, post-dispersal predation and seedling predation rates do not differ significantly between *Euclea* and *Acacia* shrubs (Aerts, unpublished data) and can therefore not explain the relative attractiveness of *Euclea* for *Olea* recruitment. Additionally, *E. racemosa* is a fleshy-fruited species, potentially offering a fruit reward to avian seed dispersers unlike the *Acacia.* This suggests that dispersal of *Olea* propagules is directed to dense Euclea shrubs with a high number of stems at ground level and as a consequence *Olea* recruitment is subject to passive facilitation by *Euclea.*

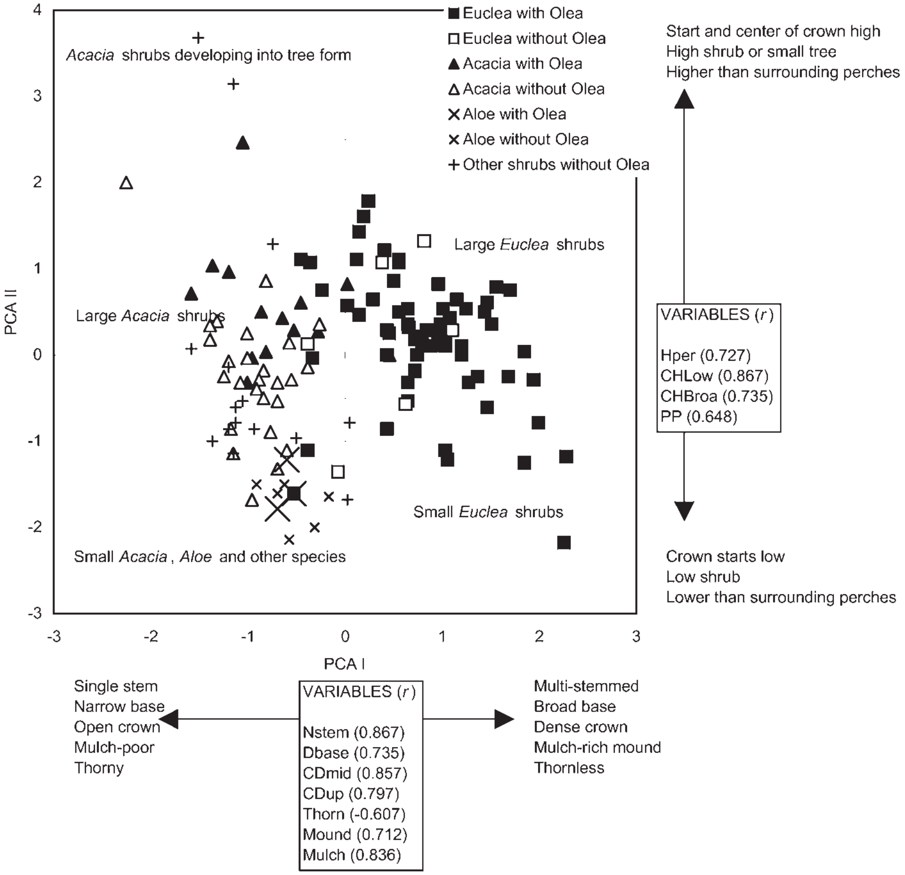

FIG. 2. Ordination of shrubs in central Tigray, Ethiopia, based on PCA. Perches are labelled with main species and presence or absence of *Olea europaea* recruit: *Euclea racemosa* with (■) and without (□) recruit; *Acacia etbaica* with (▲) and without (△) recruit; *Aloe* sp. with (✕) and without (×) recruit; other species (+) without recruit.

4 Conclusions

Dependence on animals for seed transport means that the plants are susceptible to dispersal failure when their seed vectors become rare or extinct (Willson, 1992). Small-fruited, vertebrate dispersed species such as *O. europaea* tend to have many dispersal agents, and the loss of one vector species may have minor consequences for plant population biology (Willson, 1992). However, if remnant forest stands continue to be decimated, many dispersers will be lost and potentially severe consequences for tree species survival are to be expected. Natural regeneration strategies should provide adequate protective measures for both source (e.g. church forests) and target areas (e.g. protected areas) as well as for the seed disperser population (in the case of *Olea*, frugivorous birds).

In the study area in central Tigray, *E. racemosa* shrubs are the most favorable microsites for *O. europaea* regeneration. *E. racemosa* shrubs are natural structures that probably act as preferential perching sites for frugivorous birds. Although further research is needed to identify the critical steps in the entire succession process, primary dispersal directed to *E. racemosa* seems to dominate in the study area.

Even small changes in shrub structure can alter the suitability of the microsite for olive recruitment. All this suggests that the application of appropriate protection of early successional shrubs combined with simple silvicultural measures (e.g. pruning and back-cutting to develop dense shrubs with a high number of stems at ground level and direct sowing of regurgitated or defecated seeds under *Euclea* shrubs) can significantly enhance natural regeneration of indigenous woodlands in the region without having to rely on expensive plantation activities.

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DISTRIBUTION OF PTERIDOPHYTES ALONG AN ALTITUDINAL GRADIENT IN BWINDI IMPENETRABLE FOREST, UGANDA

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Abstract

Data on the distribution of Pteridophytes were gathered along an altitudinal gradient in Bwindi Impenetrable Forest, Uganda. A total of 104 species of pteridophytes in 41 genera and 18 families were recorded in 246 samples of 25 m^2 quadrats at 100 m elevational intervals between 1200 m and 2600 m. Pteridophyte distribution varied continuously with altitude. Species richness was highest in the 2200–2400 m range and abundance varied with habitat preference of the different species. The proportion of terrestrial pteridophytes increased with altitude while the proportion of epiphytic species decreased. Differences in soil fertility, moisture and canopy cover along the altitudinal gradient may account for the drop in diversity.

Résumé

Distribution des ptéridophytes le long d'un gradient altitudinal dans la Forêt Impénétrable de Bwindi, Ouganda. Des données sur la distribution des ptéridophytes ont été rassemblées le long d'un gradient altitudinal dans la Forêt Impénétrable de Bwindi en Ouganda. Au total, 104 espèces de ptéridophytes, réparties au sein de 41 genres et de 18 familles, ont été enregistrées dans 246 quadrats de 25 m^2 entre 1200 et 2600 m d'altitude et à des intervalles de 100 m. La distribution des ptéridophytes se modifiait continuellement avec l'altitude. La richesse spécifique la plus élevée a été enregistrée entre 2200 et 2400 m alors que l'abondance variait en fonction des préférences des différentes espèces en matière d'habitat. La proportion de ptéridophytes terrestres augmentait avec l'altitude, en parallèle avec la diminution de la proportion d'espèces épiphytiques. Les différences de fertilité du sol, d'humidité et de couverture de la canopée le long du gradient altitudinal peuvent être envisagées pour expliquer l'augmentation de la diversité.

Key words: altitudinal gradient, pteridophytes, species richness, Bwindi Impenetrable Forest, Uganda

1 Introduction

Ferns constitute the most primitive group of plants with a vascular system. They range from small aquatic plants, for example *Azolla*, to large tree-like genera such as *Cyathea* (Alston, 1959; Holttum, 1965; Jones, 1987). Ferns and fern allies are most common in wet climates. More species of pteridophytes are found in rainforests than in any other vegetation type (Alston, 1959; Richards, 1969; Jones, 1987). These rainforest habitats range from lowland rainforest to forest of high altitudes. Jones (1987) reported that the highest altitude at which ferns have ever been recorded is 4400 m above sea level. Pteridophytes are not, however, restricted to rainforests, as many types of vegetation provide conditions favourable to their growth.

Recently, several detailed studies have focused on trends in composition, structure and diversity of tropical forests along various ecological gradients including rainfall (Gentry, 1988), edaphic conditions (Huston, 1980; Gartlan *et al.*, 1986; Gentry, 1988; Ashton, 1989; Clinebell *et al.,* 1995), successional time (Terborgh *et al.*, 1996) and rate of tree mortality (Phillips *et al.*, 1994). A number of studies have examined such community properties along substantial altitudinal gradients (Beals, 1969; Gentry, 1988; Beaman & Beaman, 1990; Lieberman *et al.*, 1996) but few have sampled a substantial number of elevations.

The taxonomic basis of pteridology in Africa is already fairly well founded. Pteridophytes have been presented in a number of Flora treatments dealing with individual countries or major geographic regions (e.g. Alston, 1959; Faden, 1974). A useful systematic account has been published by Schelpe (1970) for the Flora Zambesica. On the other hand, chorological and ecological data on African pteridophytes still remain scarce. Standard floras contain only a few distribution records per species, normally no more than a few per country or other major geographic division, e.g. an administration province.

Little has been reported on habitat preferences and life history of African pteridophytes. The only work concentrating on the African rainforest epiphytes is that of Johannson (1973). In 1955, Demaret published his work on the pteridophytes of Tanganyika with special emphasis on water ferns and Brummitt (1973) produced a systematic list of Nyika botanical collections mainly focusing on the pteridophytes. Pichi Sermolli (1983) made a contribution to the knowledge of the pteridophytes of Rwanda, Burundi and Congo. In Uganda, pteridophytes have only occasionally been collected together with other vascular plants by botanists and sometimes by individual travellers (Katende, pers. comm.). Therefore, ferns in the more accessible parts of the country situated along the main roads and tourist attraction centres are well represented.

This paper reports on the results of an intensive investigation of the distribution and abundance of pteridophytes along elevational gradients between 1200 m to 2600 m in Bwindi Impenetrable Forest (hereafter BIP).

2 Study area

Bwindi Impenetrable Forest is located in south-west Uganda between latitudes of 00°33'S and 1°08'S and longitudes of 29°35'E and 29°50'E (Fig. 1). It is one of the major forests in Uganda and covers an area of about 321 km^2.

Geology

Bwindi Impenetrable Forest occupies the highest block of the Rukiga highlands which stretch to the edge of the western Rift Valley. The topography of BIP is extremely rugged and it is much dissected in the southern sector. The valleys are very steep-sided and narrow, and are bounded by hills lying between 1400 m in the northern sector and 2600 m in the southern sector. The highest point in the forest is Rwamanyonyi Hill (2607 m) from where the elevation gradually descends to 1160 m at the northernmost point (Fig. 2).

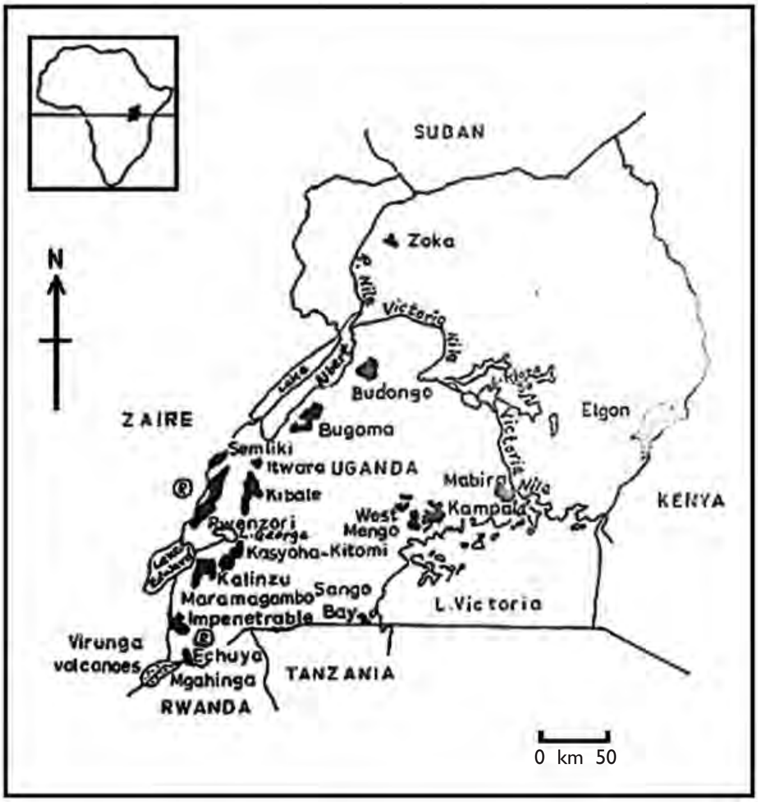

FIG. 1. Location of the Bwindi Impenetrable Forest. Source: Butynski (1984).

The soils of BIP and the surrounding areas were derived primarily from Precambrian phylliite of the Karagwe-Ankole system (Leggat & Osmaston, 1961). There are two types of soils in and around the forest (Uganda Atlas, 1969) namely: non-differentiated humic ferrallitic soils and non-differentiated ferrallitic soils with a dark horizon. Leggat & Osmaston (1961) described the soils of the BIP as tropical red earths overlain with spongy humus, and the swampy valley bottoms having clays under a layer of peat.

Harrop (1960) reported two soil series within the BIP. There is the Mafuga series which covers the upland sites and consists of latosols and loams which are usually acidic, stoneless and weakly structured, and the Ntendule series consisting of poorly structured clay loams and silt clay loams, which are even more acidic than those of Mafuga series with a pH as low as 2.9 and extremely deficient in bases.

Drainage

BIP is an important water catchment area. It gives rise to several major rivers which flow to the drier country to the north, and eastwards to the densely populated agricultural areas of the south. About four-fifths of the drainage is to Lake Edward via the Ivi, Muyaga, Ntengyere, Ihihizo, and Ishasha rivers. The remaining drainage is into Kigeyo swamp via the Ndegu river.

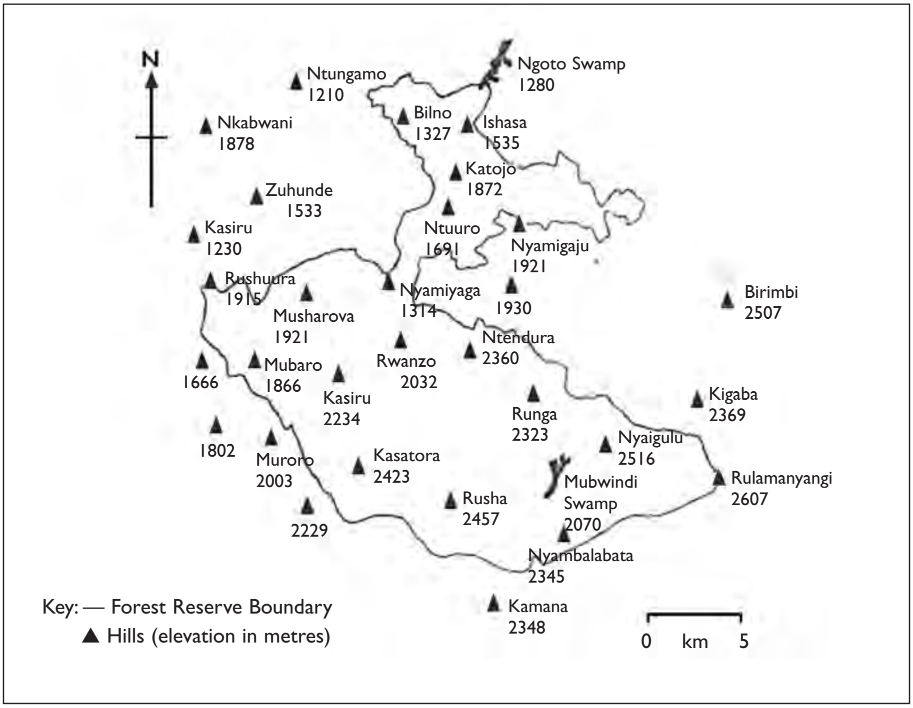

FIG. 2. Elevation in Bwindi Impenetrable Forest. Source: Butynski (1984).

Climate

BIP experiences two dry seasons per year, Dec.–Jan. and June–Aug., the latter being more severe. The wet periods are Feb.–May and Sept.–Nov. The coolest periods coincide with the dry season of June–July. The prevailing winds over the BIP especially during the dry season are from the southwest (Leggat & Osmaston, 1961).

Vegetation

The vegetation of BIP has been variously classified (Langdale-Brown, 1960; Langdale-Brown & Osmaston, 1964). However, the most recent by Hamilton (1982) classifies BIP as a moist low-montane forest. Osmaston (1968) indicates that the vegetation of BIP is very complex and greatly affected by altitude, topography and soil depth.

3 Methods

During 1989–91, a total of six sites, referred to as sample blocks, were located in BIP for this research project, namely Byanderema, Ruhiija, Kyangoroka, Buhoma, Ngoto and Ishasha.

Taking into consideration the different altitudinal gradients, four 1 km transects radiating out in major compass directions (N, S, E and W) from the same origin were established in each sample block. Forty-one 5m × 5m quadrats were placed at 100 m intervals along the transects in relatively undisturbed vegetation. All pteridophytes species within a quadrat were tallied and their abundance and growth habit recorded. Pteridophytes were identified in the field whenever possible, but in doubtful cases vouchers were collected (not listed in this paper) and deposited at Makerere University Botany Department herbarium (MHU). Species determinations were made by staff of MHU and the East African Herbarium, Nairobi (EA).

4 Results

The pteridophytes along the altitudinal gradient totalled 104 species in 41 genera and 18 families. However the distribution of these species varied along the altitudinal gradient. The epiphytic pteridopytes had a unimodal distribution whereas terrestrial pteridophytes had a bimodal distribution. The maximum number of epiphytic pteridophytes was calculated to be in the range of 1600–1800 m and that of the terrestrial pteridophytes in the range of 2200–2400 m (Fig. 3).

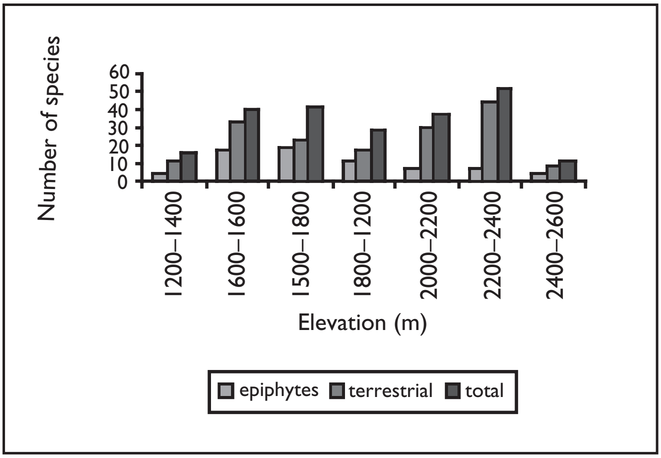

FIG. 3. Distribution of pteridophytes along altitudinal gradient.

There is no significant correlation between the number of species and the altitude (r = -0.319, p = 0.000 for epiphytic pteridophytes, r = 0.032, p = 0.000 for terrestrial pteridophytes and r = 0.013, p = 0.000 for all pteridophyte species). However when the blocks are handled independently, only Buhoma block (r = -0.540, p = 0.000) does show a significant correlation between altitude and the number of species.

Species may be classified by their distribution among habitats defined by fixed topographic features of the plots (Hubbell & Foster, 1985). Thus there are some species found in much greater abundance on the steeper slopes than on flatter terrain whereas other species are more common on the plateau and less so on the slopes. In the study, the results indicate that marked differences have been displayed in the altitudinal distribution of individual species in BIP. On this basis four groups have been distinguished.

There are 13–14 species that are confined to low-lying valleys of Ishasha block, with an altitude below 1300 m (Table 1).

Table 1. Species confined to low-lying valleys (under 1300 m above sea level)

Asplenium anisophyllum Kunze
Asplenium boltonii Schelpe
Asplenium cf. *boltonii* Schelpe
Asplenium inaequilaterale Willd.
Asplenium rutifolium (Berg.) Kunze
Blotiella currorii Hook.
Menisorus pauciflorus (Hook.) Alston
Microsorium punctatum L. Cop.
Nephrolepis biserratta (Sw.) Schott
Oleandra distenta Kunze
Pellaea adiantoides (Willd.) J.Sm.
Pellaea viridis (Forssk.) Prantl
Pteris catoptera Kunze
Pyrrosia schimperana (Mett. ex Kühn) Alston

Some species are widely distributed and occur in a wide altitudinal range (1300–2000 m) but are not present in the low-lying valleys. This includes the majority of the species in the forest and includes 37 species (Table 2).

Table 2. Species confined between 1300–2000 m altitudinal range.

Asplenium africanum Desv.
Asplenium ceii Pic.Serm.
Asplenium cancellatum Alston
Asplenium dregeanum Kunze
Asplenium holstii Hieron.
Asplenium hypomelas Kühn
Asplenium macrophlebium Baker
Asplenium protensum Schrad.
Asplenium erectum Willd.
Asplenium elliotii C.H.Wright
Asplenium monanthes L.
Asplenium sandersonii Hook.
Asplenium theciferum (Kunth) Mett.
Athyrium schimperi Fée
Antrophyum mannianum Hook.
Blechnum attenuatum (Sw.) Mett.
Blotiella gracilis Alston
Coniogramme africana Hieron.
Doryopteris concolor Kühn
Drynaria laurentii (Christ) Hieron.
Lomariopsis warneckei (Hieron.) Alston
Lonchitis mannii Faden
Lycopodium ophioglossoides Lam.
Lycopodium saururus Lam.
Marattia fraxinea J.F.Gmelin
Microlepia speluncae (L.) Moore
Nephrolepis undulata (Decne.) Pic.Serm.
Odontosoria africana Ballard
Pityrogramma aurantica (Hieron.) C.Chr.
Polypodium mildbraedii Hieron.
Pteris acanthoneura Alston
Pteris marginata Sw.
Pteris togoensis Hieron.
Thelypteris affer (Christ) Reed
Thelypteris bergiana Ching
Thelypteris chaseana Schelpe
Vittaria guineensis Desv.

Fourteen species of 10 genera and eight families were restricted to altitudinal ranges above 2000 m but did not exceed 2500 m, possibly because there is such a small area available above this altitude (Table 3).

TABLE 3. Species occurring in altitudinal range 2000–2500 m.

Asplenium blastophorum Hieron.
Asplenium mildbraedii Hieron.
Asplenium aff. friesiorum C.Chr.
Athyrium scandicinum (Willd.) Presl
Hypolepsis sparsisora (Schrad.) Kühn
Lastreopsis currori (Mett.) Tindale
Lonchitis hieronymii (Kumm.) Faden
Lonchitis tisserantii Alston & Tard.
Lycopodium verticillatum L.
Osmunda regalis L.
Polypodium polypoides (L.) D.Watt.
Polystichum setiferum (Forssk.) Woynar
Pteris linearis Poir.
Pteris preusii Hieron.

35 species are widely spread along the altitudinal gradient and are more or less irregular in their distribution. Such species can occur at all altitudinal ranges (Table 4).

TABLE 4. Species with irregular or wide altitudinal distribution.

Asplenium aethiopicum (Burm.f.) Bech.
Asplenium friesiorum C.Chr.
Asplenium linckii Kühn
Asplenium linearilobum Peter
Asplenium lividum Mett. ex Kühn
Asplenium lobatum Pappe & Rawson
Asplenium mannii Hook
Asplenium gemmiferum Schrad.
Asplenium megalura Hieron. ex Brause
Asplenium aff. *boltonii*
Asplenium aff. *cancellatum*
Athyrium glabratum (Mett.) Alston
Blechnum tabulare (Thunb.) Kühn
Cyathea borbonica Hook.
Cyathea manniana Hook.
Didymochlaena trunculata (Sw.) J.Sm.
Diplazium zanzibaricum (Bak.) C.Chr.
Dryopteris kilimensis (Kühn) C.Chr.
Hymenophyllum ciliatum Swartz
Loxogramme lanceolata (Sw.) C.Presl
Lycopodium cernua (L.) Pich. Serm.
Lycopodium clavatum L.
Pellaea doniana Hook.
Platycerium elephantotis Schweinf.
Pleopeltis excavata (Bory ex Willd.) Sledge
Pleopeltis macrocarpa (Bory ex Willd.) Kaulf.
Pteridium aquilinum (L.) Kühn
Pteris dentata Forssk.
Pteris prolifera Hieron.
Pteris pteridioides (Hook.) Ballard
Selaginella kraussiana (Kunze) A.Braun
Tectaria angelicifolia (Schumach.) Copel
Thelypteris dentata (Forssk.) E.S.John
Thelypteris longicuspis (Bak.) Schelpe

Abundance

The abundance of pteridophytes varied greatly along the altitudinal gradient, different species dominating at different altitudes (Fig. 4).

The distribution of the common epiphytic and terrestrial pteridophytes also varied along the altitudinal gradient (Figs. 5a & 5b).

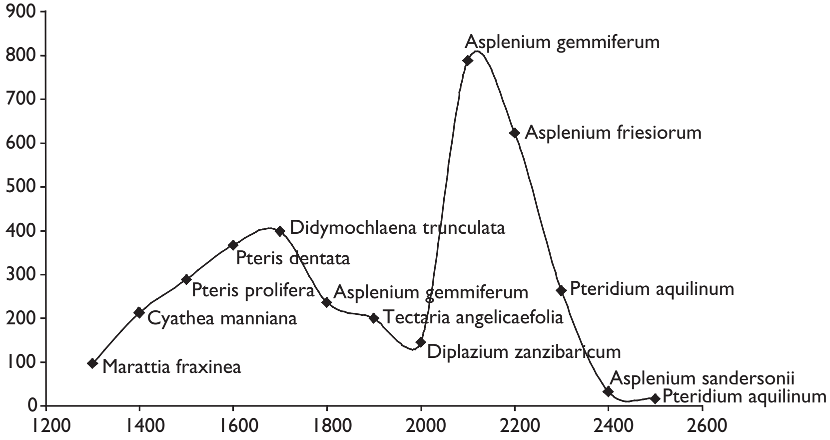

FIG. 4. Abundance of dominant pteridophyte species along the elevation gradient.

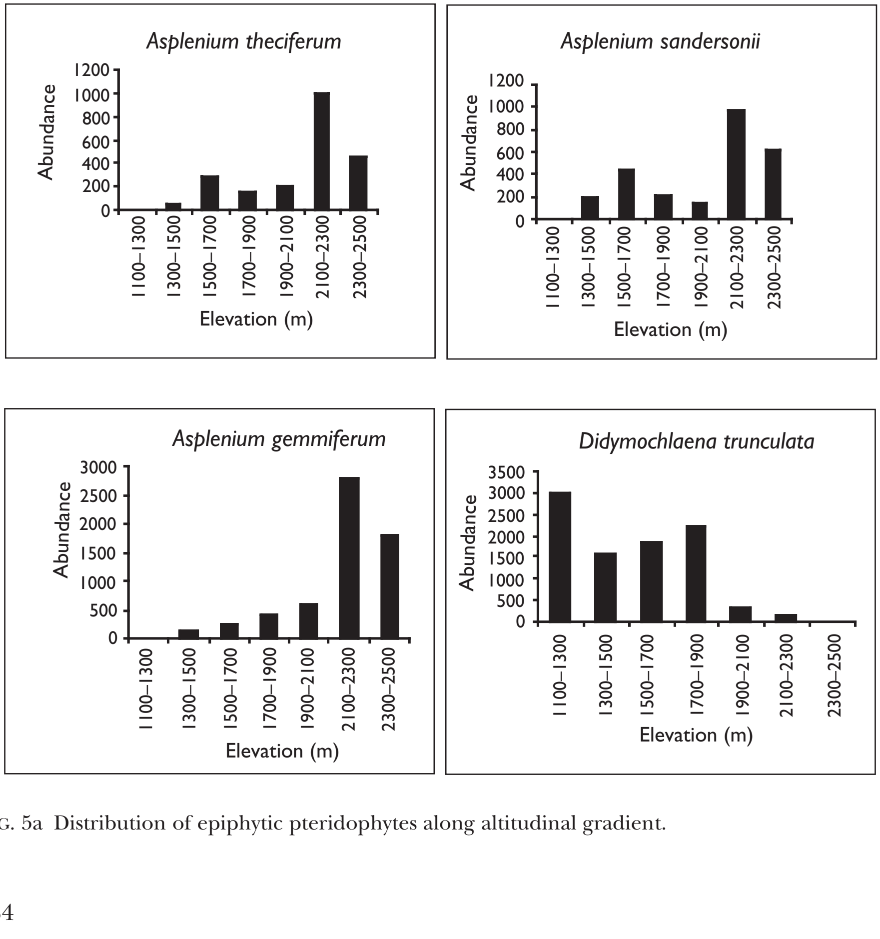

FIG. 5a Distribution of epiphytic pteridophytes along altitudinal gradient.

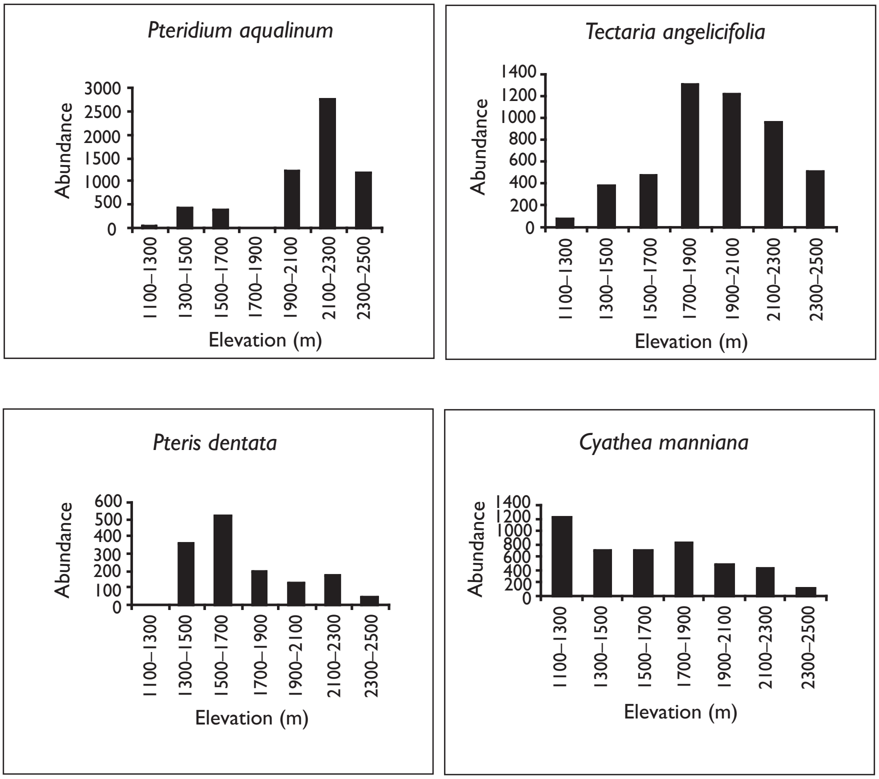

FIG. 5b Distribution of common terrestrial pteridophytes along altitudinal gradient.

5 Discussion

There is great local variation in the pteridophytes of BIP. The variation is both in the structure and in floristic composition. This variation appears to be related to differences in physical factors and structure of tree layers which contribute much to the percentage cover of pteridophytes (Badaza, 1994).

In closed and relatively dark forest such as that along the northern transect in Kyangoroka block, although individual herbs are widely spaced, the total fern diversity is very high. Often shade-tolerant ferns such as *Coniogramme africana, Pteris catoptera, Pteris linearis, Asplenium elliottii, Asplenium friesiorum, Asplenium erectum, Asplenium inaequilaterale* and *Lastreopsis currori* account for more cover in the herb stratum than that of any of other plant group. As a result the number of pteridophyte species is highest in the Kyangoroka block (with a high percentage of dense forest along the transects) and lowest in Ngoto block (with a very open forest canopy along the transects). In places where light can penetrate, such as forest gaps, epiphytic ferns such as *Pleopeltis macrocarpa, Pleopeltis excavata,* and *Loxogramme lanceolata* are very common, as is the terrestrial *Pteridium aquilinum.* Such patchy distribution has been reported in other studies in Rwanda by Pichi Sermolli (1983). These sun-loving species are the only ones favoured when an area of forest is felled and since the ecology of the felled forest is not as static as that of undisturbed forest, some species, especially the sun-loving epiphytes, eventually decline in numbers as regeneration continues (Johansson, 1974).

The distribution of pteridophytes along an altitudinal gradient (Fig. 4, Tables 2–6) support the individualistic hypothesis of community organization (Gleason, 1926), which posits that the distribution of each species is determined by its own ability to survive, compete and reproduce successfully in different environments, resulting in each species having its own distinctive niche, and in community composition changing more or less continuously along ecological gradients. Numerous studies, mainly in temperate areas support the invidualistic hypothesis (Curtis, 1959; Whittaker, 1960; Whittaker & Niering, 1965; Peet, 1978; Ogden & Powell, 1979; Austin, 1985; Syuzo, 1991; Auerbach & Schmida, 1993; Palmer & Cowling, 1994; Rawal & Pangtey, 1994).

The distribution of pteridophytes along altitudinal gradient varied greatly. Such wide range of variation is probably due to the different habitat characteristics at the different gradients. Generally there is a decrease in species diversity from high to low altitude zones. However blocks like Buhoma and Ishasha, although at a lower altitude, had relatively high numbers of species. This may be due to the diverse types of microhabitats created by the streams and rivers. Byanderema, characterised by bamboo forest, had the lowest species diversity.

According to Hutchinson (1953) the discontinuities in the substrata of a forest would be very important in determining the distribution of ferns, but only one instance of sharp discontinuity was detected on the very steep slopes and cliffs, where the only species of pteridophytes found were the lithophytic types such as *Oleandra distenta* and *Lycopodium* species. On steep hill slopes the substrate is unstable leading to a complex variation in the fern composition, often with small areas of monospecific dominance forming e.g, where there is a large amount of dead wood, of *Asplenium lobatum* and *Asplenium aethiopicum* (Badaza, 1994).

It has been suggested that differences in vegetation might be responsible for the consequent difference in fern composition and distribution in a given forest (Axelrod, 1972). This agrees with the results obtained during this study and is exemplified in Kyangoroka block. Areas of undisturbed forest interspersed several phases of regenerating forest might give rise to the observed high fern species diversity and abundance.

Moisture levels also appear to have an effect on the distribution and abundance of pteridophytes in BIP. *Marattia fraxinea, Cyathea manniana* and *Pteris* species are the most frequently seen along streams at all altitudes. Inside the forest in relatively drier habitats *Asplenium erectum* and *Tectaria angelicifolia* dominate. In forests where the floor is shaded but the canopy not dense, a dense fern layer of *Asplenium gemmiferum* and *Asplenium friesiorum* dominated.

Although BIP is expected to have a relatively low fern diversity when compared to tropical forests in South America, it has a high diversity when compared to most African forests. Such diversity is probably due to the representation in BIP of the fern-diverse altitudinal range 1160–2600 m, the high diversity of fern habitat and the forest being part of a Pleistocene refugium. According to Kornas (1979), Africa is known to be rather poor in pteridophytes when compared to similar areas in tropical America and Southeast Asia because of the great climatic changes and floral migrations in Africa during the cenozoic era as opposed to the long-lasting evolution in the hygrophilous floras in the American and Eastern Asian Tropics (Wulff, 1943; Axelrod, 1972; Szafer, 1975).

Hutchinson (1953) explained that when two or more species, ecologically similar except for one factor, are growing along a gradient of that factor, there will be a definite point along the gradient below which one species will succeed to the exclusion of the other, above which the other species will succeed to the exclusion of the first. In support of this, in this study it was noted that whenever there is a gap in the closed canopy forest, *Pteridium aquilinum* out-competes all the others. Cole (1960) suggested that two or more species may co-exist in an equilibrium which is dependent on factors like the number of seed/spores produced by each, their density and their spatial pattern. In this study, there is evidence that stable plant communities do occur, without competition, as exemplified in the fern communities of *Asplenium gemmiferum* and *Asplenium friesiorum* referred to above. This may be due to the fact that species require different resources.

Although Pichi Sermolli (1991) suspected that the diversity, abundance and distribution of pteridophytes is influenced by both topography and edaphic factors, results of this study indicate that the different vegetation types along the altitudinal gradient play a major role in the distribution, diversity and abundance of pteridophytes in BIP.

6 Conclusion

104 species of pteridophytes were recorded along the altitudinal gradient (from 1140 m to 2600 m) in BIP. The highest diversity and abundance of species was recorded between 2200 m and 2400 m. Most of the species were habitat-specific and apparently controlled by changes in forest ecology.

Note: Since the submission of this paper several of the names listed in Tables 1, 2, 3 & 4 have changed. Please consult the latest fascicles of FTEA on ferns and fern allies for an update on name changes. Eds.

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THE PLANT FOSSIL RECORD AND IMPLICATIONS FOR PHYTOGEOGRAPHY IN TROPICAL AFRICA

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Abstract

This paper reviews the paleobotanical record for tropical and northern Africa for the period 70 to 3 million years ago. While the record is sparse for some time periods and some regions, broad patterns emerge that are relevant to phytogeographic history. For example, high angiosperm pollen richness in Cameroon during the Oligocene may represent expansion of lowland wet forest, although palm pollen richness declines at the Eocene/Oligocene boundary. Ongoing investigation of Late Oligocene fossils from the Ethiopian Highlands documents a more significant role for palms than is usually the case in African forests today. The earliest woodland structurally equivalent to miombo is known from the Middle Eocene of Tanzania and, like today, is dominated by caesalpinioid legumes. Some families, such as Leguminosae and Meliaceae, common in living African plant communities appear often early in the Cenozoic. Others, such as Poaceae, appear early, but do not become common until much later in the Tertiary. A relatively good record for the Neogene of East Africa indicates that forest taxa with West African affinities were present in the Rift Valley until as late as 3 million years ago, but change there was complicated by topographic heterogeneity and climate change. There was not a monotonic change from forest to savanna during the course of the Neogene.

Résumé

Mise en évidence de fossiles végétaux et implications pour la phytogéographie en Afrique tropicale. Cet article passe en revue les découvertes paléobotaniques en Afrique tropicale et du nord pour la période s'étendant de -70 à -3 millions d'années. Bien que les témoins soient rares pour certaines périodes et certaines régions, on peut dégager des modèles généraux pertinents pour l'histoire phytogéographique. Par exemple, au cours de l'Oligocène, la richesse en pollen d'angiospermes peut signifier l'expansion de la forêt humide de basse altitude, alors qu'entre l'Eocène et l'Oligocène, c'est une diminution du pollen des palmiers qui est observée. Les recherches en cours sur les fossiles de l'Oligocène tardif dans les montagnes d'Ethiopie démontrent un rôle significatif des palmiers dans cette région et il reste à déterminer la relation éventuelle qu'ils auraient pu avoir avec les palmiers de l'Oligocène ou plus anciens du Cameroun. La plus ancienne forêt claire, structurellement équivalente au miombo, est connue de l'Eocène Moyen en Tanzanie et, comme à l'heure actuelle, était dominée par des légumineuses caesalpinioïdes. Certaines familles, comme les Leguminosae et les Meliaceae, communes dans les communautés végétales africaines actuelles apparaissent souvent tôt au Cénozoïque. D'autres, comme les Poaceae, apparaissent tôt mais ne deviennent communes que beaucoup plus tard au cours du Tertiaire. Un relativement bon échantillon pour le Néocène est-africain indique que les taxons forestiers à affinités ouest-africaines étaient présents dans la Vallée du Rift jusqu'il y a au moins 3 millions d'années, mais que le changement a été enfreint par l'hétérogénéité topographique et un changement climatique. Aucun changement monotonique de la forêt en savane n'a eu lieu au cours du Néocène.

Key words: Africa, Cenozoic, paleobotany, paleoecology, Tertiary

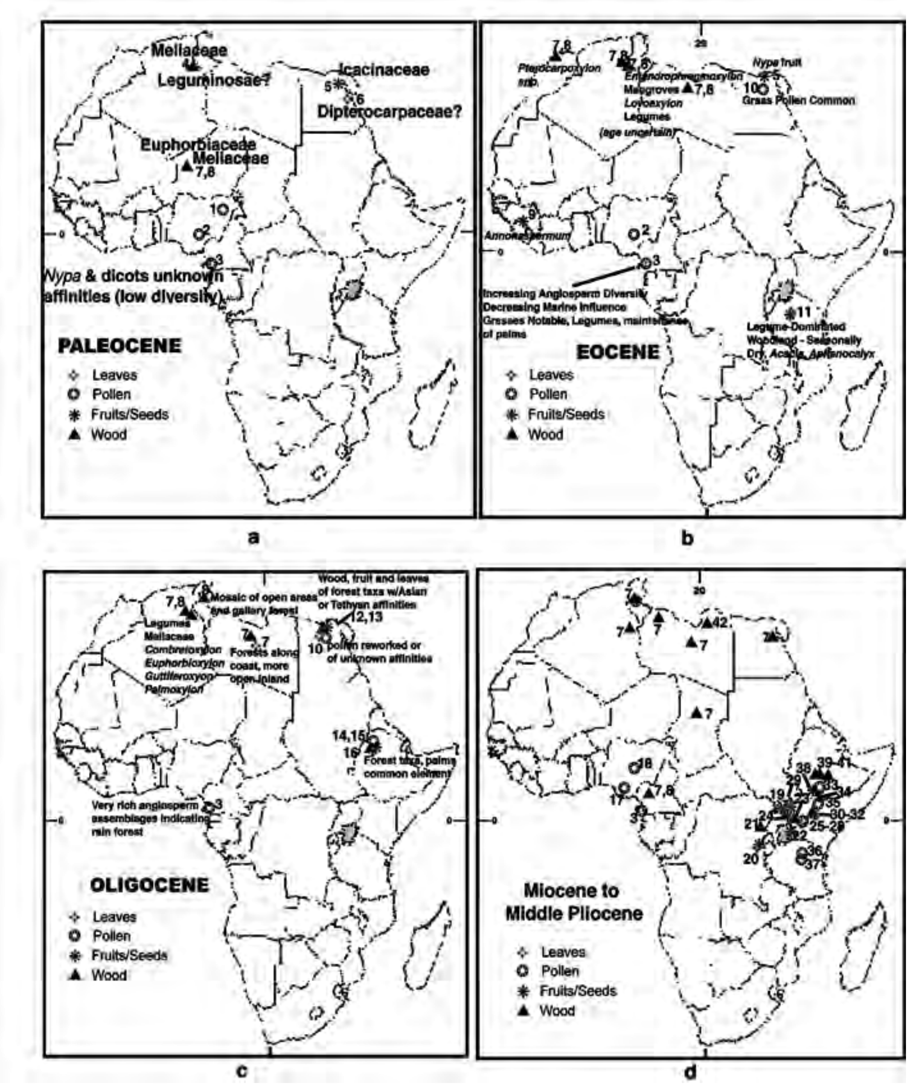
1 Introduction

The African paleobotanical record documents large-scale patterns of vegetation change across millions of years, a smaller-scale view of plant community structure from individual fossil sites, past climate at a regional scale, and helps to identify and resolve biogeographic questions. This paper reviews the record at a relatively large scale, focusing on the time period between about 70 and 3 million years ago, from the final Stage of the Upper Cretaceous (Maastrichtian) in the Mesozoic Era to the middle Pliocene Epoch in the Cenozoic Era. Angiosperm pollen and macrofossils clearly related to living groups are first documented in the Maastrichtian, although angiosperms first become a significant part of pollen assemblages in the Cenomanian, about 95 Ma. The fossil record is described for three principal regions: northern Africa including the area currently occupied by the Sahara, Central and West Africa comprising the modern tropical wet zone, and East Africa. Some significant phytogeographic points arising from the data are discussed.

The kind and amount of paleobotanical information varies. Fossil woods, which provide the most abundant source of information for northern Africa, are often dated imprecisely because they lack geologic context, and names such as *Leguminoxylon* leave their botanical affinity uncertain. It should be kept in mind that pollen samples are derived from a wider source area than plant macrofossil assemblages and will thus inform about regional, as opposed to local, vegetation. Finally, although an effort was made to cite all the literature relevant to the time interval and areas of interest, the citation list is not exhaustive. However, the citations contained herein will lead to the remaining literature, and the reader should be aware of the following review papers for additional insight: Germeraad *et al.* (1968), Dupéron-Laudoueneix and Dupéron (1994), Jacobs *et al.* (1999), Morley (2000), and Jacobs (2004). The geographic distribution of Cenozoic fossil sites is provided in Fig. 1.

1.1 Northern Africa

A pollen record from El Kef, Tunisia, spanning the time interval from the Late Cretaceous through the Paleocene is the primary source of information about change encompassing the Mesozoic-Cenozoic boundary in northern Africa. It documents the Late Cretaceous co-occurrence of plants from Northern Hemisphere landmasses (i.e. Laurasia) with those from tropical areas to the south (Méon 1990). Late Cretaceous assemblages are dominated by conifer pollen (Araucariaceae), spores, and angiosperms represented predominantly by Laurasian Normapolles Province taxa (Juglandales; Muller 1984), together with Arecaceae pollen typical of the Late Cretaceous of tropical Africa. After the Mesozoic-Cenozoic boundary, and by the end of the Paleocene (56 Ma), conifers and palms are absent from the El Kef pollen site and only northern taxa remain (Méon 1990). A Late Paleocene–Early Eocene pollen



Paleobotanical sites in northern and tropical Africa for the Paleocene (a), Eocene (b), Oligocene (c) and Miocene to Middle Pliocene (d). Numbers refer to citations. **Fig. 1a**: **1**, Adegoke (1978); **2**, Van Hoeken-Klinkenberg (1966); **3**, Salard-Cheboldaeff (1978, 1981) and Salard-Cheboldaeff and Dejax (1991); **4**, Boreau *et al.* (1983, p. 357); **5**, Chandler (1954); **6**, Seward (1935); **7**, Koeniguer (1971); **8**, Dupéron-Laudoueneix and Dupéron (1994). **Fig. 1b**: **9**, Chesters (1955); **10**, Kedves (1971); **11,** Herendeen and Jacobs (2000). **Fig. 1c**: **12**, Wing *et al.* (1982); **13**, Kräusel (1939); **14**, Yemane *et al.* (1987); **15**, Jacobs (this paper); **16**, Pan and Jacobs (2003). **Fig. 1d**: **17**, Morley and Richards (1993); **18**, Legoux (1978); **19**, Chaney (1933); **20**, Lakhanpal (1966); **21**, Lakhanpal and Prakash (1970); **22**, Chesters (1957); **23**, Bancroft (1933); **24**, Bancroft (1932); **25–28** (Bonnefille, 1984; Dugas and Retallack, 1993; Retallack, 1992b; Retallack *et al.*, 1990); **29**, Hamilton (1968); **30–32** (Jacobs and Kabuye, 1987; Jacobs and Kabuye, 1989; Jacobs, 2002); **33**, Bonnefille (1994); **34**, Bonnefille and Letouzey (1976); **35**, Bonnefille and Vincens (1980); **36**, Bonnefille and Riollet (1980); **37**, Bonnefille and Riollet (1987); **38**, Tiffney *et al.* (1994); **39–41** (Lemoigne, 1978; Lemoigne and Beauchamp, 1972; Lemoigne *et al.*, 1974); **42**, Dechamps (1987).

record from southern Morocco, dominated by Normapolles pollen, substantiates the floristic link between northern Africa and Europe at this time (Ollivier-Pierre 1982).

Koeniguer (1967) reports the earliest record of Euphorbiaceae (*Euphorbioxylon* wood) from the Late Cretaceous of Tunisia. Thus, a long African history is documented for this family, which is diverse and ecologically important in African plant communities today.

Boureau *et al.* (1983) and Aubréville (1970) report *Entandrophragmoxylon normandii* Louvet, wood related to the living forest genus *Entandrophragma* (Meliaceae), and several species of legume wood of uncertain ecology from the Paleocene Tinrhert area of Algeria. These are interpreted as indicating the presence of dense forest near the coast, while a drier forest community is thought to have been present further inland based on wood identified as *Combretoxylon bussonii*, *Guttiferoxyon barryi*, and *Palmoxylon aschersonii*. *Trichilioxylon* (Meliaceae) is present in the Paleocene of Niger, consistent with forest vegetation along the ancient shoreline (Koeniguer, 1971; Boureau *et al.*, 1983). Although the date is imprecise, Paleogene (65–23 Ma) *Pterocarpoxylon* wood from Morocco is indicative of gallery or semi-deciduous forest (Boureau *et al.*, 1983).

In northeastern Africa, Late Cretaceous pollen records from Egypt and Sudan indicate a mixture of Laurasian species of *Aquilapollenties* and the Normapolles pollen group, together with taxa more typical of tropical Africa (Kedves, 1971; Kaska, 1989; Méon, 1990; Schrank, 1991; Mahmoud, 2003). However, Northern Hemisphere forms are less prevalent here than in either Morocco (Ollivier-Pierre, 1982) or Tunisia (Méon, 1990). Interestingly, among the palm pollen taxa is the genus *Spinizonocolpites*, which appears to be related to the living mangrove palm *Nypa* (Arecaceae) today limited to Southeast Asia, but present in Egypt from the Late Cretaceous to the early part of the Cenozoic from the Libyan border to the Red Sea (Schrank, 1991, 1994). In an earlier review of pollen samples from Egypt, Kedves (1971) mentions the presence of palm pollen in Late Cretaceous and Paleogene samples, but does not specify whether these are relatives of *Nypa*.

Fruits and seeds from the Paleocene Kosseir region of Egypt include *Nipa* (*Nypa*), *Anonaspermum* (Annonaceae), *Lagenoidea* (Euphorbiaceae), *Icacinicarya* (Icacinaceae), *Palaeowetherellia* (Euphorbiaceae?), and *Thiebaudia* (Flacourtiaceae?), indicating biogeographic ties to both the Eocene London Clay flora and to modern Southeast Asia (Chandler, 1954). These are interpreted as indicating a wet climate, in part due to the presence of *Nypa* (Chandler, 1954). A wet climate is also reported for southwestern Egypt based on Cretaceous-Paleocene fruits including Arecaceae (Nypoideae and Coryphoideae), Fagaceae, Flacourtiaceae, Icacinaceae, and Olacaceae (Gregor & Hagn, 1982).

Fossil leaves documented by Seward (1935) from the Nubian Sandstone of Egypt are of uncertain age, either Campanian-Maaastrichtian (Schrank, 1992) or Paleocene (Axelrod & Raven, 1978; Morley, 2000), but due to their large size, are widely cited as representing tropical wet conditions (Axelrod & Raven, 1978; Schrank, 1992; Morley, 2000). The leaves include *Dipterocarpophyllum* spp. (possibly, but not necessarily related to the living Dipterocarpaceae), *Dicotylophyllum* spp. (unknown affinity), and *Nelumbium* sp. (Nelumbonaceae).

Aubréville (1970) and Boureau *et al.* (1983) review Eocene to Oligocene (56–23 Ma) wood and leaves from Algeria, Tunisia and Libya, documenting mangroves and the continued presence of forest vegetation along the northern coast of Africa. However, between the Early Eocene and Late Oligocene, dry forest and "savanna" expanded from south to north, narrowing the strip of coastal forest. The role of grasses, if any, in the more open landscape is not documented. A marine regression during the Eocene, and Africa's northward movement to near its current position by the Oligocene, are cited as the cause of this environmental change. However, the effects of significant global Eocene and Oligocene climate change (e.g. Zachos *et al.*, 2001) should be considered a contributing factor.

Eocene and Oligocene coastal (gallery?) forest representatives from Algeria and Tunisia include the wood of *Lovoaxylon, Entandrophragmoxylon* (Meliaceae), *Ficoxylon, Copaiferoxylon* (Leguminosae) and *Tetrapleuroxylon* (Leguminosae). In Libya, Eocene mangroves are represented by the wood of *Sonneratioxylon* (related to *Sonneratia*), *Flacourtioxylon* (probably related to Rhizophoraceae), and the fruit, *Nipadites.* Wood of *Combretoxylon* (*Anogeissuxylon*) *bussonii* (close to extant *Anogeissus leiocarpa*) and the leaves of several legume species comparable to those found in savannas today (e.g., species of *Detariophyllum, Pterocarpus, Caesalpinities*) represent more open inland vegetation in the Oligocene (Boureau *et al.*, 1983).

Pollen and sedimentological records from the Lower to Middle Eocene of southern Morocco document mangrove vegetation, behind which was salt marsh and probably xeric vegetation in the uplands (Mohr, 1986). Mangrove taxa include *Nypa, Rhizophora,* and *Brownlowia.* Inland pollen diversity among the samples is low, and the presence of diagenetic dolomite and gypsum in the sediments indicate an arid climate (Mohr, 1986).

In northeastern Africa, the Early Eocene is represented by a pollen core from Kharga, Egypt, which documents abundant cycad and grass pollen occasionally mixed with saltwater indicators (Kedves, 1971). Egyptian pollen samples from the Middle to Upper Eocene share taxa with Europe, but the assemblages are dominated by a majority of grass pollen that Kedves (1971) suggests may have been riverine.

Oligocene wood, fruit and leaves from the Fayum, which include *Quercoxylon* and the Asian genus *Epipremnum,* document forest vegetation near the coast of Egypt having phytogeographic links to other areas around the Tethys Seaway (Boureau *et al.*, 1983; Dupéron-Laudoueneix & Dupéron, 1994; Kräusel, 1939; Wing *et al.*, 1982).

Late Oligocene or Early Miocene wood from central Tunisia represent two legume species with affinities to *Cynometra* and *Swartzia,* and a third taxon with affinities to the genus *Terminalia* (Combretaceae). The paleoenvironmental interpretation based on the association of taxa is gallery forest (Delteil-Desneux, 1981).

The Miocene to Middle Pliocene (23 to about 3.5 Ma) in northern Africa is documented by fossil woods, most of which are poorly dated, but which indicate increasingly open environments and aridity compared with earlier time intervals. Miocene and Early Pliocene wood assemblages from Libya document a dry, warm, seasonal climate, which supported a harsh setting for trees near the sea, along streams, or in the desert associated with groundwater (Boureau *et al.*, 1983; Deschamps, 1987). Woods from Algeria, Tunisia, Libya, Chad and Egypt are dominated by legumes and thought to indicate savanna or wooded savanna conditions and a seasonally dry climate (Boureau *et al.*, 1983).

1.2 Central and West Africa

Central and West African vegetation history is documented primarily by pollen from cores associated with petroleum exploration. This is true particularly for the Late Cretaceous through Paleogene time interval as demonstrated in reviews by Morley (2000) and Germeraad *et al.* (1968), and the publications of Jardiné and Magloire (1965), Salard-Cheboldaeff (1978, 1979, 1981), Salard-Cheboldaeff and Dejax (1991), and Herngreen *et al.* (1996). Maastrichtian West and Central African pollen assemblages are dominated by palm pollen including *Spinizonocolpites* . The presence of palms related to extant *Nypa* here and in contemporaneous samples from northern

Africa represented by both pollen and fruits, is of phytogeographic interest. Relatives of the genus *Nypa* have also been documented at fossil sites in Eurasia, South America, and North America (Herngreen *et al.*, 1996; Westgate & Gee, 1990; Collinson, 2000; Gee, 2001), with the greatest worldwide distribution during the Early Eocene. Today the genus is limited to Indo – Australasia, where mangrove plants representing a variety of families are most diverse (Ricklefs & Latham, 1993). The reason for *Nypa*'s absence in Africa and elsewhere after the Eocene is not certain, but is generally ascribed to global climate change (i.e. cooling) documented in marine and higher-latitude terrestrial settings (Gee, 2001; Zachos *et al.*, 2001; Collinson *et al.*, 1981).

West and Central African Late Cretaceous samples also share Illiciaceae, Linaceae (*Ctenolophon*), Proteaceae, and Restionaceae pollen. Illiciaceae and *Ctenolophon*, which commonly occurred in tropical African pollen assemblages at this time, are limited in distribution among forest communities today, while Proteaceae are currently found at higher latitudes of the Southern Hemisphere. Proteaceae pollen from the Maastrichtian of Nigeria may be related to some living genera such as *Gevuina* (Germeraad *et al.*, 1968). The pollen genus *Proteacidites*, a form-genus which includes taxa having a variety of botanical affinities, is extinct at the Cretaceous – Paleogene boundary (Muller, 1981). Clearly, conditions for Proteaceae became unfavorable in the tropical zone, but were better to the south.

Cretaceous plant macrofossils are rare in tropical Africa, but Chesters (1955) reported the seeds of Annonaceae (*Anonaspermum*) from Nigeria, which are Maastrichtian based on associated marine fauna. Other seed specimens from Nigeria thought to be Maastrichtian include *Icacinicarya* (Icacinaceae) and a possible relative of Passifloraceae (Chesters, 1955). Fruits and seeds from Senegal dated at about the Campanian – Maastrichtian boundary are similar to extant Arecaceae, Meliaceae, Leguminosae, Rubiaceae and Annonaceae (Monteillet & Lappartient, 1981). However, the authors note that these identifications are tentative due to an absence of diagnostic characters. Reports of Mesozoic leaf fossils from West Africa are especially rare. Menzel (1909) reports leaves from Cameroon of possible Late Cretaceous age among which are legume leaflets similar to extant *Albizzia*. However, unequivocal legume fossils are not known from well-dated Mesozoic deposits (Herendeen *et al.*, 1992).

A pollen core from coastal Cameroon that spans the time period from the Late Cretaceous to the Early Miocene shows increasing angiosperm diversity from the Paleocene into the Late Eocene accompanied by decreasing marine taxa (Salard-Cheboldaeff, 1978, 1979, 1981). Salard-Cheboldaeff (1981) indicates that these taxa are likely to be from developing angiosperm lowland rainforest. Up to 4% grass pollen is present in Paleocene pollen samples from Nigeria (Adegoke *et al.*, 1978), and there is a Middle Eocene grass biozone present in the Cameroon record (Salard-Cheboldaeff, 1979), first established in pollen cores from Venezuela by Germeraad *et al.* (1968). Pollen samples from modern grass-dominated environments contain grass pollen percentages of between 20% and > 60%. Quantitative data are not provided for the Cameroon samples, but the grass biozone indicates the presence of some open areas or perhaps the establishment of monocot-dominated wetlands (Morley 2000).

The pollen core from Cameroon shows tremendous angiosperm richness in the Oligocene, especially among dicots, which Salard-Cheboldaeff (1981) interprets as the flourishing of West and Central African lowland rainforest. Although palm taxa continue to be present, and more diverse in the Oligocene than they are in forest communities today, there are several last occurrences of palm taxa at the Eocene-Oligocene boundary (Salard-Cheboldaeff & Dejax, 1991, see also Morley, 2000; Pan *et al.*, in press).

Lowland forest vegetation persists into the Miocene as documented by samples from the Cameroon pollen core, which include mimosoid legume pollen related to extant forest genera (Guinet & Salard-Cheboldaeff, 1975). Morley and Richards (1993) document grass pollen, cuticle, and charred cuticle in a core from the Niger Delta as an indication of the extent of open savanna in West Africa. Charred cuticle and grass pollen are present in low quantities in the Early Miocene, consistent with the Cameroon pollen record, but by the Late Miocene there is a peak indicating marked aridity, seasonal rainfall, and broad savanna in West Africa.

1.3 East Africa

The East African plant fossil record from the Late Cretaceous to the Middle Pliocene consists almost entirely of Neogene (Miocene and younger) macrofossil localities, although recent efforts have improved the Paleogene sample. Substantial Neogene development of the East African Rift created physiographic heterogeneity increasing opportunities for fossilization (Fig. 1d). Fossil sites reveal a complex phytogeographic history relevant to hypotheses of human origins and to botanical disjunctions on either side of the Rift Valley. Specifically, the timing of development of open habitats in East Africa has traditionally been associated with the origin of the human family, a hypothesis that can be tested by plant fossils. The fossil record also informs the hypothesized vicariance of African forest genera found in lowland and sub-montane forests of the West and East. The following section will review the Neogene record to address these hypotheses, and will focus on recent additions to the Paleogene record in East Africa.

Cretaceous and Paleocene data are lacking, but the Middle Eocene Mahenge site from north central Tanzania provides paleobotanical data. The site consists of fossiliferous mudstones and shales formed in a crater lake created soon after a volcanic eruption dated at ± 45.8 million years ago (Harrison *et al.*, 2001). The sediments preserve leaves, fruits, fish, a frog with stomach contents, and a bat (Báez, 2000; Gunnell *et al.*, 2003; Harrison *et al.*, 2001; Herendeen & Jacobs, 2000; Murray, 2000, 2003). Plant fossils are dominated by legumes, which comprise about 60% of all leaves at the site. About a third of the 19–21 leaf morphotypes are legumes. These include the earliest record of *Acacia* in Africa (*A. mahengense*), *Aphanocalyx singidaensis*, 3–4 caesalpinioid species, and 2 unknown mimosoids (Herendeen & Jacobs, 2000; Jacobs & Herendeen, 2004). The flora is interpreted as representing woodland structurally equivalent to modern miombo, which is also dominated by a few caesalpinioid genera. Thus, the Mahenge flora documents the first such woodland in the fossil record, and indicates that miombo structure (if not species composition) is at least as old as 46 million years. Climate reconstruction, based on regression equations derived from the leaf areas of modern tropical species in relation to rainfall, indicates rainfall at Mahenge was about the same as it is today (660 mm/yr), and perhaps less seasonal (Jacobs, 2002; Jacobs & Herendeen, 2004).

The Oligocene is represented by plant localities in the northwest Ethiopian Highlands approximately 60 km west of Gonder in the Chilga region (Kappelman *et al.*, 2003; Jacobs *et al.*, 2005, Pan *et al.*, in press). Plant fossils occurring just above a tuff radiometrically dated at 27.36 ± 0.11 Ma include *Anonaspermum* (Annonaceae) seeds, legume pods, and fruits and seeds that are preliminarily identified as palms. About 20 meters below the dated tuff, but above basalt dated at 32.4 ± 0.11 million years old, are excellently preserved leaf and flower compressions in fine mudstones. These include legume leaves and leaflets; palm rachises, leaf fragments, and flowers; and the leaves of *Dioscorea* sp. and other as yet unidentified plants. At least two localities stratigraphically equivalent to the dated tuff consist of *in situ* silicified trunks of forest trees having a maximum diameter of 2 m, and sometimes having buttresses.

The occurrence of palms in nearly all the paleobotanical assemblages at Chilga indicates that they may have had a larger role to play in Oligocene communities of East Africa compared with today just as they did in West Africa based on pollen samples from Cameroon (Salard-Cheboldaeff, 1979; Pan *et al.*, in press). The paleofloras and land sediments of Chilga demonstrate that the region was occupied, at least at times during the Late Oligocene, by forests that must have required a wet climate (Jacobs *et al.*, 2005). Yemane *et al.* (1987) reported a pollen section from Chilga that reflected a rich angiosperm flora with Central and West African affinities. They indicated the section was Late Miocene, but geological evidence supports an Oligocene age (Kappelman *et al.*, 2003), and comparison with the macrofossils will provide complementary data.

Fossil evidence from East Africa of forest with West and Central African floral elements includes leaves and woods thought to be Early Miocene from the Ethiopian Highlands (Lemoigne, 1978; Lemoigne *et al.*, 1974), flowers, fruit and leaves from Bukwa, Uganda, which are older than 22 Ma (Brock & Macdonald, 1969; Hamilton, 1968), leaves from the Republic of Congo cited as middle Tertiary and representing *Sclerosperma* swamp forest (Lakhanpal, 1966), abundant fruits and seeds from Rusinga Island in Lake Victoria (17 Ma) interpreted as gallery forest (Chesters, 1957), and 16 Ma fruits and seeds of *Antrocaryon*, *Parinari*, and Annonaceae from Fejej, Ethiopia (Tiffney *et al.*, 1994). Younger occurrences of plants with West and Central African forest affinities include a 12.6 Ma assemblage of leaves and some fruit in the Tugen Hills of the Kenya rift (Jacobs & Kabuye, 1987, 1989), and *Antrocaryon* from the Pliocene Omo Valley (Bonnefille & Letouzey, 1976). Clearly, forest communities with West African elements, or at least isolated taxa not found in East Africa today, were present well into the Miocene, and as late as the middle Pliocene. It should be noted, however, that Pliocene pollen records (Bonnefille & Riollet, 1987) show essentially modern conditions in East Africa with relatively small-scale variations in the extent of forest relative to savanna in response to climate and physiographic change.

There is some evidence of open woodland or dry forest from the Early Miocene based on leaves, fruit, and wood from Bugishu, Uganda (Chaney, 1933), and the environment at Fort Ternan in western Kenya, dated at 14 Ma, most likely represents woodland (perhaps with open areas [Retallack *et al.*, 1990]) or dry forest (Cerling *et al.*, 1997; Cerling & Quade, 1991; Retallack, 1992a, 1992b). Fossil leaves from the Tugen Hills sequence in Kenya indicates that a low-diversity community dominated by legumes in a seasonally dry climate was present at about 10 Ma, and woodland or dry forest existed in the same region at 6.8 Ma (Jacobs, 2002).

Savanna vegetation, which expands substantially in West Africa during the Middle to Late Miocene as documented by a pollen core from the Niger Delta (Morley & Richards, 1993), must have developed in a more complex pattern in the East African Rift. Stable carbon isotopes, which document the relative abundance of C_4 (mainly warm-climate grasses) vs C_3 (cool-climate grasses and most dicots) plants on the landscape or in the diet of mammals, indicate that the Kenyan rift valley was a mix of C_3 and C_4 vegetation throughout the Middle Miocene and Pliocene (Kingston *et al.*, 1994). However, strictly C_4 diets are documented in the Kenyan rift beginning about 8.5 Ma (Morgan *et al.*, 1994) indicating that savanna grasses were abundant enough to support specialized grazers at that time (see also Jacobs *et al.*, 1999). Thus, the development of open vegetation in East Africa, and its potential association with the origin of the human family about 6 million years ago, was not a one-directional progression from forest to savanna after the Miocene (as once thought) but a complex mix of open and closed vegetation (Jacobs, 2002).

2 Summary and conclusions

The plant fossil record for tropical Africa is sparse relative to the Northern Hemisphere, but recent work shows that there is great potential to document plant evolution, ecosystem development, and to address biogeographic questions. Palms, for example, were an important component of Paleocene, Eocene and Oligocene forests, but do not play this role today. The fossil record offers the best access to information about what happened to palm diversity and ecological importance since the isolation of Africa after the breakup of Gondwana in the Cretaceous. West and Central African rainforests may have flourished first during the Oligocene, approximately 30 million years ago, and the composition of the eastern extent of these forests will continue to be investigated through the study of fossils from the Ethiopian Plateau. Woodland communities dominated by legumes and structurally equivalent to modern miombo were present as early as the Middle Eocene, 46 million years ago in Tanzania. Grasses, which are known from the continent since the Paleocene, became a presence first during the Middle Eocene, but became ecosystem dominants in the Middle to Late Miocene. Forest disjunctions between East and West Africa probably have a complex history, and their times of separation may have to await additional studies of plant communities from the Early Miocene of Uganda, the Western Rift, and West Africa. Such studies are possible, but paleobotanists must revisit at least the known localities using modern methods of collection, dating, and study. Finally, the Neogene in the East African Rift was represented by a variety of habitats associated with complex topography and climate changes, but did not change in a unidirectional way from forest to savanna during the Miocene.

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AN OVERVIEW OF ASCLEPIAD BIOGEOGRAPHY

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Abstract

The derived subfamilies of Apocynaceae, subfam. *Periplocoideae*, *Secamonoideae* and *Asclepiadoideae*, treated until recently as the family Asclepiadaceae, contain ± 3400 species in about 230 genera. There are three main centres of diversity – eastern and southern Africa, SE Asia, and Central and South America. This paper summarises the geographic patterns of diversity at generic level within each of the major clades and subclades identified in recent taxonomic literature. The study demonstrates that the generic diversity of the Old World subfamilies *Periplocoideae* and *Secamonoideae* is centered in Africa and Madagascar respectively. In the largest subfamily, *Asclepiadoideae*, all of the major clades (recognised mostly at tribal rank) occur in continental Africa, although the New World subclade comprising subtribes *Metastelmatinae*, *Oxypetalinae* and *Gonolobinae* is represented in Africa only by species assumed to be recent introductions. The three remaining clades of *Asclepiadoideae* found in the New World are represented there by single genera of predominantly Old World clades. Counter-intuitively, each of the early-divergent lineages *Fockeeae* (sister to all other tribes of subfam. *Asclepiadoideae*), *Eustegia* (sister to tribes *Marsdenieae* & *Ceropegieae*) and *Astephaninae* (sister to Old World & New World clades of tribe *Asclepiadeae*) occur in arid or seasonally arid regions of Africa and Arabia, suggesting the move into dry environments occurred very early in the evolution of the *Asclepiadoideae*.

Résumé

Un aperçu de la biogéographie des Asclepias. Les sous-familles des *Periplocoideae*, *Secamonoideae* et *Asclepiadoideae*, dérivées des Apocynaceae, et traitées jusqu'à récemment comme Asclepiadaceae, contiennent ± 3400 espèces réparties dans 230 genres environ. On leur attribue trois centres principaux de diversité – l'Afrique orientale et australe, l'Asie du sud-est et l'Amérique centrale et du sud. Cet article résume les modèles géographiques de diversité générique au sein des principaux clades et sous-clades identifiés dans la littérature taxonomique récente. L'étude démontre que la diversité générique des sous-familles *Periplocoideae* et *Secamonoideae* de l'Ancien Monde est centrée respectivement sur l'Afrique et sur Madagascar. Au sein de la plus large sous-famille, les *Asclepiadoideae*, les principaux clades (reconnus surtout au niveau de la tribu) sont présents en Afrique continentale, alors que le sous-clade du Nouveau Monde comprenant les sous-tribus des *Metastelmatinae*, *Oxypetalinae* et *Gonolobinae* n'est représenté en Afrique que par des espèces supposées être des introductions récentes. Les trois clades restants au sein des *Asclepiadoideae* et qui ont été trouvés dans le Nouveau Monde y sont représentés par des genres appartenant surtout à des clades de l'Ancien Monde. Contrairement à ce qu'on pourrait penser, chacune des lignées différenciées précocement, les *Fockeeae* (sœur de toutes les autres tribus de la sous-famille des Asclepiadoideae), *Eustegia* (soeur des tribus *Marsdenieae* et *Ceropegieae*) et *Astephaninae* (soeur des clades de la tribu des Asclepiadeae de l'Ancien et du Nouveau Monde) est observée dans des régions arides de façon permanente ou saisonnière en Afrique et en Arabie, ce qui suggère qu'un déplacement vers des environnements secs a eu lieu très tôt dans l'évolution des *Asclepiadoideae*.

Key words: Apocynaceae, arid, Asclepiadaceae, geography, radiation

1 Introduction

Good (1947 & later editions, 1952) mapped the distributions of many taxa in the subfamilies *Asclepiadoideae*, *Secamonoideae* and *Periplocoideae*, and concluded that southern Africa and Madagascar are key areas of diversity for these groups. He also suggested that the presence of leaves in the genus *Frerea* argued for an Indian origin of the stem-succulent stapeliads.

However, in the light of recent advances, it is apparent that several generic and suprageneric delimitations were seriously misunderstood at the time of Good's papers, leading to doubts about many of his conclusions. For example, two groups with unusual disposition of pollinia, the Old World genus *Tylophora* and the New World genera *Matelea* and *Gonolobus* are now understood to be members of the *Asclepiadeae* on the basis of both morphological and molecular studies (Swarupanandan *et al.*, 1996; Liede, 2001). Good (1952) placed *Tylophora* in the *Marsdenieae*, and recognised a separate tribe, the *Gonolobeae*, for the New World group. Other groups where the generic limits or assumed affinities employed by Good have been discredited include the global concept of *Cynanchum*, and the *Sarcostemma*, *Philibertia*, *Funastrum* complex where similar floral morphology is the result of convergent evolution.

The current classification of Apocynaceae recognises five subfamilies, three of which (*Periplocoideae*, *Secamonoideae* and *Asclepiadoideae*) were formerly placed in the Asclepiadaceae. There is now good morphological and molecular evidence that these three groups arose from the more derived end of the old Apocynaceae – i.e. subfamily *Apocynoideae* (Endress, 1994; Endress & Bruyns, 2000; Goyder, 2000; Potgieter & Albert, 2001), but adequate analyses on the two basal subfamilies are still lacking.

The *Periplocoideae* were recently revised at the generic level by Venter & Verhoeven (2001), taking account of both palynological and gross morphological investigations by these and other authors. Considerable progress has been made on the *Secamonoideae* by Klackenberg (1992a, 1992b, 1995, 1996a, 1996b, 2001), Civeyrel *et al.* (1998) and Civeyrel & Rowe (2001) in a series of morphological, palynological and molecular studies. And most major groups of *Asclepiadoideae* now have some molecular framework (Liede, 2001; Liede & Kunze, 2002; Liede & Täuber, 2000, 2002; Liede *et al.*, 2002a, 2002b; Meve & Liede, 2002a, 2002b; Rapini *et al.*, 2003; Verhoeven *et al.*, 2003) to supplement morphological & species level studies (Swarupanandan *et al.*, 1996; Omlor, 1998, and many other workers), although some obvious lacunae remain, particularly concerning the *Marsdenieae*.

Fifty years on from Good's papers, I have chosen to re-examine his findings on the origin and diversity of the main groups by looking at geographic patterns of generic diversity within each major clade.

2 Methods

Genera referable to Apocynaceae subfamilies *Periplocoideae, Secamonoideae* and *Asclepiadoideae*, broadly defined where there are competing taxonomies, were mapped onto the TDWG Level 2 geographic units of Brummitt (2001). This gave a broadscale pattern of generic diversity for these subfamilies worldwide. The data were analysed further by studying the patterns of geographic diversity shown by each of the principal clades identified in recent molecular systematic studies of these groups. The phylogenetic overview presented by Rapini *et al.* (2003) based on *trnL-F* is used as the principal framework for discussion as all the major clades are represented (Fig. 1), but reference is made to more detailed investigations where appropriate.

2.1 Overview of subfamilies

Subfamily Periplocoideae (31 genera, 181 spp.)

An entirely Old World subfamily, 16 genera are found in continental Africa, 13 in tropical Asia, and 5 in Madagascar.

Venter & Verhoeven (2001) published a morphological cladistic analysis but the resulting cladogram was unresolved basally, and no large-scale molecular survey has been attempted as yet. Little inference can be made on the phytogeography of this group until more data become available.

Subfamily Secamonoideae (7 genera, 170 spp.)

Also restricted to the Old World, this subfamily is clearly centred on Madagascar, where 5 of the 7 genera occur. *Secamone* R.Br., by far the most species-rich genus in the subfamily, is also centred on Madagascar with ± 65 species on the island. Following the generic reallignment of Klackenberg (2001), *Secamone* is the only genus of this group found on the African mainland. A further 2 species occur in tropical Asia in addition to the genera *Toxocarpus* Wight & Arn. and *Genianthus* Hook. f.

The morphological cladogram published by Klackenberg (1996b) implies a Madagascan origin for the Secamonoideae, and a subsequent move into SE Asia. However, as with the Periplocoideae, no large-scale molecular survey has been published – the work of Civeyrel & Rowe (2001) covers only three secamonoid genera, and no material from Asia.

Subfamily Asclepiadoideae (± 180 genera, 3000 spp.)

The Asclepiadoideae are distributed worldwide, with three main centres of generic (and species) diversity – tropical Central and South America with 47 genera, eastern and southern Africa with 86 genera, and tropical Asia with 38 genera. Generic diversity in Madagascar is relatively low with just 12 genera represented, or 8 if *Sarcostemma* and allies are included within *Cynanchum.* Phytogeographic relations between Africa and Madagascar were discussed by Meve & Liede (2002a), who concluded that except for *Cynanchum*, where dispersal appears to have been from Madagascar to continental Africa, in all other cases where there are species in common between the two regions, dispersal has been in the opposite direction.

Recent morphological overviews of this subfamily have been published by Swarupanandan *et al.* (1996) and Endress & Bruyns (2000). Liede and co-workers have instigated many molecular studies focussing on particular tribes or subtribes, resulting in the detection of a number of major clades. The patterns of geographic distribution for each of these clades is discussed below using the recent outline published by Rapini *et al.* (2003). An overview of large-scale patterns is followed by a clade by clade summary, commenting on more detailed molecular studies as appropriate.

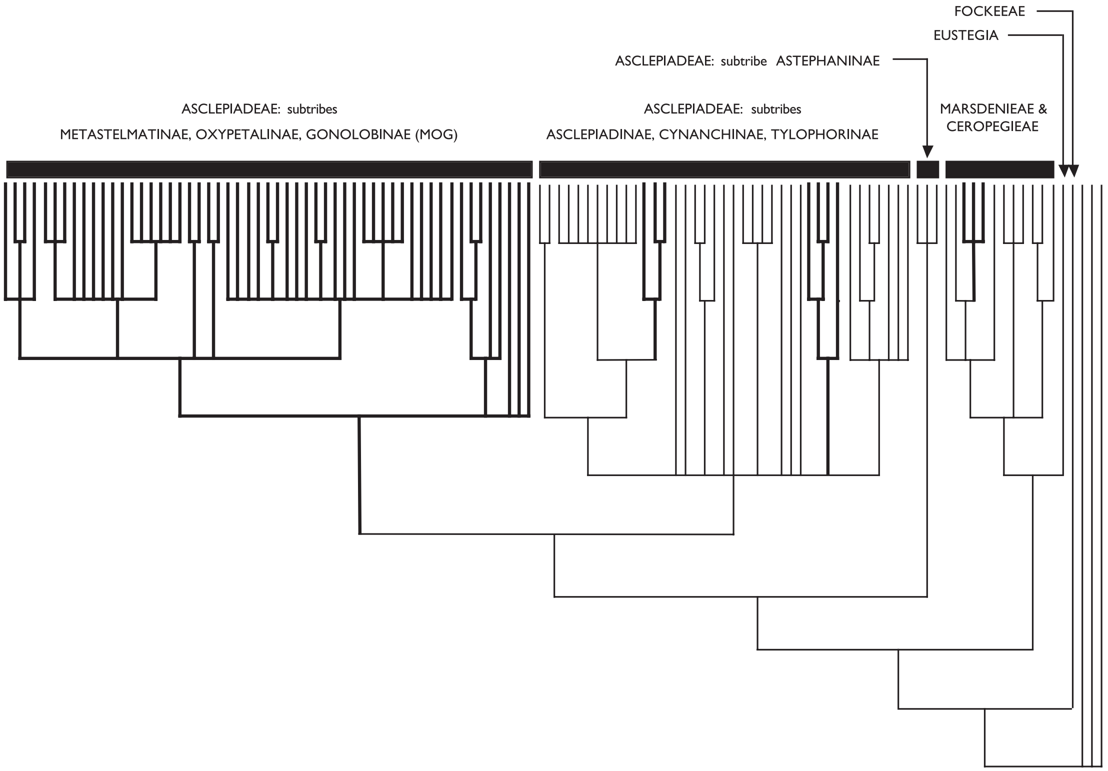

FIG. 1. Consensus tree of Apocynaceae subfamily *Asclepiadoideae* (posterior probability >94%) resulting from 40,000 trees generated from Bayesian analysis of *trnL-F*. See Rapini *et al.* (2003: Fig. 4) for bootstrap values, percentages of posterior probability and names of terminal taxa. Principal clades are labeled with the current tribe and subtribe, and the four New World clades are highlighted in bold – from left to right these are: MOG, New World species of *Asclepias*, *Cynanchum* and *Marsdenia*. The three unlabeled and unresolved outgroups are *Secamone glaberrima* (subfamily *Secamonoideae*), *Periploca graeca* (subfamily *Periplocoideae*) and *Apocynum androsaemifolium* (subfamily *Apocynoideae*). Redrawn from Rapini *et al.* (2003).

2.2 'Major' clades in subfamily Asclepiadoideae

The tribes Marsdenieae and Ceropegieae appear in an unresolved clade in the molecular overview of Rapini *et al.* (2003), but in the study by Verhoeven *et al.* (2003) on the relationships of *Fockea*, and the work of Meve & Liede (2004) on the Ceropegieae, they appear as separate clades.

Tribe Marsdenieae

The principal area of generic diversity is SE Asia, with 18 genera. A broadly delimited *Marsdenia* is the only member of this tribe in the New World. It also occurs in Madagascar and continental Africa, along with an additional 1 and 2 genera respectively. Until the tribe Fockeeae was erected by Kunze *et al.* (1994), the Marsdenieae had been regarded as the least morphologically derived tribe of the Asclepiadoideae.

Omlor (1998) published a morphological revision of the tribe, but representation of genera in this group is poor in the molecular surveys published to date. The study by Meve & Liede (2004) reveals two main clades – one comprising pantropical *Marsdenia* and its segregates (treated here under a broadly defined *Marsdenia*), and the other the largely SE Asian *Hoya/Dischidia* group. Although SE Asia is considerably more humid than other regions of asclepiad diversity, many species of the latter group occur in the forest canopy, and possess many xeromorphic adaptations. *Marsdenia*, at least in Africa and South America, occurs in seasonally dry forest. Further phytogeographic insight is limited by fact that only half of the marsdeniad genera were available for analysis.

Tribe Ceropegieae

The Ceropegieae are more or less vicariant with respect to the Marsdenieae. The centre of generic diversity is southern Africa – 38 genera are found on the African continent, eight in tropical Asia, and just three in Madagascar.

This is the part of the Asclepiadoideae that has received by far the most systematic study, but investigations have been skewed heavily towards the derived succulent genera. Within this groups of stapeliads, Meve (1997) documented polyploid series in *Duvalia*, which tracked the evolution of taxa from NE Africa to Arabia in one direction, and to southern Africa in the other. *Duvalia* sect. *Arabica* (NE Africa) is predominantly diploid, while sect. *Duvalia* (southern Africa) has diploid, tetraploid and hexaploid species. Bruyns' (2000b) cladistic biogeographic study based on a morphological analysis (Bruyns, 2000a) also argued for a NE African origin for the stapeliads, with radiations into India and southern and south-western Africa.

Meve & Liede (2004) have demonstrated that sister to the core group of *Ceropegia* and the stem succulent stapeliads, is a second group of African genera which they designate the Anisotominae. Sister to both of these clades is a small group of genera whose members are highly adapted for arid environments. These include the ephemeral, montypic *Conomitra*, which occurs on the southern margins of the Sahara, and *Orthanthera* and *Leptadenia*, which have African 'arid corridor' and Saharo-Sindian distributions. The earliest-divergent clade, however, sister to the rest of the tribe, comprises *Heterostemma*, a wet forest genus from SE Asia.

Tribe Asclepiadeae

Two vicariant clades are apparent in Rapini *et al.* (2003). These are, firstly, a clade comprising the subtribes Asclepiadinae, Cynanchinae and Tylophorinae – an Old World radiation centred on eastern and southern Africa (with 38 genera in the continent, seven in Madagascar and 12 in SE Asia). Just two genera occur in the New

World – *Asclepias*, which has a radiation centred on Mexico and the United States, and the small section of *Cynanchum*, subgen. *Mellichampia*, comprising just 12 species in Central and South America.

The second of the two major vicariant clades comprises the subtribes Metastelmatinae, Oxypetalinae and Gonolobinae – 44 genera restricted to Central and South America with the single exception of *Gonolobus*, which is presumably a recent introduction to West Africa.

The older lineages in each of the major groups of the Old World radiation occur in dry to arid regions of Africa and Asia. In the *Asclepias* group (Goyder *et al.* in prep.), *Kanahia*, *Calotropis* and *Pergularia* appear to be most 'basal', and are widely distributed in dry parts of tropical Africa and Asia. In the *Cynanchum/Glossonema* group, *Schizostephanus alatus* appears basal (Liede & Täuber, 2002), and occurs from the Horn of Africa south to Kruger National Park on the South Africa – Mozambique borders, largely on on rock outcrops in semiarid areas. Phylogenetic relationships in the *Tylophora* group (Liede *et al.*, 2002b) are not clear, but *Pentatropis* (Indian Ocean margins) and the East African clade *Diplostigma*, *Goydera*, *Pleurostelma* and *Blyttia* appear to have diverged early.

Much more work is needed to work out relationships in the New World radiation, but there are some suggestions that the older lineages are to be found in central (*Pentacyphus*) or southern Andean regions (*Diplolepis*) (Liede-Schumann *et al.*, 2005). Further study of the frequent reduction in basic chromosome numbers in members of the *Metastelmatinae* and *Oxypetalinae* (frequently reduced to x = 10, rarely x = 9* (*Funastrum*, *Diplolepis*, *Orthosia*, *Philibertia**, *Araujia*, *Oxypetalum**, *Tweedia*)) may also give valuable insights (Albers & Meve, 2001). The principal genera of the *Oxypetalinae* have a strong geographic element to their distributions, with *Oxypetalum* itself centred on Brazil, *Morrenia* and *Araujia* on the Chaco region, *Tweedia* restricted largely to Chile, and *Philibertia* in a newly enlarged delimitation) centred on the Andean dry valley systems of Bolivia and northern Argentina (Goyder, 2004). The large and problematic genera *Ditassa* & *Metastelma* were not in the survey, and the few *Gonolobinae* surveyed did not shown comparable chromosomal reductions.

2.3 'Minor' early-divergent clades in subfamily Asclepiadoideae

The following three early-divergent clades appear as sister groups to the major tribal and subfamilial radiations in Rapini *et al.* (2003).

Subtribe *Astephaninae*

The *Astephaninae*, as redefined by Liede (2001), is sister to all other members of the tribe *Asclepiadeae*. It consists of 3 genera (*Astephanus*, *Microloma* and *Oncinema*) which straddle the summer/winter rainfall divide in the Cape region of southern Africa. The group shows some highly derived characters, such as the reduced basic chromosome number (x = 10) and floral adaptations for bird-pollination in *Microloma*. Other characters such as the presence of clear latex are presumed to be plesiomorphic.

Eustegia

The position of the monotypic genus *Eustegia*, sister to the *Marsdenieae* and *Ceropegieae* clades, was noted by Liede (2001) and again by Rapini *et al.* (2003). This placement is surprising, as its affinities have always been assumed to be with the *Asclepiadeae* due to its pendant pollinia. It will be interesting to see if other molecular markers support this position. Nevertheless, the possession of clear rather than white latex could be cited as a link to the *Ceropegieae*, where clear latex occurs more or less throughout the tribe, and the *Marsdenieae*, where its occurence is frequent.

Bruyns (1999) studied the ontogeny of the ‘triple’ corona - actually of two series, an outer ± continuous ring broken up into 20 lobules, and an inner series of five discrete lobules opposite the anthers. He noted that the early stages were similar to those of *Fockea* (the most ‘basal’ of the early-divergent lineages, below) and some *Cynanchum* and *Schizoglossum*, except for the lack of fusion of the lobules. He noted that the inner & outer series were homologous to the two series in *Ceropegia* and the stapeliads (found also in many *Asclepiadeae*). Assuming affinities with the *Asclepiadeae*, Bruyns’ morphological analysis included no members of the *Marsdenieae* or *Ceropegieae* and suggested links to Arabian *Blyttia*. The enigmatic genus *Emicocarpus*, endemic to Maputo in southern Mozambique and not collected since the 1960s, has a very similar corona and, if it can be rediscovered, should be included in any future study of this group.

Eustegia is restricted to the winter rainfall area of the Western Cape.

Tribe Fockeeae

The Fockeeae are sister to all other tribes of subfamily *Asclepiadoideae*. The tribe contains just two genera – *Fockea* occuring across southern & eastern Africa from Namibia & the Cape to eastern Kenya – and *Cibirhiza*, with one species in Oman, and the other in Zambia and Tanzania. Both genera occur principally in seasonally dry summer rainfall regions, but *Fockea comaru* occurs in the SW Cape winter rainfall area (Court, 1987).

The combined distribution of the two genera conforms to the classic ‘arid corridor’ of Verdcourt (1969), de Winter (1971) and White & Leonard (1991).

4 Discussion

All three subfamilies clearly originated in the Old World, although more precise details are lacking particularly for the *Periplocoideae*. The *Secamonoideae* are clearly centred on Madagascar, and all tribes of the *Asclepiadoideae* occur in Africa, although the *Marsdenieae* are most diverse in SE Asia. Rapini *et al.* (2003) demonstrated that the vast majority of the *Asclepiadoideae* in the Americas are the result of a single massive radiation which parallels a similar African and Asian radiation. The three remaining clades of New World asclepiads presumably result from later dispersal events as, in each case, they are represented by single genera from otherwise Old World groups.

Several ancient lineages of the *Asclepiadoideae* fall into Verdcourt’s arid corridor (Verdcourt, 1969) or extensions of it into Saharo-Sindian territory suggesting that the move into dry environments occurred very early in the evolution of the *Asclepiadoideae* – the more ‘basal’ subfamilies *Rauvolfioideae* and *Apocynoideae* are most diverse in more mesic environments. The direction of migration has been tracked for some stapeliads southwards across Africa but it is not clear if this is repeated in other groups, although Bruyns & Linder (1991) argued that there was an early divergence into summer and winter rainfall zones in *Microloma* – a date dependent obviously on the creation of such weather patterns by the Benguella current.

In the New World, overall distribution shadows the pleistocenic arc of Pennington *et al.* (2000) and Prado & Gibbs (1993), but generally in higher, drier or more open habitats, and with older lineages in the central and southern Andes.

Van der Laan & Arends (1985) argued for an African origin for the Apocynaceae s.l. as most genera with basic chromosome numbers deviating from x = 11 occur outside Africa. Albers & Meve (2001) came to a similar conclusion based on chromosome size and numbers. But the fossil record has been of little use in substantiating these claims.

Although the 'basal' subfamilies are well-represented by pollen and megafossil records dated to the Early Eocene – mostly *Rauvolfioideae* – and subfamily *Apocynoideae* from the Middle Miocene, few if any records exist for the more derived subfamilies. There are records of *Tacazzea* (*Periplocoideae*) type pollen from the Oligocene in Cameroon, but no well-substantiated fossil record for either the *Secamonoideae* or the *Asclepiadoideae* (Magallón *et al.*, 1999; Collinson *et al.*, 1993; Muller, 1981). Collinson *et al.* (1993) regarded all records in the Plant Fossil Record database (Holmes, 1991) as unconfirmed for these subfamilies. One further key area of ignorance is what the apocynoid sister groups are for each of the asclepiad subfamilies, altough Middleton and co-workers are currently addressing this problem through a densely sampled molecular study.

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THE LOBELIACEAE ORIGINATED IN SOUTHERN AFRICA

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Abstract

The Lobeliaceae are a medium size plant family (± 1300 species in 34 genera) distributed throughout the world and particularly abundant in temperate and high elevation tropical areas. One center of diversity is southern Africa, but Australasia and the neotropics also have high generic and infrageneric diversity. Is one of these centers of diversity also the area of origin? A chloroplast DNA-based phylogenetic estimate for the Lobeliaceae is being developed with DNA sequence data from *atpB*, *rbcL*, and their intergenic spacer region. Results unambiguously identify southern Africa as the area of origin. This conclusion is strengthened by the sister-group relationship of the Lobeliaceae with the Cyphiaceae, a monogeneric African family with its center of diversity and area of origin in southern Africa.

Résumé

Les Lobeliaceae sont originaires d'Afrique australe. La famille des Lobeliaceae a une taille moyenne (± 1300 espèces au sein de 34 genres) et est distribuée à travers le monde mais est particulièrement abondante dans les régions tempéréres et tropicales de haute altitude. Un de ses centres de diversité est l'Afrique australe mais l'Australasie et les néotropiques présentent également une diversité générique et infragénérique importante. Un de ces centres de diversité serait-il également le centre d'origine? Une étude phylogénétique des Lobeliaceae, basée sur l'ADN chloroplastique, est en cours. Elle considère les données de séquençage de l'ADN à partir de *atpB*, *rbcL* et de la région non codante entre ces gènes. Les résultats permettent d'identifier sans ambiguïté l'Afrique australe comme étant le centre d'origine. Cette conclusion est renforcée par le fait que les Lobeliaceae et les Cyphiaceae sont des clades sœurs. Cette dernière famille monogénérique africaine a un centre d'origine et de diversité localisé en Afrique australe.

Key words: biogeography, *cp*DNA, *Cyphia*, Lobeliaceae, phytogeography

1 Introduction

The Lobeliaceae comprise ± 1,300 species in 34 genera (Wimmer, 1943, 1953, 1968). They are higher dicots (Order Campanulales, Class Asteridae) and so have floral parts mostly in fives, with the sepals alternate with the petals which are alternate with the stamens. In *Lobelia* (Fig. 1), the calyx is fused at the base and surrounds an inferior ovary containing two locules that develops into a dry capsule containing numerous small seeds. The corolla is also fused (in the case of *L. gregoriana* Bak.f. to the tips of the petals; Fig. 1), but during flowering it characteristically splits to the base on the back of these resupinate flowers (i.e. twisted 180°). The fused staminal column is a characteristic that readily distinguishes the family and is an important part of the pollination mechanism. During anthesis the pollen is released into the center of this hollow cylinder. The elongating style extends through the staminal column, putting pressure on the pollen mass. The tips of the anthers possess small bristles that are contacted by incoming pollinators, thereby opening the apical orifice and allowing deposition of pollen. Eventually the style emerges and opens to expose a bi-lobed stigma, making these plants protandrous. The remaining 33 genera were recognized based on a sexual system of classification, and thus have modifications of this basic organizational plan, such as fusion or freeing of floral parts, a shift in ovary position, reduction to a single locule, loss of resupination, or the production of baccate (fleshy) fruits.

The Lobeliaceae are distributed throughout many parts of the world and are most abundant in temperate and high-elevation tropical areas. There are several regions of the world with high generic and infrageneric diversity, most notably southern Africa, Australasia, and the neotropics. Is one of these centers of diversity also the area of origin?

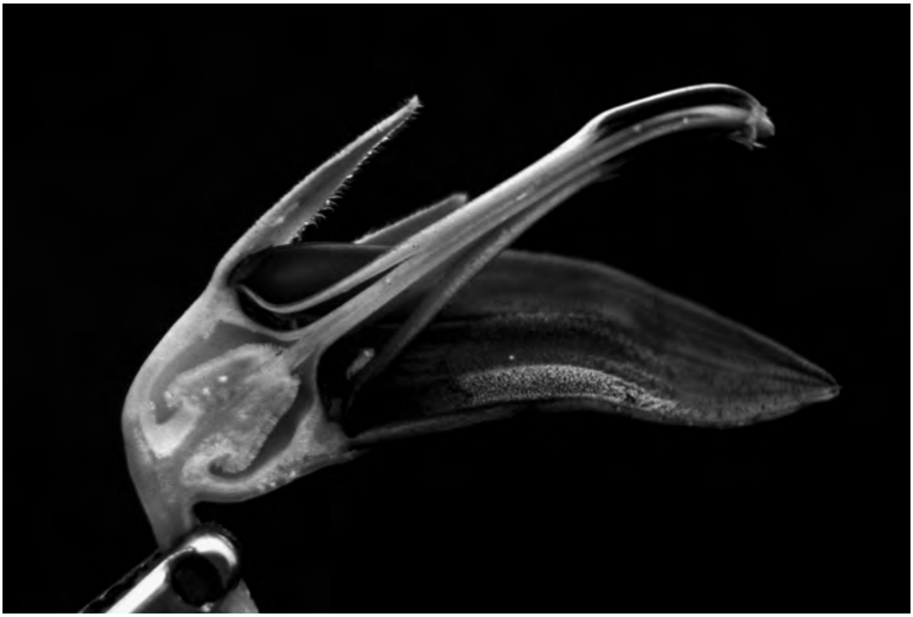

FIG. 1. Longitudinal section of a flower of *Lobelia gregoriana* Baker f. subsp. *sattimae* (R.E.Fr. & T.C.E.Fr.) E.B.Knox from the Aberdare Mountains, Kenya. The fused staminal column plays an important role in the pollination mechanism and is a characteristic feature of the Lobeliaceae.

2 Materials and methods

A phylogenetic estimate for the Lobeliaceae (and closely related Cyphiaceae) is being developed with DNA sequence data from the chloroplast genes *atpB* and *rbcL* and their intergenic spacer region. This segment of the plastid genome comprises ± 3800 nucleotides, and the combination of slowly evolving genes and the more rapidly evolving intergenic region provides good resolution and robust results. About 350 samples have already been sequenced, with 150 additional samples currently being processed. Outgroup taxa include *Nicotiana* (Solanaceae), *Stylidium* (Stylidiaceae), and four genera (*Canarina*, *Codonopsis*, *Musschia*, and *Trachelium*) that form pairs on either side of the most basal branch within the Campanulaceae (W.M.M. Eddie and R.K. Jansen, pers. comm.). A full presentation of the DNA results will be published elsewhere after the current laboratory work is complete, but an overview and some initial conclusions are reported here.

Most of the plant material has been field-collected, and we are indebted to many botanists who have contributed material that we otherwise would not have obtained. Previous molecular work with *Downingia* (western North America; Schultheis, 2001), *Lysipomia* (South America; T. J. Ayers *et al.*, pers. comm.), and the giant lobelias from Hawaii (Givnish *et al.*, 1994, 1995) and eastern Africa (Knox & Palmer, 1998) obviates the need for extensive sampling within each of these groups. The most intensive collecting is from South Africa and Australia/New Zealand, where we have achieved almost complete taxonomic sampling.

The aligned DNA data-matrix was analyzed with PAUP* (Swofford, 1998). The resulting phylogenetic estimate (strict consensus) was used as a constraint for determining the minimum geographic distances among sampling sites following the methods of Knox & Palmer (1998; see also Knox, 1999). Briefly, this is an optimization technique for biogeographic reconstruction that starts at the tips of the phylogenetic estimate and uses the latitude and longitude of each collecting site to plot a minimum distance map according to the relationships of the phylogenetic estimate. The result is a projection of the phylogenetic relationships onto a map of the collecting sites.

3 Results

The Lobeliaceae form a clade that is sister to the monogeneric Cyphiaceae (Fig. 2). *Lobelia* is the 'core genus' of the Lobeliaceae, with the remaining genera being segregates based on unusual morphological modifications of the reproductive features shared by the lobelias. The phylogenetic positions of *Cyphia* and the African genera of Lobeliaceae (Table 1) are shown in Fig. 2.

Biogeographic reconstruction on a continental scale (Fig. 3) unambiguously identifies Africa as the continent of origin for the Lobeliaceae. This same conclusion is reached even if the exclusively African Cyphiaceae are removed from the analysis. However, not all African Lobeliaceae result from autochthonous diversification on the continent. Two immigration events from the Asia/Pacific region best account for the phylogenetic placement of the Madagascan *Dialypetalum* and the African giant lobelias. In contrast, the high diversity of Lobeliaceae in Australasia is due to the combined effect of multiple immigration events from various sources at different times and autochthonous diversification following the early colonizations. Although more than half the species of Lobeliaceae grow in the neotropics, this high diversity results primarily from the rapid radiation of the shrubby 'CBS' clade (*Centropogon*, *Burmeistera*, and *Siphocampylus*), a dramatic example of co-evolution of the plants with hummingbird and bat pollinators and frugivorous seed-dispersers.

TABLE 1. Genera of Cyphiaceae and Lobeliaceae in Africa.

Family Genus (# of species)	Distribution	Species Sampled
Cyphiaceae		
Cyphia (± 80)	Southern and Tropical Africa	36
Lobeliaceae		
Lobelia (± 350)	Worldwide	130
Solenopsis (4)	Mediterranean	1
Dielsantha (1)	West African Highlands	1
Dialypetalum (5)	Madagascar	1
Monopsis (15)	Southern and Eastern Africa	14
Grammatotheca (1)	Southern Africa	1
Unigenes (1)	South Africa	1
Wimmerella (11)	South Africa	10

Recall that a cladogram is a one-dimensional model (with time as the only axis and all living samples taken from the Present) and that it can be rotated (like a hanging mobile) at each internal node. As a result, a horizontal model of the relative recency of common ancestry has no fixed vertical organization except for the obvious requirements that the ultimate outgroup (in this case, *Nicotiana* in the Solanales) occupy either the very top or the very bottom position and that the lines do not cross. Within the constraints of the cladistic structure, the vertical layout remains a discretionary matter, and the organizational principles used to guide the lay-out decisions for each cladogram should be made explicit. In this case, the African giant lobelias are placed at the bottom. The vertical organization of clades along the resulting 'backbone' thus tells the story of 'the other groups that evolved at each step of diversification that led to the giant lobelias'. Within each of these clades, samples are generally organized from the north and west (top) to the south and east (bottom).

The biogeographic reconstruction for the African Lobeliaceae and Cyphiaceae (Fig. 4) unambiguously places the origin of both families in southern Africa, most likely in the Western Cape region. If this place of origin is correct, then the biogeographic history within Africa involves repeated dispersal east and north along the mountainous 'spine of Africa', repeated dispersal to the West African highlands, and repeated dispersal from the mainland to Madagascar. These patterns are seen more clearly when presented for individual clades, which follow the progression along the backbone of the cladogram from *Cyphia* to the giant lobelias.

The sampling to-date indicates an unambiguous origin of *Cyphia* (Fig. 2) in the winter rainfall areas of the Western Cape region of South Africa (Fig. 5a). The species in the summer rainfall areas of southern Africa (the Eastern Cape region, northward) do not form a clade and were derived from at least three different lineages from the diversification in the Western Cape. Similarly, the tropical species represent a minimum of three derivations from the temperate, summer rainfall area.

The first two clades of Lobeliaceae along the backbone comprise *Lobelia* species with apical bristles on all five anthers (subgenus *Lagotis* section *Holopogon*) and the derived, segregate genera with the same condition (see Wimmer, 1943, 1953, 1968 for the most recent monographic treatment). The first clade (Fig. 5b) contains the monotypic *Dielsantha galeopsoides* (Engl. & Diels) E.Wimm. (Fig. 2) from West Africa, most of the

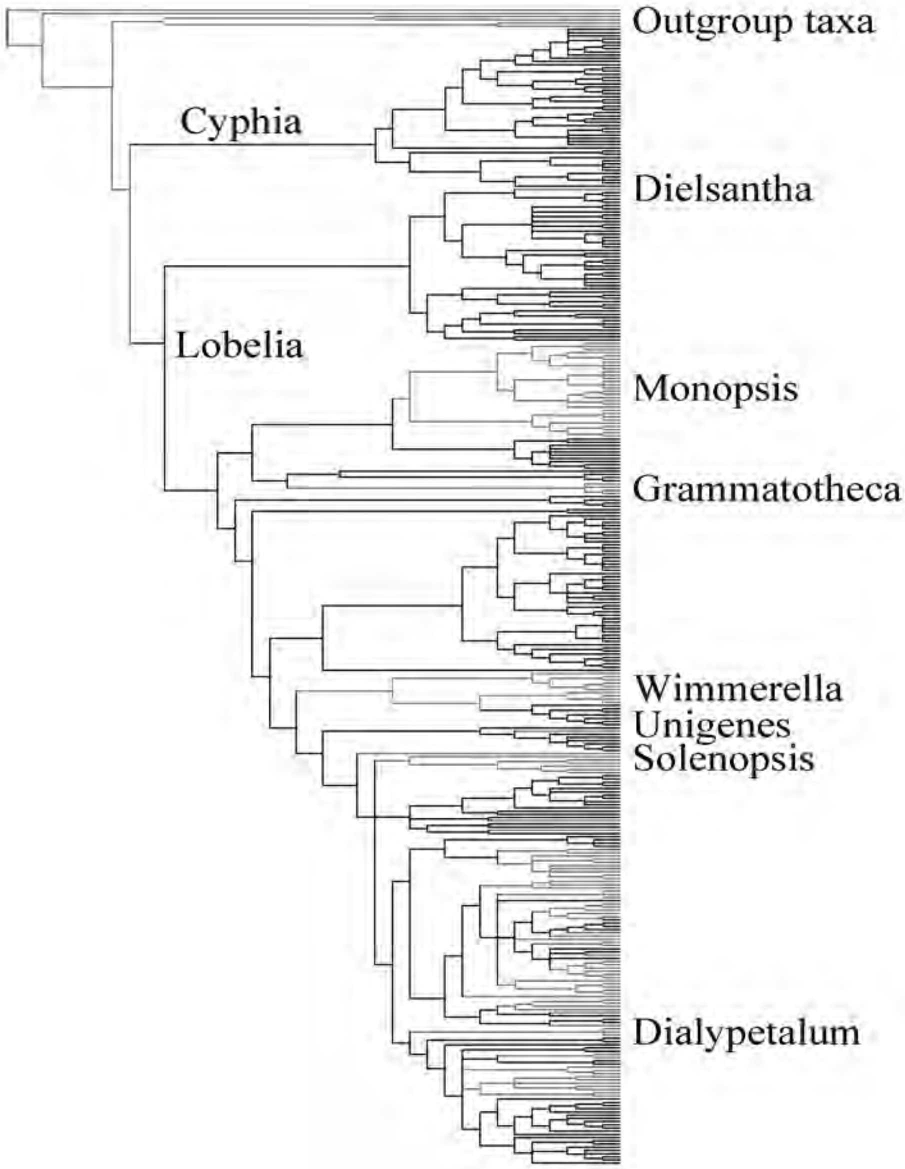

FIG. 2. Phylogenetic estimate for the Cyphiaceae and Lobeliaceae based on DNA sequence variation of the chloroplast genes *atpB* and *rbcL* and the intergenic region between them. *Cyphia* (labeled to the left and indicated in black) forms a monogeneric family sister to the Lobeliaceae. *Lobelia* (also labeled to the left and indicated in black) is the 'core genus' of the Lobeliaceae, being paraphyletic to the remaining 33 segregate genera. Only the segregate genera present in Africa (Table 1) are indicated.

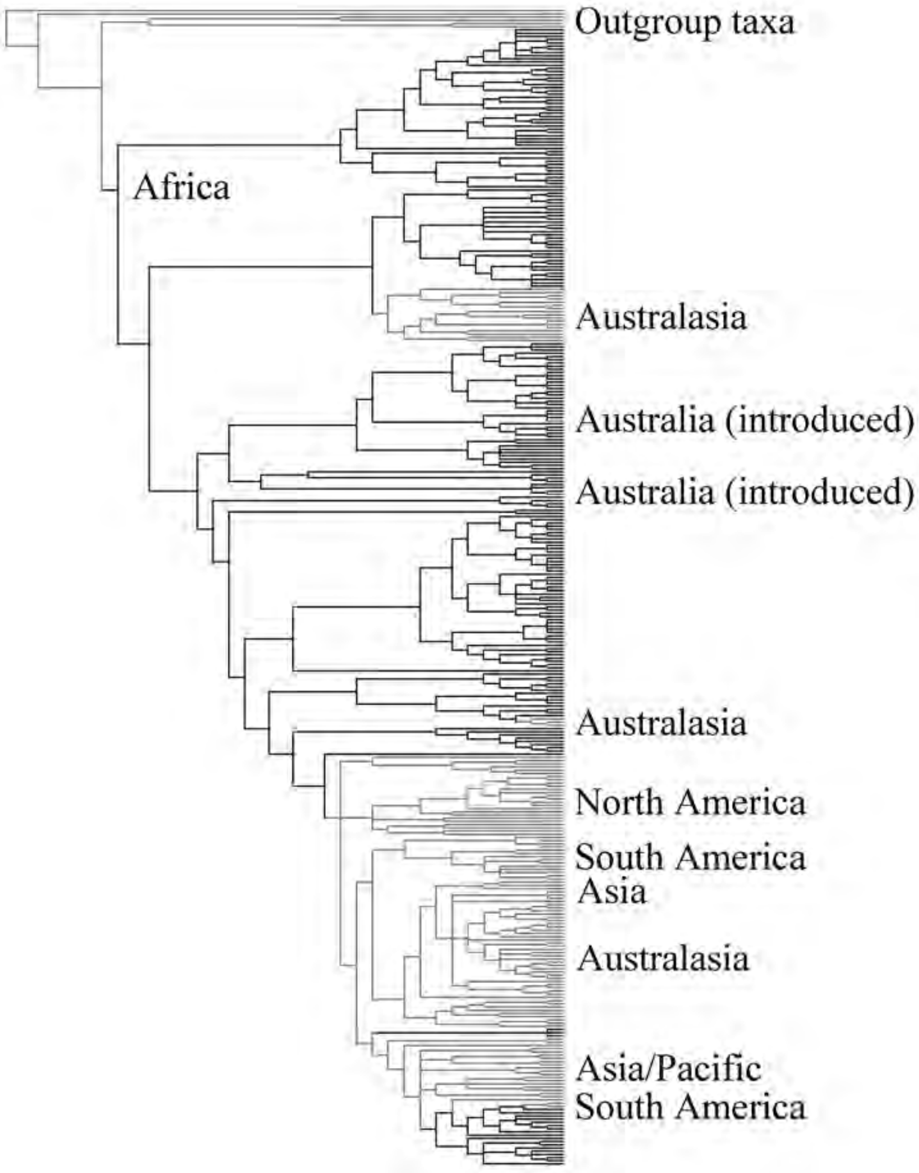

FIG. 3. A continental-scale biogeographic reconstruction for the Cyphiaceae and Lobeliaceae based on the phylogenetic estimate (Fig. 2) indicates that the Cyphiaceae originated and are restricted to Africa and that the Lobeliaceae originated in Africa, colonized other parts of the world, and then returned at least twice to Africa and Madagascar. The terminal and inferred ancestral lineages marked in black indicate those that diversified in Africa, whereas the lineages marked in gray indicate the undetermined biogeographic reconstruction for the outgroup species and the non-African portions of the diversification of the Lobeliaceae.

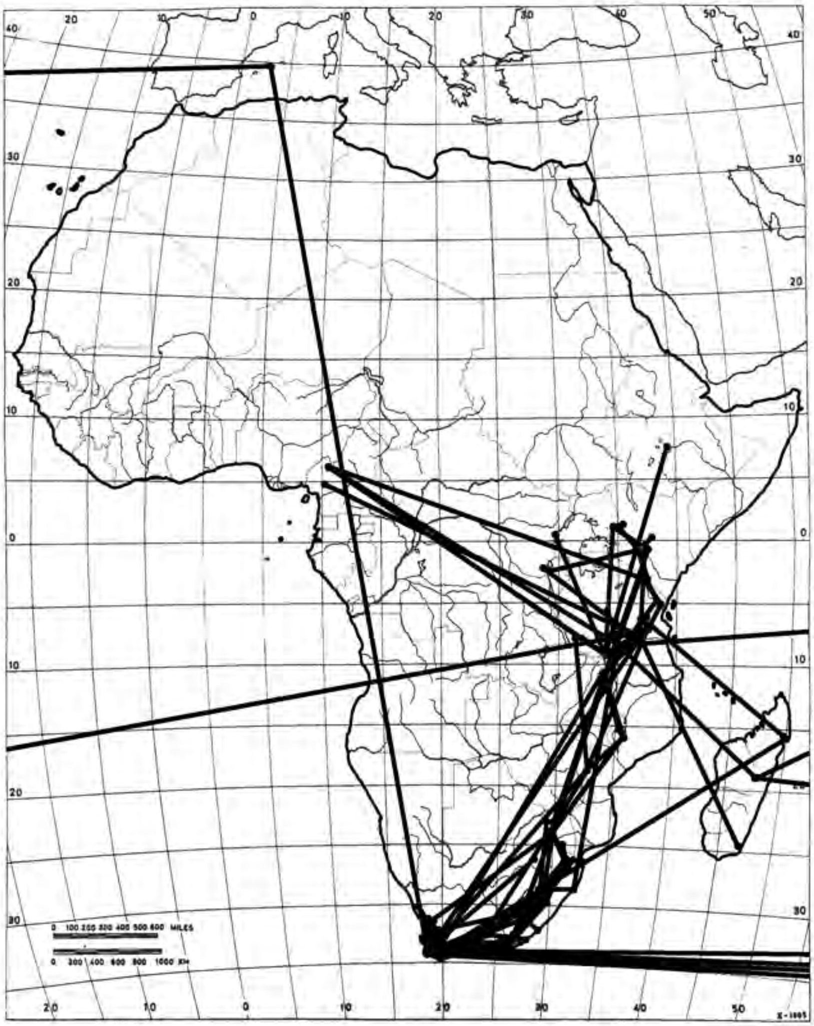

FIG. 4. Biogeographic projection of minimum distance among sampling sites as constrained by the phylogenetic estimate (Fig. 2). The reconstruction indicates that the area of origin for the Cyphiaceae and Lobeliaceae is southern Africa, and most likely the Western Cape region for the initial diversification. Various lineages then repeatedly moved from the winter-rainfall habitats of the Western Cape to the summer-rainfall habitats of the Eastern Cape and points to the north, moved repeatedly along the mountains that comprise 'the spine of Africa' to reach the tropics, dispersed repeatedly to reach the West African highlands and Madagascar, and in at least one instance reinvaded southern Africa. Dispersal on four occasions reached Australia, two of which pre-date human exploration and two of which are likely human introductions. Amphitropical dispersal accounts for Mediterranean endemic *Solenopsis*, which is sister to the lineage that colonized and diversified in North America, South America, Australasia, the Asia/Pacific region, eventually reaching Africa again and continuing on to Brazil. Dots indicate sampling sites. Lines indicate projected branches of the phylogenetic estimate (Fig. 2) that minimize total geographic distance.

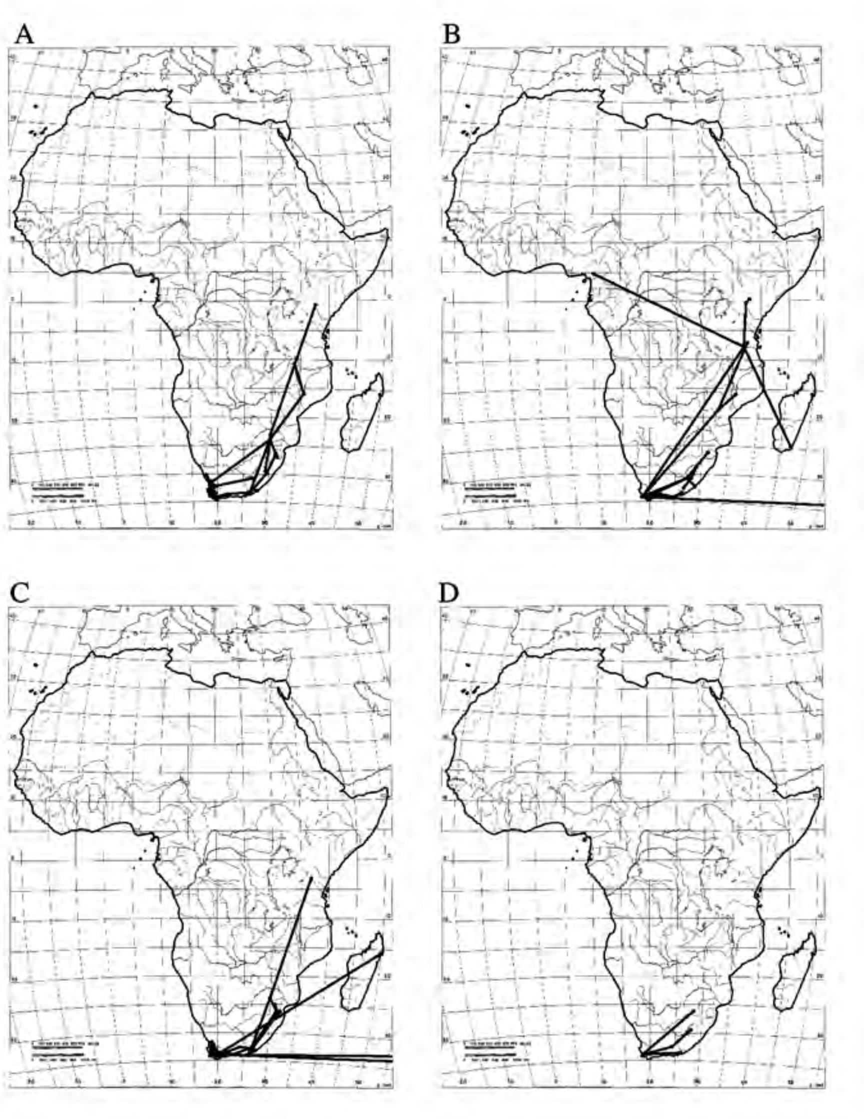

FIG. 5. Clade-by-clade biogeographic reconstruction along the 'backbone' of the phylogenetic estimate (part 1). A. *Cyphia* originated in the Western Cape and is restricted to Africa. B. The first holopogonoid *Lobelia* clade reached the summer-rainfall areas, the tropics, West Africa (giving rise to *Dielsantha*), Madagascar, and Australasia (giving rise to *Colensoa*). C. The second holopogonoid *Lobelia* clade reached the summer-rainfall areas, the tropics, and Madagascar, and gave rise to *Monopsis* and *Grammatotheca*, which diversified in South Africa and were likely introduced to Australia. D. The first and second mezlerioid *Lobelia* clades primarily occur in southern Africa, but have occasionally been collected in eastern Africa.

African holopogonoid lobelias, and a well-delimited group of holopogonoid lobelias from Australia (that subsequently gave rise to the segregate genus *Colensoa* in New Zealand and Australasia). Within Africa, the holopogonoid lobelias have diversified in the Western Cape region, dispersed at least once to the summer rainfall areas, where they diversified, with one small clade (*L. patula* L.f., *L. dasyphylla* E.Wimm., and *L. ardisiandroides* Schltr.) re-entering the Western Cape. At least two lineages dispersed up the spine of Africa, with subsequent dispersal to the West African highlands and to Madagascar. The second Lobeliaceae clade (Fig. 5c) contains a complex group of holopogonoid lobelias from the Western Cape with a 'broom' growth-form, a few odd members of the African holopogonoids that lacked clear affinities (based on morphology), and the segregate genera *Monopsis* and *Grammatotheca* (Fig. 2). The biogeographic projection again starts in the Western Cape, with at least two points of dispersal into the summer rainfall area, at least one point of dispersal back into the Western Cape, one species that spread into tropical Africa, and one dispersal to Madagascar. *Monopsis debilis* (L.f.) C.Presl subsp. *depressa* (L.f.) Phillipson and *Grammatotheca bergiana* (Cham.) C.Presl are present in Australia, presumably as naturalized introductions in hay shipped with cattle from South Africa, an interpretation bolstered by the very limited molecular variation present in each species.

The next two small clades (Fig. 5d) contain small, annual species that comprise a clear group within *Lobelia* subgenus *Mezleria*. They typically occur along the moist margin of a drying vlei (i.e. a vernal pool), or in a comparable ecological setting, but do not necessarily germinate every year. More sampling is clearly desirable from the species with widespread distribution in southern Africa, but these must be acquired opportunistically. However, the emerging biogeographic reconstruction shows a pattern consistent with that of other clades.

The next clade (Fig. 6a) comprises most of the African members of *Lobelia* subgenus *Lagotis* section *Hemipogon* subsection *Leiospermae*, including the widely planted ornamental *L. erinus* L. and its wild ancestor. The biogeographic reconstruction indicates an origin for this clade in South Africa. One South African lineage is represented only by the Drakensberg species, *L. laxa* MacOwan. The other South African lineage gave rise to *L. erinus* (which has migrated up the spine of Africa) and at least seven derivative species, which are geographically restricted and ecologically specialized. A third lineage is inferred to have diversified in eastern tropical Africa, giving rise to one species that reached the summer rainfall area of South Africa [*L. flaccida* (C.Presl) A.DC.], two dispersal events to Madagascar (*L. fervens* Thunb. and *L.* cf. *vagans* Balf.f.; the latter lineage having also reached the Mascarene Islands), and three dispersal events to the West African highlands (*L. adnexa* E.Wimm., *L. rubescens* De Wild., and *L. neumannii* T.C.E.Fr.).

The next clade (Fig. 6b) comprises *Wimmerella* and *Lobelia anceps* L.f. *Wimmerella* comprises eleven species with completely fused corollas, four of which are small, fragile cave-dwellers. *Wimmerella* clearly originated in the Western Cape, and two species have ranges extending into the Eastern Cape and slightly beyond. *Lobelia anceps* clearly originated in South Africa and dispersed to Australia and New Zealand. The depth of molecular variation among the samples suggests that colonization of Australia and New Zealand by *L. anceps* predated human exploration of the world. *Lobelia anceps* also grows in Chile, on both the mainland and the Juan Fernandez Islands. These populations have not been sampled yet to determine whether they were colonized directly from South Africa or via Australia/New Zealand.

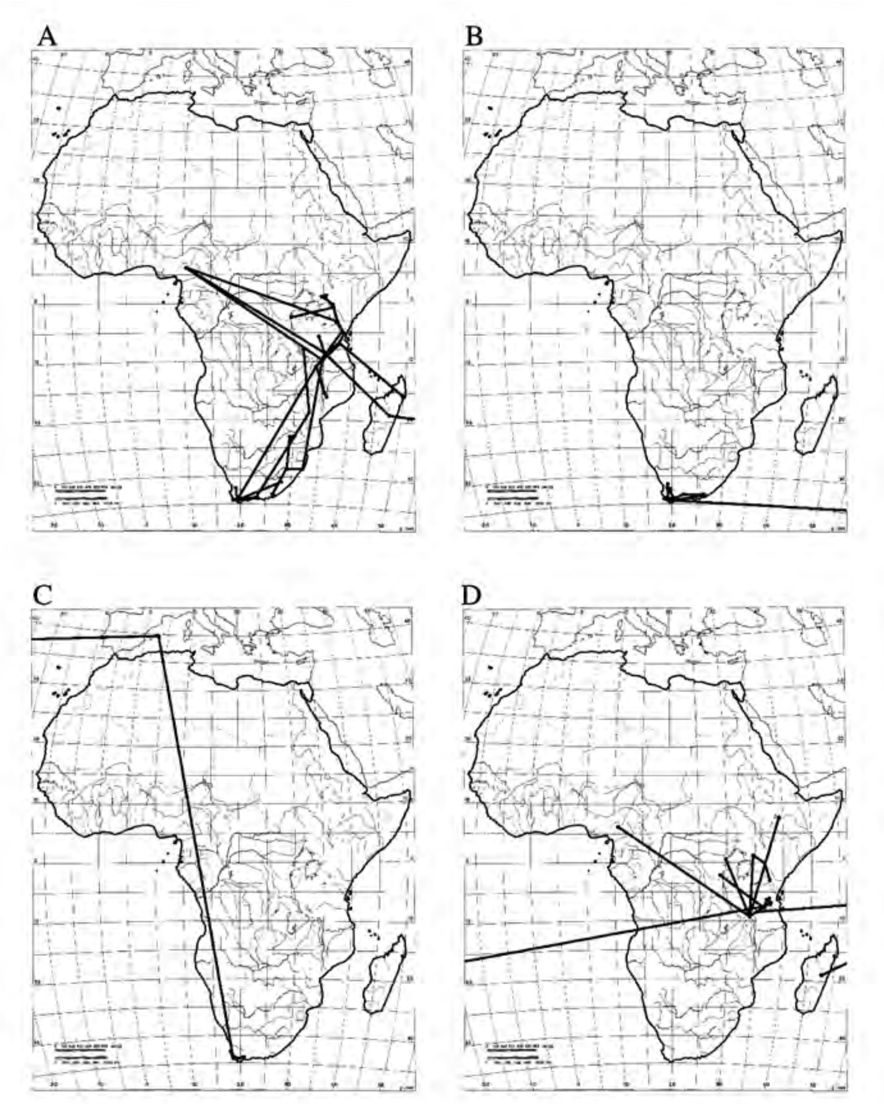

FIG. 6. Clade-by-clade biogeographic reconstruction along the ‘backbone’ of the phylogenetic estimate (part 2). A. The erinoid *Lobelia* clade reached the summer-rainfall areas, the tropics, West Africa (repeatedly), Madagascar (and Mauritius), with one lineage re-entering southern Africa from the tropics. B. The *Wimmerella* clade is restricted to South Africa except for *Lobelia anceps*, which has reached Australia and New Zealand [and also occurs on the mainland and Juan Fernandez Islands of Chile (not yet sampled)]. C. The third mezlerioid *Lobelia* clade is restricted to the Western Cape and is sister to the Mediterranean *Solenopsis* and most non-African Lobeliaceae. D. The Lobeliaceae reached Africa at least twice from the Asia/Pacific region, giving rise to the Madagascan *Dialypetalum* and the African giant lobelias that subsequently dispersed to Brazil.

The next two clades (Fig. 6c) comprise a small group of five species that are restricted to the Western Cape and then a lineage represented only by the segregate genus *Solenopsis*, which is restricted to the Mediterranean. The small Western Cape clade includes the remaining species of *Lobelia* subgenus *Mezleria* and the segregate genus *Unigenes*, which has a superior ovary bearing a single seed. *Solenopsis*, like *Wimmerella*, has the corolla completely fused.

The next stage along the backbone of the phylogenetic estimate encompasses the main colonization and diversification in North America, South America, Australasia, and eastern Asia/Pacific islands (Fig. 3). More sampling of Asian Lobeliaceae is needed to fully reconstruct their biogeographic history, but the current sampling clearly indicates that the Madagascan *Dialypetalum* (Fig. 2) and the African giant lobelias arose as re-introductions from non-African ancestors (Fig. 6d). *Dialypetalum* comprises five species that are large plants with racemes of numerous, small flowers with five equal petals that are free to the base. The giant lobelias in Africa are part of a pantropical radiation that also includes dispersal from Africa to Brazil.

4 Discussion

The conclusion that the Cyphiaceae and Lobeliaceae originated in southern Africa (and most likely in the Western Cape) seems obvious from the available evidence (Figs. 3–6). With the work in progress, we will have attained almost complete taxonomic sampling for the Lobeliaceae in South Africa. Our goal in this effort was to reconstruct completely the phylogenetic relationships of the species in this area of origin, but has this extensive sampling biased the results? The answer is no, for two reasons.

First, we also have almost complete taxonomic sampling for the Lobeliaceae in Australia and New Zealand. This extensive Australasian sampling merely elaborates the pattern of multiple introductions that was already apparent based on more limited sampling. Hence, there is nothing about extensive sampling *per se* that biases the phylogenetic estimate or the associated biogeographic reconstruction. The initial results we obtained were suggestive of a South African origin, and the extensive sampling now available merely clarifies the full extent of the diversification in the region.

Second, although the extent of sampling in South Africa has been matched in Australasia, the inverse question could be asked concerning groups that were possibly undersampled. Stated differently, should we still expect this conclusion of a South African origin to be supported if we had almost complete taxonomic sampling throughout the family? The answer to this hypothetical question is probably yes because there is not enough outstanding (i.e. unsampled) diversity (based on morphological variation or species numbers) in Asia or the neotropics to counteract the strong African pattern already established (Fig. 3). Most of the segregate genera and the infrageneric taxa within *Lobelia* have been sampled. Expanded sampling in other regions is predicted to elaborate the bold continental patterns already discovered (where most of the morphological variation results from autochthonous diversification), and to add a few more instances of intercontinental dispersal, as locally anomalous species are shown to have geographically distant relatives.

The general conclusion of an African origin for the Lobeliaceae is unambiguously refined to southern Africa, and most likely to the Western Cape, based on our biogeographic reconstruction. For *Cyphia* and the first seven clades of Lobeliaceae (along the backbone), (1) all have representatives in the Western Cape, (2) most are unambiguously reconstructed as having originated in the Western Cape, and (3) one is restricted to the Western Cape. The aggregate pattern (Fig. 4) shows fairly clearly the southerly origin, the repeated movement up and down the spine of Africa, the repeated dispersal to the West African highlands, Madagascar, and Australia, the arrival from the Asia/Pacific region of *Dialypetalum* and the giant lobelias, and the westward dispersal of herbaceous lobelias in North America and of the giant lobelias to Brazil.

Although this reconstruction based on minimum biogeographic distance provides clear conclusions on a broad scale, it obviously over-simplifies many of the terminal events. For example, the phylogenetic relationships clearly establish that there were at least four dispersal from the mainland to Madagascar (Fig. 4), but the actual points of departure and arrival are not necessarily those currently occupied by the populations sampled. The connections in the biogeographic reconstruction merely represent the shortest distances based on the contemporary sampling. This over-simplification, however, is not a short-coming of biogeographic reconstruction *per se* because sampling must occur at a level of organization below the phenomenon of interest. Additional geographic sampling across the range of each terminal taxon would provide an indication of the amount of variation (and its geographic structure) present within each taxon. A species that recently diverged and greatly expanded its range may possess little of the DNA variation needed to trace such events, but in other cases geographically structured variation may show a clear historical pattern.

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RESTRICTED RANGE ENDEMISM IN EAST AFRICAN PLANTS

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Abstract

A list of 1335 East African plant species likely to be restricted to a distribution area of less than one degree square (approximately 10,000 km^2) has been generated from the published families of Flora of Tropical East Africa (FTEA). Our list shows that of the species recorded for FTEA, about 10% might be narrow endemics. We give details on distribution and habitat for these single-degree endemics, as well as for specific areas that have a large number of narrow endemics, such as the Usambara and Uluguru Mountains. Families and genera in which narrow endemism occurs quite commonly are examined: the families with the largest number of narrow endemics are Rubiaceae and Leguminosae, but the families with the largest percentage of narrow endemics are Aloaceae and Balsaminaceae. Forest as a habitat has the largest number of narrow endemics, followed by woodland, bushland and grassland. A subset of the main list are treated in greater detail. Overall reasons for narrow endemism in East African plants and possible conservation issues are discussed.

Résumé

Endémisme à petite échelle de plantes d'Afrique de l'est. Une liste de 1335 espèces végétales d'Afrique de l'est dont l'aire de distribution semble inférieure à un degré-carré (environ 10.000 km^2) a été produite à partir des familles publiées dans la 'Flora of Tropical East Africa' (FTEA). Notre liste montre, parmi les espèces traitées dans FTEA, qu'environ 10% pourraient être endémiques. Nous donnons des détails sur la distribution et l'habitat de ces endémiques limitées à un degré-carré et nous nous intéressons à des régions, comme les Monts Usambara et Uluguru, qui abritent un nombre important de ces espèces. Les familles et les genres au sein desquels un endémisme à petite échelle est fréquemment observé sont examinés: les familles avec le plus grand nombre de telles endémiques sont les Rubiaceae et les Leguminosae, mais les familles avec le plus haut pourcentage d'endémiques à petite échelle sont les Aloaceae et les Balsaminaceae. La forêt, en tant qu'habitat, abrite le plus grand nombre de ces endémiques, suivie de la forêt claire, des formations buissonnantes et de la savane. Une partie de la liste principale est traitée en détail. Les causes générales de l'endémisme à petite échelle chez les plantes d'Afrique de l'est et les implications possibles en matière de conservation sont discutées.

Key words: East Africa, FTEA, conservation, narrow endemism, single-degree endemics

1 Introduction

In Uganda, Kenya and Tanzania – the countries covered by the Flora of Tropical East Africa (FTEA) – endemism is not uncommon; but the occurrence of this endemism is uneven, some areas being rich in endemics, others poor. The East Coast has figured in the main centres of plant endemism from Hamilton (1982) to Linder (2001), and so have the Eastern Arc forests from Polhill (1968) to Taplin & Lovett (2003), and because of (unquantified) high numbers of endemics and high levels of threat these two areas combined have appeared as one of the hotspots of Myers (e.g. Myers *et al.*, 2000). We have set out to quantify narrow range endemism in East Africa to some degree.

The IUCN Red Data categories (IUCN, 2001) are an authoritative tool for conservation, providing quantitative thresholds for population size and range size, and taking trends into consideration. The resulting conservation assessments can be used in decision-making. However, for tropical Africa the number of conservation assessments is still very low: for East Africa, the total number is 426 (IUCN, 2002), or less than 5% out of a Flora of over 12,000 species. We provide the following method as a rapid assessment tool, requiring relatively little time and flagging species that are prime candidates for proper conservation assessments; a restricted range may be of key importance for conservation (Hall & Moreau, 1962) and species with restricted range may also have small population sizes (Brown, 1984). People with detailed knowledge of both species distribution and local conditions are required to make the final conservation assessment for each of these species; this will require much time and effort. On the other hand, our method can be used as a conservation tool in its own right, as it points out areas with high numbers of species with very restricted distribution: obviously prime areas for conservation.

2 Materials and methods

In a rapid read-through we have scanned the parts of FTEA appeared so far (up to December 31, 2002), and listed the full species that seemed to have restricted distribution, i.e. that looked as if they might be restricted to an area of less than 12,320 km^2. This rather arbitrary area is equivalent to one degree square at the equator, or 110.567 by 111.321 km. Subspecific taxa are excluded, unless all subspecific taxa of a species are within the 'narrow endemic' range. "Imperfectly known species", hybrids and non-described species ("sp. A") were excluded.

Such a group of possible restricted range endemic species is easy to assemble: possible candidates can be picked up through a look at the Flora parts by an informed observer. A similar rapid assessment, albeit more in-depth and with different parameters, has been done on the rare trees of Kenya (Beentje, 1988) and another one is in progress on the rare trees of Tanzania (Luke & Beentje, in prep.)

This one-degree distribution requirement is not the same as that used by Crisp and others in Australia (Crisp *et al.*, 2001) or Brooks *et al.* (2001) for African animals – their single degree distribution was linked to latitude/longitude grid cells. In our definition the 'single degree' part of the name refers to the extent of occurrence as defined by IUCN (2001), and the boundaries of such areas are determined by the georeferencing of the species. Such boundaries could have any shape – two groups of plant specimens 10,000 km apart would also fit in an 12,320 km^2 extent of occurrence. But we are trying to deal with more or less contiguous populations, as one of our main purposes is to come up with narrowly endemic species; therefore, we have set the extreme for linear distributions at 300 × 40 km.

This initial list will be quite imperfect: on one hand, it will miss species published since the FTEA part appeared for that family. On the other hand, many of the species included on the initial list will have a distribution wider than 12,320 km^2, or a more linear distribution than we allow for. Only georeferencing, mapping based on herbarium specimens and other records, will decide on this.

3 Results

Does our definition of narrow, 'single-degree endemism' (SDE) apply to enough species to make the concept useful? The initial run-through of FTEA parts appeared so far, in which 9,000 species were involved, produced a long list of possible candidates: 1335 species, or almost 15% of the total.

Some listings follow, in which all results should be taken as preliminary.

Single degree endemics (SDE) per country:
Uganda 139
Kenya 318
Tanzania 990
Note: SDE may occupy cross-border areas.

From the initial list, a subset of 160 taxa, or 12% of the total on the initial list, has been georeferenced from specimens deposited in the Kew herbarium and/or mentioned in the Flora. The taxa involved were chosen because they represent several different habitats: *Euphorbia* (with mostly drylands distribution: 62 possible SDE species out of 160 occurring in the Flora area; Carter, 1988); *Impatiens* (with mostly wet forest distribution: 36 SDE species out of 70; Grey-Wilson, 1982), *Cyphostemma* (with mixed habitat preference: 30 SDE species out of 93; Verdcourt, 1993) and all SDE Caesalpinioideae (dry to moist habitats: 32 SDE species out of 150; Brenan, 1967).

Twenty-five species turned out to have a wider distribution than our definition of SDE allowed, and were removed from the list.

The initial list has also been checked against the preliminary results of the 'Atlas of the endemic trees of Tanzania' (Luke & Beentje, in prep.) which deals with, and maps, 306 species. This partial control showed that 10 species had been overlooked in the first run-through of FTEA; and that 15 species had been published in those families since the relevant FTEA parts were published.

4 Discussion

The number of possible SDEs, 1335, from the original FTEA scan represents 15% of the 9000 species examined. Of the subset which was georeferenced, 16% turned out to be mistakenly included; if this percentage is subtracted from the initial list of 1335, we can extrapolate just over 1100 SDEs – which is still 12% of the species concerned.

Table 1 shows the eight families with the largest numbers of SDEs. The largest families in the region figure prominently, but it is interesting to note that the percentages of SDEs within these families vary considerably, being rather high (25%) in Rubiaceae and Euphorbiaceae, and about half of this percentage in Leguminosae and Compositae, while Gramineae only has about 5%. Some smaller familes show exceptionally high percentages: Aloaceae and Balsaminaceae have over half their consituent species as SDEs.

TABLE 1. Families with the largest number of single-degree endemics occurring in FTEA area.

Family	Number of SDE	Total species of family in FTEA area	% of SDE per family
Rubiaceae	192	756	25
Leguminosae	169	1227	14
Orchidaceae	138	682	20
Euphorbiaceae	131	527	25
Compositae I,II	69	571	12
Aloaceae	47	83	57
Balsaminaceae	36	70	51
Gramineae	41	864	5

TABLE 2. Genera with the largest number of single-degree endemics occurring in FTEA area.

Genera	number of SDE	Total species of genus in FTEA area	Percentage of SDE per genus
Euphorbia	62	160	39
Aloe	47	83	57
Crotalaria	43	199	21
Polystachya	38	85	45
Impatiens	36	70	51
Psychotria	33	81	41
Cyphostemma	30	93	32
Monadenium	28	39	72
Rytigynia	20	45	44

TABLE 3. Areas with the largest number of single-degree endemics.

	Occurrence in total (may occur outside as well)	Occurrence in this area only
Uluguru Mts (incl. 'Morogoro')	141	92
Usambara Mts	138	89
Iringa District	112	
Njombe District	70	
Mbeya District	60	
Morogoro District	55	
Lindi District	54	
Rungwe District	53	

Table 2 shows the nine genera with the largest numbers of SDEs. Percentages of SDEs per genus vary considerably, with *Aloe* (57% of the species are SDEs), *Impatiens* (51%) and *Monadenium* (72%) standing out.

Table 3 shows the eight areas with the highest number of SDEs. All these areas are in Tanzania. It has to be pointed out that well-known areas of high endemicity such as the Rondo Plateau do not show up as high as expected, probably because in the Flora they are not cited consistently as such; specimens might be cited as coming from Lake Lutamba, the Rondo itself, or other specific sites. It can be assumed that most SDEs occurring in 'Lindi District' are from the Rondo. Only complete georeferencing will show up focused 'hotspots'. The occurrence at the top of this list of the Usambara and Uluguru Mountains, both well-known areas of high endemicity, is in agreement with existing literature on the subject, such as Iversen (1991) for the Usambara and Burgess *et al.* (2002) for the Uluguru; it is interesting that Burgess *et al.* number the endemic plant species as 135, while the SDE recorded for the Uluguru are 141, with 92 restricted to the Uluguru (this study). These differences can be explained by the fact that not all endemics are necessarily SDEs, as some could have slightly larger ranges; and that some of the SDEs are not true Uluguru endemics, as they also occur elsewhere.

Table 4 lists all the neighbouring countries, all of which have SDEs in common with either Uganda, Kenya or Tanzania. This list is quite imperfect: several of the border regions are quite under-collected, especially in the cases of Sudan and Mozambique. Note that many of these might be false single degree endemics; distribution within these countries has not been checked with specimens, apart from in the species listed in appendix 2; however, there were reasons to assume distribution does not exceed a single square degree, such as distribution data cited in Floras.

Fig. 1 shows the number of SDEs per altitude class, based on the data in FTEA. A taxon may straddle more than one altitude class. The pattern, with a peak in the 1000–1499 and 1500–1999 m classes, is familiar from existing literature (e.g. Rahbek, 1997; Lovett, 1998) and also corresponds with the main (remaining) acreage of forest on several mountain blocks including, for example, the Uluguru Mountains (Burgess *et al.*, 2002).

TABLE 4. Neighbouring countries with which single-degree endemics occurring in FTEA area are shared.

Countries	SDE occurring in FTEA area shared
Somalia	12
Ethiopia	13
Sudan	5
Congo (Kinshasa)	60
Rwanda	22
Burundi	11
Zambia	29
Malawi	29
Mozambique	19

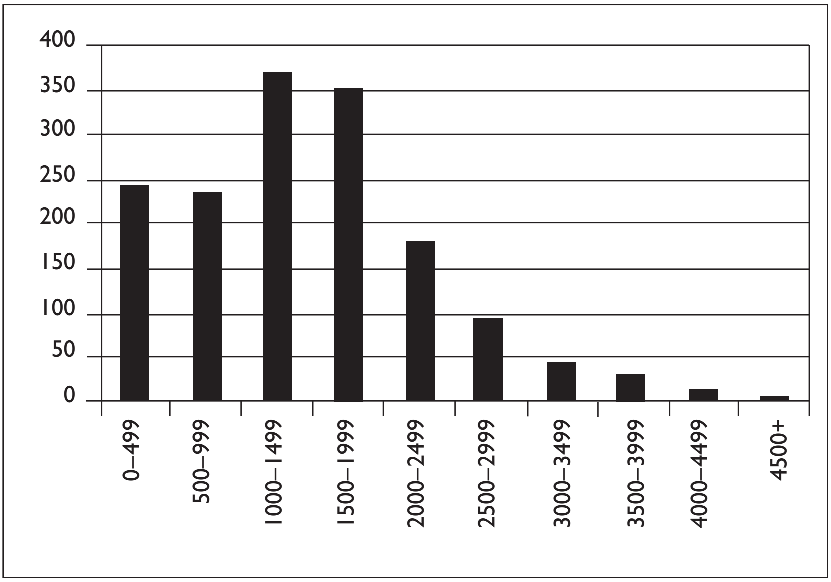

FIG. 1. Horizontal axis: altitude classes; vertical axis: number of SDEs within that altitude class.

Table 5 shows the distribution of SDEs by habitat type, based on FTEA data. It is no surprise that forest (all types) is the richest habitat type for SDEs, as it is the most diverse habitat for species *per se*. Other reasons could be that in a forest there are probably more microclimates than in grassland or woodland, and hence possibly more narrow endemics. Pollinators may also prove a factor – families with high numbers of SDE are insect-pollinated. The choice of genera for the subset precludes habitat conclusions, as they were chosen on the basis of habitat! Bushland, woodland and grassland are about equal in second place; more specific habitats contain smaller numbers of SDEs, and taxa may straddle several classes (e.g. rocky slope in bushland).

There are various subtypes of SDE: from the georeferenced subset, 28 are single-collection species (e.g. *Euphorbia fuscorum*, *Cyphostemma adenocarpum*); 20 are only known from 2 collections, and another 17 are only known from 3 collections. A total of 65 species represented by three or fewer collections out of a total of 135 is almost 50%. This may result from the species occurring in undercollected areas, such as in *Euphorbia dauana*, known from 2 collections in the Ramu area, NE Kenya; when such areas are explored better, such taxa might have to be removed from the SDE list. Other species, e.g. *Euphorbia tanaensis*, are apparently genuinely very rare; the species mentioned is known from 3 specimens collected in the Witu Forest; it has been searched for in likely sites, but it seems genuinely restricted to its single known site. *Stephanostemma stenocarpum* is known from only 40 individuals in a graveyard near Dar es Salaam (cited in Clarke *et al.*, 2000).

In some cases recent collections have extended the known distribution areas: *Stuhlmannia moavi* was restricted to the Tanga/Pangani area, but recent collections by Luke & Luke have extended this to the Selous, almost (but not quite) removing it from the SDE list. *Karomia gigas* was known from a single tree at Mwarakaya in Kenya; this tree was cut down in the 1980s (Beentje, 1988). Subsequently, this species was rediscovered in a tiny fragment of forest in SE Tanzania (Clarke, 1995) – it is not a SDE any more, but certainly highly endangered.

TABLE 5. Habitat distribution, by habitat class.

Habitat	**Total**	**Pure**	**Mixed**
Forest	546	456	90
Bushland	170	118	52
Woodland	165	115	50
Grassland	164	124	40
Rocks/rocky slope	98	72	26
Thicket	52	23	29
Riverine, stream	44	31	13
Swamp/bog	38	29	9
Moorland	30	24	6
Wooded grassland	26	15	11

Other species have large numbers of collections from a small area, e.g. *Impatiens kilimanjari* with 29 collections from Kilimanjaro. *Chassalia albiflora*, a strict single-degree endemic from the Usambara Mountains, is known from no less than 38 collections. Clarke *et al.* (2000) cite the example of *Cynometra brachyrrachis*, known from only four forests in the Pangani River basin, but which may account for 75% of the canopy trees where it does occur.

What are the reasons for narrow endemism? They can be many, but the list can be divided into 'false narrow endemism' and 'true narrow endemism'.

False narrow endemism – undersampling is the main reason for this, and this will mean they should not be included in a list of single-degree endemics. Undersampling may be caused by general lack of collecting in an area, and this may be true for large tracts of east Africa (see map in Beentje, 2002). Undersampling may also be due to the biology or appearance of the plant itself – it may have a very short season in which the plant itself is visible (as in the case of ephemerals, or plants which sprout from underground parts after rain or burns), or in which leaves and flowers or fruit are present; it may superficially resemble a common species; it may be really awkward to collect; or it may be exceedingly rare with only a few specimens present over a fairly large range.

True narrow endemism can result from habitat rarity, or from historical causes: if a species is restricted to a certain habitat (vegetation type and/or edaphic type coupled to rainfall), and that habitat is rare, the species can be restricted to a narrow range. The habitat can be rare because its original distribution area has been severely diminished by man (historical causes); or where a small area has been stable during climate change, the so-called 'refugium'. The Usambara Mts have been suggested to be such a refugium (Hamilton, 1976, 1982; Lovett & Friis, 1996; Sosef, 1996). Lovett & Friis (1996) conclude that patterns of endemism in NE and East Africa woody flora appear to be due primarily to climatic history determined by tectonic events which created areas of climatic stability; environmental stability encourages speciation by allowing survival of local segregates. They feel geological heterogeneity is a factor in creating floristic heterogeneity, and that it is not necessary to invoke the refugium theory to explain the present-day distribution of restricted range taxa. Crisp *et al.* (2001) considered topographic variation might be an important factor for rarity.

Another example is the mountain-top endemic; several of these exist in East Africa, often with related taxa living on adjacent mountain tops.

Two more categories are discussed in existing literature:

paleo-endemics: species with no obvious close affinities, or species with close affinities to geographically distant sister taxa. Both these types can be regarded as geographical relics (Cronk, 1992; Lovett & Friis, 1996). We have no specific examples of this type.

neo-endemics: species with putative ancestors living nearby; speciation by survival of local segregates; possibly caused by geological heterogeneity (Lovett & Friis, 1996). This type is debatable – there is usually no saying when evolution took place.

It is interesting to note that endemism patterns are different for various life-forms, in accordance with the findings of Cowling *et al.* (1994): endemic 'forbs' or leafy herbs such as *Impatiens* are common in high rainfall areas; endemic shrubs and trees were not restricted to any specific areas; endemic geophytes and succulents such as *Euphorbia* were more common in semi-arid areas.

4.1 Discussion of different approaches

Data were compiled on birds, mammals, snakes and amphibians by Brooks *et al.* (2001), using a 1° grid scale for sub-Saharan Africa. One of the areas of particular high species richness they found is that of the mountains of Kenya, Tanzania and Malawi, and the Eastern Arc was one of their five top conservation priorities. The most endemic-rich areas were in the montane forests, while the poorest were in drylands and plains areas. In comparison our data agree with the high values for montane forests; but in plant species, dryland areas are not necessarily the poorest in endemics.

Kier & Barthlott (2001) adjusted the index of Williams (1993) combining endemism and species richness, and used this on the phytochoria of White (1983). Williams' method needed complete information on all species distributions for a given area, a rather impractical need for most parts of the tropics. Kier & Barthlott's method does not require data on all species, but requires knowledge of the global distribution of a species and works with pre-defined grid cells. So far, the Kier & Bathlott method has been employed at the phytochorion scale, using a standard area of 10,000 km^2.

Linder (2001) did a continental study of plant diversity based on the larger 2.5 × 2.5 degree grid cells, probably the best cell size for continent scale; he uses 2-grid endemics as his narrow endemics. The value of methods like this is that there is no cut-off point as in the SDE method; on the other hand, the SDE method is simple in the extreme, and works very fast on a local scale; it can contribute to larger continental studies as well as a local start-up method. Linder's main areas of narrow endemics include the East African coast and the Zambesi/Congo watershed. Linder finds that his 'corrected weighted endemism' is not significantly related to rainfall, nor correlated to grid diversity, and that this pattern is consistent with the Lovett & Friis hypothesis of climatic stability. He suggests that "... using a smaller grid size would enable a more detailed analysis of the topographically complex areas of East Africa ...", and we hope that this SDE scale will allow such a study; we will continue our research. Of course, to a certain degree "patterns of endemism are scale-dependent" (Major, 1988; Andersson, 1994; Ruggiero & Lawton, 1998; Vilkenkin & Chikatunov, 1998).

Taplin & Lovett (2003) have mapped over 3600 plant species on a 1° grid scale for sub-Saharan Africa. Like Linder, they used inversely range-weighted species richness ('range-size rarity'), but unlike Linder, did not divide range-size rarity scores per cell by the number of species present; they felt sampling bias and total range errors would introduce errors. They found that the two most important factors associated with high levels of both species richness and range-size rarity were a low absolute annual maximum temperature, ideally 25–31°C, and a low level of mean monthly potential evapotranspiration. However, correlation was not very strong. They point out that under-sampling also affects the data.

Many of the mapping studies so far are based on the same sets of maps, the wonderful 'Distributiones Plantarum Africanarum' (various authors; published by the National Botanic Garden of Belgium, Meise; 1500 maps published) with its 5° grid high among them; our current set of data is based on totally different taxa, so 'new' results will hopefully emerge.

5 Conclusions

As a conservation tool, FTEA on its own is not much use – though it can be used to produce lists of possible candidates for conservation, this needs to be combined with careful checking in herbarium cupboards at the very least to give an indication of possible conservation value. A third step, ground truthing, or at the very least recent information from the area concerned, is essential for solid conservation assessments.

For East Africa, and many other regions in the tropics, plant Red Data listings are far and few between, and often inadequate to set conservation priorities. For East Africa plant Red Data listings have not been made across the board and programs to conserve what is currently on the Red List will be unbalanced, with the usual lean to what is known rather than with a broader scientific view in mind. As an intermediate conservation tool, the concept of single-degree endemism is somewhat useful at this half-truthed, herbarium-check-only, stage; it pinpoints plants with small distribution areas, point-endemics or otherwise; from our initial list, and its georeferenced subset, it appears that a percentage as high as 10% of the total number of species of FTEA may be involved. Looking at many such taxa, one pinpoints concentration areas of such species which are very likely prime targets for conservation: see Map 1 in Appendix 2. This method is also advocated by Brooks *et al.* (2001); due to the small range area employed by us their 'greedy complimentarity' method is, in practice, already employed in our SDE method. We certainly feel the SDE method is more objective than the 'hotspot' method, which is based on well-known richness sites rather then on objective data. At this stage the SDE concept is useful to flag up possibly vulnerable taxa, and more truthing will focus this: coupled with knowledge of the area, habitat and threats will lead to sound conservation assessments for such species.

The high number of possible SDEs, well over 1000 species, confirms Brenan's observation (Brenan, 1978) that plant endemism in East Africa tends towards narrow distribution ranges, while endemics in the Guineo-Congolian forests generally have a wider distribution.

Preliminary results from the geo-referenced sample (Appendix 1) show that for this selected group of taxa SDEs occur all over East Africa; and that the areas richest in SDEs are the Eastern Arc mountains of Tanzania, followed by the coastal forests of Kenya and Tanzania and mountains such as Mt Kenya and the Nyandarua/Aberdares.

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APPENDIX 1. Georeferenced taxa from selected genera.

Species	**number of specimens**	**number of localities**	**distribution area**
Baikiea ghesquiereana	1	1	T8: Kilwa
Bauhinia kalantha	4	3	T56: Ruaha, Gulwe; recent collection T7
Bauhinia mombassae	6	3 or 4	K7 Kilifi
Bussea eggelingii	2	1	T8: Rondo
Caesalpinia dauensis	2	2	K1: Malka Murri
Cynometra brachyrrhachis	4	3	T3: Amani
Cynometra engleri	7	2	T3: Sigi Valley, Kwamgumi FR
Cynometra filifera	4	3	T8: Lindi
Cynometra gillmannii	1	1	T8: Kilwa
Cynometra greenwayi	6	3	K7: Watamu, Waa
Cynometra longipedicellata	4	2 or 3	T3: Amani
Cynometra lukei	5	4	K1/4: lower Tana River; possibly T6 Selous
Cynometra ulugurensis	1	1	T6: Kimboza
Cyphostemma adenocarpum	1	1	T4: Tabora
Cyphostemma bidgoodiae	1	1	T8: Rondo
Cyphostemma chrysadenium	1	1	T2: Kilimanjaro
Cyphostemma cryptoglandulosum	2	2	T7: Chunya
Cyphostemma eminii	1	1	T1: Mwanza
Cyphostemma feddeanum	1	1	T6: Bagamoyo
Cyphostemma gracillimum	3	3	T6: Mt Nguru to Ulanga
Cyphostemma grahamii	3	2	K4: Embu, Kitui
Cyphostemma greenwayi	4	3	T6/&: Ruaha River
Cyphostemma kibweziense	5	5	K46: Kitui, Kibwezi, Oloitokitok
Cyphostemma meyeri-johannis	1	1	T1: Biharamulo
Cyphostemma micradenium	1	1	'Masai'
Cyphostemma muhuluense	1	1	T6: Muhulu Mts
Cyphostemma nigroglandulosa	2	1	T4: Ufipa
Cyphostemma njegerre	5	1	T3: Mt Bomole
Cyphostemma odontadenium	2	1	K7: Voi

APPENDIX 1 continued

Species	number of specimens	number of localities	distribution area
Cyphostemma pseudoburgeri	1	1	T2: Tarangire
Cyphostemma rivae	3	2 or 3	K1 & Ethiopia: Moyale
Cyphostemma rotundistipulatum	8	5	Zambia & T4: Mbala, Kawimbwe, Ufipa
Cyphostemma sanctuariumselousi	1	1	T8: Selous
Cyphostemma schliebenii	1 or 2	1 or 2	T8: Kilwa; ?T7, Udzungwa
Cyphostemma shinyangense	3	2	T1: Shinyanga, Seregeti
Cyphostemma stegosaurus	1	1	T7: Mbeya
Cyphostemma taborense	2	2	T47: Rungwa, Kitunda
Cyphostemma villosicaule	1	1	T5: Dodoma
Cyphostemma vollesenii	3	2	T7 Mufindi
Cyphostemma zanzibaricum	3	2	Zanzibar, Pemba
Cyphostemma zimmermannii	9	7	K7 T3: Kilifi, Kwale, Amani
Englerodendron usambarense	12	4	T3: Amani, Kwamkoro
Euphorbia allocarpa	4	1	T6/7: Ruaha Gorge
Euphorbia angustiflora	5	4	T7: Chunya, Iringa
Euphorbia astenacantha	2	1	T4 Ubende Plateau
Euphorbia baioensis	3	2	K1: Baio area
Euphorbia ballyana	1	1	K6: Magadi road
Euphorbia biharamulensis	2	1	T1: Biharamulo
Euphorbia cataractarum	3	2	T4: Kalambo falls, Kawa falls
Euphorbia classenii	1	1	K7: Kasigau
Euphorbia colubrina	7	6	Ethiopia, Somalia, K1: Mandera, Ramu
Euphorbia cuprispina	3	3	K1: South Horr
Euphorbia cussonoides	3	2	K46: Ngong, Chania Gorge
Euphorbia dauana	2	2	K1: Ramu area
Euphorbia dichroa	3	3	U1: Acholi, Karamoja
Euphorbia dilobadana	1	1	T4: Mpanda
Euphorbia discrepans	9	4	T7: Njombe
Euphorbia dumeticola	8	5	T67: Ruaha R, Mbuyuni

APPENDIX 1 continued

Species	number of specimens	number of localities	distribution area
Euphorbia elegantissima	6	3	K6 T2: Nguruman, Manyara scarp
Euphorbia exilispina	1	1	T7: Njombe
Euphorbia eyassiana	10	6	T2: Oldeani, Olduvai, Seronera
Euphorbia fischeri	6	5	T57: Manyoni, Ruaha River
Euphorbia fluminis	7	6	K1/7: lower Tana River
Euphorbia fuscolanata	1	1	T7: Livingstone Mts
Euphorbia gemmea	2	2	K1: Takabba, Dandu
Euphorbia handeniensis	4	3	T3: Handeni
Euphorbia jatrophoides	12	8	Ethiopia, K1: Neghelle, Ramu
Euphorbia laikipiensis	2	2	K3: Rumuruti
Euphorbia lavicola	3	3	K2: Lodwar, Lokichoggio
Euphorbia marsabitensis	2	2	K1: Marsabit
Euphorbia meridionalis	9		K46 T2: Kapiti Plains to Longido
Euphorbia odontophora	1	1	K1: War Gedud
Euphorbia perangustifolia	4	3	Ethiopia, K1: Sof Omar, Ramu
Euphorbia petraea	7	4	U1: Acholi, Karamoja
Euphorbia petricola	4	4	K47: Mutomo to Voi
Euphorbia pilosissima	1	1	T5: Itigi
Euphorbia pseudoburuana	8	7	K6 T2: Siyabei Gorge to lisingita
Euphorbia pseudograntii	4	3	T7: Njombe
Euphorbia quadrispina	3	2	K1: Ramu
Euphorbia rubrospinosa	4	2	T4: Mpanda
Euphorbia samburuensis	12	7	K1: S Horr, El Barta, Lopit
Euphorbia saxorum	5	3	K4: Embu, Kitui
Euphorbia scarlatina	7	7	K6 T2: Suswa to lake Natron
Euphorbia selousiana	2	2	T8: Selous
Euphorbia subscandens	7	3	K1: Kulal, Baio
Euphorbia tanaensis	3	1	K7: Witu Forest
Euphorbia taruensis	3	1	K7: Taru

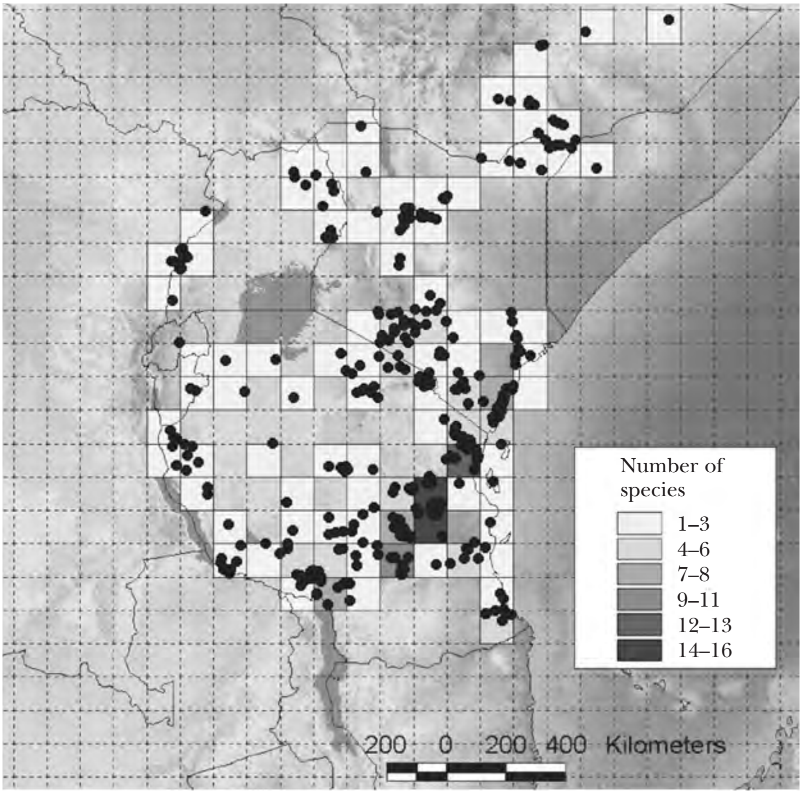
APPENDIX 1 continued

Species	number of specimens	number of localities	distribution area
Euphorbia tetracanthoides	7	4	T7: Poroto, Kinga, Njombe
Euphorbia trichiocyma	2	2	T56: Malolo, Mpwapwa
Euphorbia vulcanorum	2	2	K1: Marsabit
Euphorbia wakefieldii	9	5	K7: Voi R mouth to Mwachi
Guibourtia schliebenii	4	4	T68: Kilombero to Rondo
Impatiens apiculata	11	9	Congo, U2: Ruwenzori, Kalonga, Ankole
Impatiens barbulata	2	2	T6: Uluguru
Impatiens cinnabarina	6	1	T6: Kimboza
Impatiens cribbii	7	4	T7: Kitulo, Kipengere
Impatiens elachistrocentra	5	2	T6: Mahenge, Kwiro
Impatiens flammea	5	2	T7: Rungwe Mt
Impatiens hamata	16	5	T6: Uluguru, Mkobwe
Impatiens humifusa	2	1	T6: Uluguru
Impatiens ioides	11	7	T6: Uluguru
Impatiens joachimii	7	3	T67: Udzungwa, Mwanihana
Impatiens kentrodonta	21	8	T67: Uluguru, Mandege, Udzungwa
Impatiens kilimanjari	29	7	T2: Kilimanjaro
Impatiens leedalii	1	1	T7: Njombe
Impatiens lukwangulensis	7	2	T6: Uluguru
Impatiens mahengeensis	5	3	T6: Ulanga
Impatiens mazumbaiensis	9	6	T3: Mazumbai area
Impatiens messumbaiensis	4	4	T6: Nguru
Impatiens miniata	12	3	U3 K3: Mt Elgon
Impatiens palliderosea	23	7	T6: Uluguru & Mamiwa
Impatiens paludicola	4	2	T6: Ulanga
Impatiens polhillii	3	3	T7: Mufindi
Impatiens pseudohamata	1	1	T6: Uluguru
Impatiens rosulata	8	3	T7: Kitulo
Impatiens runssoriensis	19	7	T2: Ruwenzori

APPENDIX 1 continued

Species	**number of specimens**	**number of localities**	**distribution area**
Impatiens saliensis	1	1	T6: Ulanga
Impatiens serpens	3	2	T6: Uluguru
Impatiens simbiniensis	2	2	T6: Uluguru
Impatiens teitensis	19	9	K7 T3: Taita, Usambara
Impatiens thamnoidea	4	1	T6: Uluguru
Impatiens tricaudata	2	1	T6: Uluguru
Impatiens tweediae	10	4	U3 K3: Mt Elgon
Impatiens ukagurensis	6	4	T6: Ukaguru
Impatiens ulugurensis	29	8	T6: Uluguru, Luhomero
Impatiens usambarensis	12	9	T3: Usambara
Julbernardia unijugata	10	6	T4: Kigoma, Mpanda
Stuhlmannia moavi	8	4	T38: Tanga, Pangani, Selous
Tessmannia densiflora	4	2	T6 Rufiji: Kichi
Tessmannia martiniana	2	2	T6: Rufiji, Uzaramo
Zenkerella capparidacea	6	3	T6: Uluguru
Zenkerella egregia	10	6	T36: Usambara, Uluguru
Zenkerella grotei	10	9	T3: Usambara
Zenkerella schliebenii	4	1	T6: Uluguru

APPENDIX 2. Number of SDE per 1° grid square



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DISJUNCTIONS IN THE AFRICAN FLORA AS SEEN FROM THE FLORA OF ETHIOPIA AND ERITREA

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Abstract

This study gives a review of disjunctions both between northern and southern and between eastern and western Africa as seen from the point of view of the "Flora of Ethiopia and Eritrea." Some patterns are already well known. Northeastern-southwestern disjunctions have been documented, and it is believed that the explanation is an arid corridor between north-eastern and south-western Africa in existence during the Pleistocene. Disjunctions between northeast and east Africa and Macaronesia have been documented, and it has been postulated that the explanation is a past continuous distribution, which was broken before the Pleistocene. Disjunctions between the highlands of Ethiopia and Cameroon have been documented and discussed in connection with the debate about the Afromontane flora. Now disjunctions between Ethiopia and central and western Africa are also beginning to appear at lower altitudes, both in the forest- and in the savanna-floras. Forest disjunctions seem to reflect an earlier larger extension of the Guineo-Congolian forests, while the western savanna disjunctions seem to coincide with the large hypothetical Pleistocene lakes: Lake Arouâne in the west, Lake Mega-Chad in the middle, and Lake Sudd in the upper Nile basin. Disjunctions to Asia and other continents are not included.

Résumé

Disjonctions dans la flore africaine envisagées d'après la 'Flora of Ethiopia and Eritrea'. Cette étude constitue une révision des disjonctions nord-sud et est-ouest de l'Afrique, envisagée du point de vue de la 'Flora of Ethiopia and Eritrea'. Certains aspects sont déjà bien connus. Les disjonctions nord-est et sud-ouest ont été bien étudiées en Afrique. On les explique par l'existence probable d'un corridor aride entre le nord-est et le sud-ouest du continent au cours du Pleistocène. Les disjonctions entre nord-est et est de l'Afrique d'une part, et Macaronésie d'autre part, ont été documentées et on suppose qu'il devait exister, par le passé, une distribution continue mais qui fut brisée avant le Pleistocène. Les disjonctions entre les régions d'altitude d'Ethiopie et du Cameroun sont envisagées dans le cadre du débat sur la flore afromontagnarde. Actuellement, des disjonctions entre l'Ethiopie et l'Afrique centrale et de l'ouest commencent à apparaître à basse altitude, tant pour la flore forestière que pour celle des savanes. Les disjonctions forestières semblent refléter une extension plus large des forêts guinéo-congolaises par le passé, alors que les disjonctions des savanes de l'ouest coïncideraient avec les grands lacs hypothétiques du Pleistocène: le lac Arouâne à l'ouest, le lac Mega-Chad au centre et le lac Sudd dans le bassin supérieur du Nil. Les disjonctions avec l'Asie et les autres continents ne sont pas envisagées ici.

Key words: arid corridor, disjunctions, Ethiopia & Eritrea, Pleistocene, savanna, forest

1 Introduction

Phytogeography has always been of great interest to AETFAT (Friis, 1998, 1999). The most prominent result of this has been the phytochoria of Frank White, based on congruent plant distributions and recognition of centres of endemism (White, 1976, 1983, 1993a, 1993b). Members of AETFAT have contributed published and unpublished data to this effort, and the phytochoria of Africa have been subject of debate and testing (Lovett & Friis, 1996; Clarke, 1998, 2001; Linder, 1998; Grimshaw, 2001; Linder *et al.*, 2005). Much discussion has been dedicated to establishment of centres of endemism, but the literature on disjunct distributions is also large. Especially three types of disjunct distributions have been of interest: (1) Disjunctions between the dry parts of NE and SW Africa. (2) Disjunctions between NE Africa and Macaronesia. (3) Disjunctions between the high African mountains, which has resulted in the establishment and study of the Afromontane (White, 1965; Troupin, 1966) and Afroalpine regions (Hauman, 1955; Hedberg, 1957). In this paper the authors will review the position of the area covered by the Flora of Ethiopia and Eritrea, and also take a look at disjunctions, which have been given less attention than the three types mentioned.

1.1 Disjunctions between the arid northeastern and southwestern Africa

These disjunct distributions involve the drier parts of NE and E Africa and S and SW Africa. The first list of species and genera with this type of disjunction was published by Engler (1921: 851–853). The disjunctions have been explained by the existence during the Pleistocene of an "arid corridor" between the arid NE and SW Africa, an idea put forward by Winterbottom (1967) and further discussed by Verdcourt (1969). It has been reviewed by a number of subsequent authors (Monod, 1971; de Winter, 1971, Ihlenfeldt, 1994; Thulin, 1994). Basically, the theory about the "arid corridor" still stands.

1.2 Disjunctions between tropical NE Africa and Macaronesia

Disjunctions between tropical NE Africa and Macaronesia have also been known for a long time. Again, attention to this type of disjunction was first called by Engler, but in an earlier work (Engler, 1879). Later authors (Lems, 1960; Hedberg, 1961; Ciferri, 1962; Bramwell, 1976, 1985; Sunding, 1979; Liu, 1989; Thiede, 1994; Thulin, 1994) largely agree on the point that the Macaronesian endemics are relicts of taxa that were widespread in a humid subtropical flora in the region around the Tethys Sea, and that this flora persisted until the late Tertiary (Pliocene and Miocene). This applies both to the arid lowland taxa and taxa of the dry, broad-leaved montane forest, which in Macaronesia is known as the laurel forest. With the formation of the Sahara during the Pleistocene came the extinction of some populations (taxa) and the separation of the Macaronesian habitats from those in eastern Africa and Arabia (Yemen). Like the "arid corridor", this theory about the Tertiary connection along the Tethys Sea has not been seriously challenged.

1.3 Disjunct distributions between montane habitats in Ethiopia and Eritrea and western Africa

A number of mainly Afromontane species are known to occur in Ethiopia and Cameroon, but not in the lowlands in between. Some examples traced in a recently published checklist of plants from Cameroon (Cheek *et al.*, 2000) include: *Agauria salicifolia* Hook.f. ex Oliv. (Ericaceae), *Bersama abyssinica* Fresen. (Melianthaceae), *Maesa lanceolata* Forssk. (Myrsinaceae), *Maytenus buchananii* (Loes.) Wilczek, *M. undata* (Thunb.) Blackelock (Celastraceae), *Moraea schimperi* (Hochst.) Pic.Serm. (Iridaceae), *Nuxia congesta* R.Br. ex Fresen. (Loganiaceae), *Pittosporum viridiflorum* Sims (Pittosporaceae), *Rhamnus prinoides* L'Hér. (Rhamnaceae), *Sapium ellipticum* (Hochst.) Pax (Euphorbiaceae), *Scadoxus multiflorus* (Martyn) Raf. and *Schefflera abyssinica* (Hochst. ex A.Rich.) Harms (Araliaceae).

A theory to explain this type of disjunctions will have to be part of the general theories for Afromontane distributions. It will be too complex to discuss this in detail here, but the species mentioned above seem to fit well with what White (1993b, p. 401) has referred to as taxa providing evidences for a "southern migratory track between [the Afromontane habitats in] east and west Africa by way of the Zambesi-Zaire watershed to near the mouth of the Zaire River, and then northwards through Congo, Gabon and Cameroun to the Cameroun-Gongola highlands, and also with southern cul-de-sac in Angola." There are, of course, also disjunctions in the high-altitude Afromontane and Afroalpine floras to the mountains to the south of Ethiopia and Eritrea, e.g. to Mt Kenya, Elgon, Kilimanjaro, etc., but these will not be further discussed here. The theories of this type of disjunction are still the subject of discussion.

1.4 Disjunct distributions between northern and southern Africa

Although many species are widespread throughout eastern Africa, there are a few cases of disjunct distributions at lower altitudes.

> *Jodrellia fistulosa* (Chiov.) Baijnath (Asphodelaceae) occurs in northern Ethiopia, Tanzania, Zambia and Zimbabwe (Baijnath, 1978, 1979; Sebsebe & Nordal, 1997). The explanation for the large gap between Ethiopia and Tanzania is not clear. There is only very little and old Ethiopian material, so it is possible that two taxa may be involved rather than one.
>
> *Ochna inermis* (Forssk.) Schweinf. (Ochnaceae) occurs in the Somalia-Masai region, including Yemen, in Zimbabwe, S Mozambique and Botswana, but not in Tanzania, Zambia, Malawi and N Mozambique (Lebrun & Stork, 2003).
>
> *Pouzolzia mixta* Solms (Urticaceae) occurs in Yemen, eastern Sudan and central and eastern Ethiopia and in Tanzania, Zambia, Malawi, Zimbabwe, Mozambique, Angola and the northern parts of S Africa (Transvaal, Natal). It also occurs in Madagascar, but avoids southern Ethiopia, Congo D.R., Uganda, Kenya and Somalia (Wilmot-Dear & Friis (*in press*), where a distribution map is published).
>
> *Croton zambeziacus* Muell. Arg. (Euphorbiaceae) is split into an Ethiopian population, a South African one, extending from southern Angola to Mozambique and South Africa (Natal), and a west African population, from Gambia to the Sudan (Gilbert, 1995a; Smith, 1987). The species thus seems to show both a north-south and an east-west distribution, although the north-south disjunction is the most prominent.

No theories have been formulated to explain this disjunction pattern with an interval in Kenya and/or N Tanzania. It seems possible that this could be a phytogeographically heterogenous group.

1.5 Disjunction between Ethiopia and the forests of the Guineo-Congolian region

Examples of disjunctions between the humid part of Ethiopia and the forests of the Guineo-Congolian region in broad sense (including transgression into transition zones and regional mosaics) exist both at the species level and at the level of species pairs or -groups. Here only a few selected examples are mentioned. A generalised distribution map of this type of Ethiopian disjunctions is shown in Fig. 1.

Byttneria catalpifolia Jacq. subsp. *africana* (Mast.) Exell & Mendonça (Sterculiaceae, now proposed transferred to Malvaceae) is widespread in the Guineo-Congolian region and transition zone (Lebrun & Stork, 2003), with a disjunct record in low-altitude forests of SW Ethiopia (Vollesen, 1995).

Flabellaria paniculata Cav. (Malpighiaceae) is widespread in Guineo-Congolian region, and is known from Kakamega forest in Kenya (Lebrun & Stork, 2003); with one disjunct record in humid low-altitude forests of SW Ethiopia (Launert, 1995).

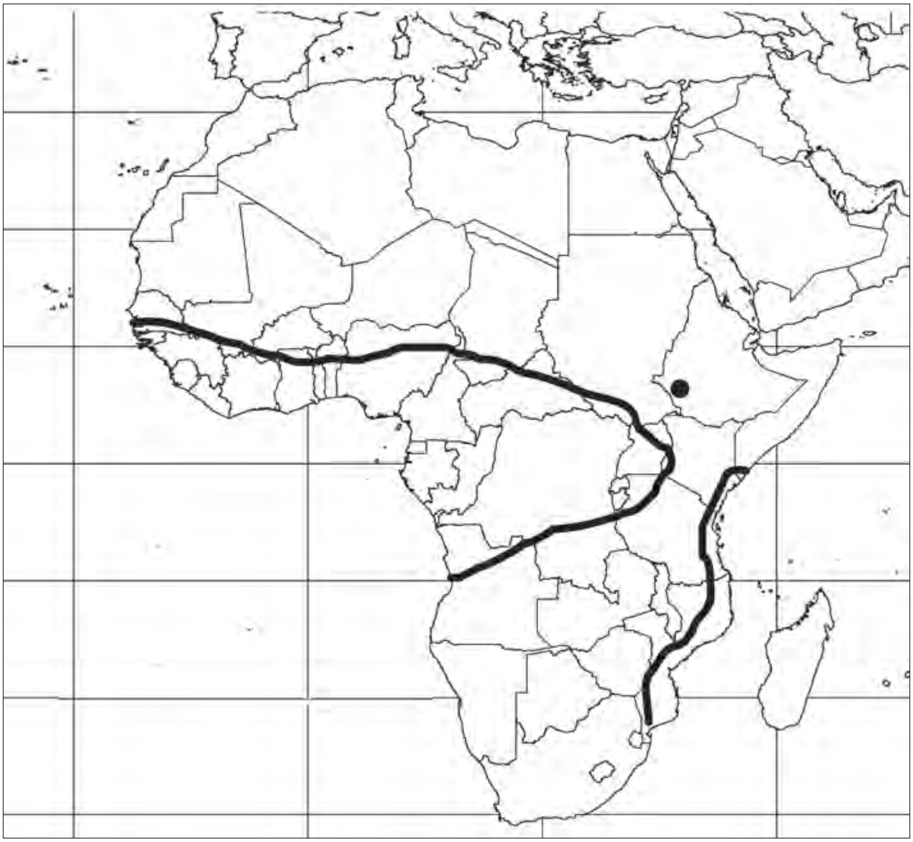

FIG. 1. The Guineo-Congolian region and its transition zone to surrounding phytochoria (jointly indicated by the line to the left) and the Zanzibar-Inhambane regional mosaic (indicated by the line to the right) in relation to the approximate locality (indicated by dot) where most of the disjunctions between Ethiopia and the Guineo-Congolian region are found.

Calvoa orientalis Taub. (Melastomataceae) is widespread in the eastern part of the Guineo-Congolian region, in the Lake Victoria mosaic and in the Zanzibar-Inhambane mosaic (Lebrun & Stork, 2003), with a disjunct record in humid low-altitude forests of SW Ethiopia (Gilbert, 1995b).

Melastomastrum capitatatum (Vahl) A. & R.Fernandes (Melastomataceae) is widespread in the Guineo-Congolian region and in the transition zones north and south of it (Lebrun & Stork, 2003), with one disjunct record in a riverine forest in SW Ethiopia (Gilbert, 1995b).

Begonia wollastonii Bak. f. (Begoniaceae) is known from the easternmost part of the Guineo-Congolian region, the Lake Victoria mosaic (Lebrun & Stork, 2003); the species is also known from a disjunct distribution area in low and medium altitude forests of S and SW Ethiopia (Sands *et al.*, 1995).

Pyrenacantha sylvestris S.Moore (Icacinaceae) is known from large parts of the rainforest area of Congo D.R., from Cabinda and Uganda (Boutique, 1960), and from a disjunct record in the humid low-altitude forests of SW Ethiopia (Vollesen, 1989).

Rinorea friisii M.G.Gilbert, *R. dentata* (P.Beauv.) Kuntze and *R. oblongifolia* (C.H.Wright) Chipp is a group of three closely related species; two (*R. dentata* and *R. oblongifolia*) have a Guineo-Congolian distribution (Lebrun & Stork, 2003), while *R. friisii* is known from a few records from the humid low-altitude forests of SW Ethiopia (Gilbert, 2000).

These low-altitude forest disjunctions seem to reflect an earlier larger extension of the Guineo-Congolian forests. The disjunctions are often on the species level or represent pairs of closely related species. Small patches of Guineo-Congolian type forest exist in Southern Sudan, for example Talanga, Lotti and Laboni forests in the foothills of the Imatong Mountains (Friis & Vollesen, 1998), and some forests in the western Ethiopian lowland, e.g. the Gog forest, have been classified as Dry peripheral semi-deciduous Guineo-Congolian forest (Friis, 1992). It seems reasonable to explain this type of disjunctions by either the existence of an undocumented continuous forest in southern Sudan during more humid periods of the Pleistocene or a pattern of forest patches and riverine and gallery forests that may have acted as stepping stones for the now disjunct species.

1.6 Disjunct distributions between open submontane and lowland savanna and woodland habitats in Ethiopia and Eritrea and western Africa

The examples of lowland species or group of species that that have east-west disjunctions have only fairly recently been noticed, and no attention has been called to them in the literature. The examples given here are documented with new distribution maps: *Cephalocroton incanus* M.G.Gilbert (Euphorbiaceae), has a widely disjunct distribution between Ethiopia and northern Nigeria (Gilbert, 1995a); Fig. 2.

Gomphocarpus abyssinicus Decne (Asclepiadaceae, now proposed transferred to Apocynaceae), has a disjunct distribution with records from Ethiopia, western Sudan and Guinee (Goyder, 2003); Fig. 3.

Pancratium centrale (A.Chev.) Taub. (Amaryllidaceae), previously known from Central Africa and Chad, but recently discovered in Western Ethiopia (Sebsebe & Nordal, 2004); Fig. 4.

Zygotritonia praecox Stapf (Iridaceae) was only known from central Africa and Chad, but was recently discovered in W Ethiopia (Sebsebe *unpublished*); Fig. 5.

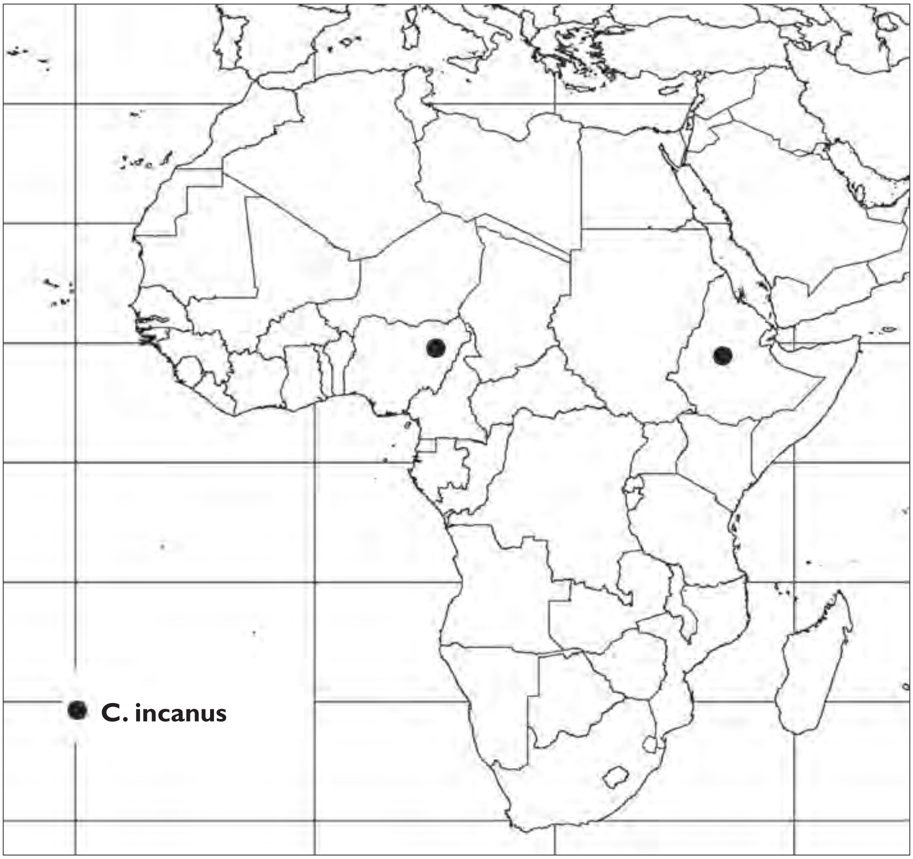

FIG. 2. Distribution of *Cephalocroton incanus* M.G.Gilbert (Euphorbiaceae). Data from herbarium material at ETH and K.

These disjunctions are all located within the Sudanian region of White, not in two different phytochoria or in disjunct phytochoria with other phytochoria in between. As with other cases of disjunction, there are the possibilities of long distance dispersal versus a split between previously continuous populations. An ancestral population of the species may some time in the past have been widespread throughout the Sudanian region from east to west. With the drying up of Africa, possibly coinciding with the formation of the Sahara during the Pleistocene, the populations in the drier parts may have gone extinct and thus separating the populations to develop the disjunct pattern now observed. An important future task will be to look for common patterns in these western disjunct distributions.

From the few examples we know, there seems to be a common gap between populations in Ethiopia and populations in areas with slightly higher ground in Central and West Africa: (1) a common and usually very uniform gap represented by the Nile Valley, (2) a gap from somewhere on the watershed between the Nile and the Niger

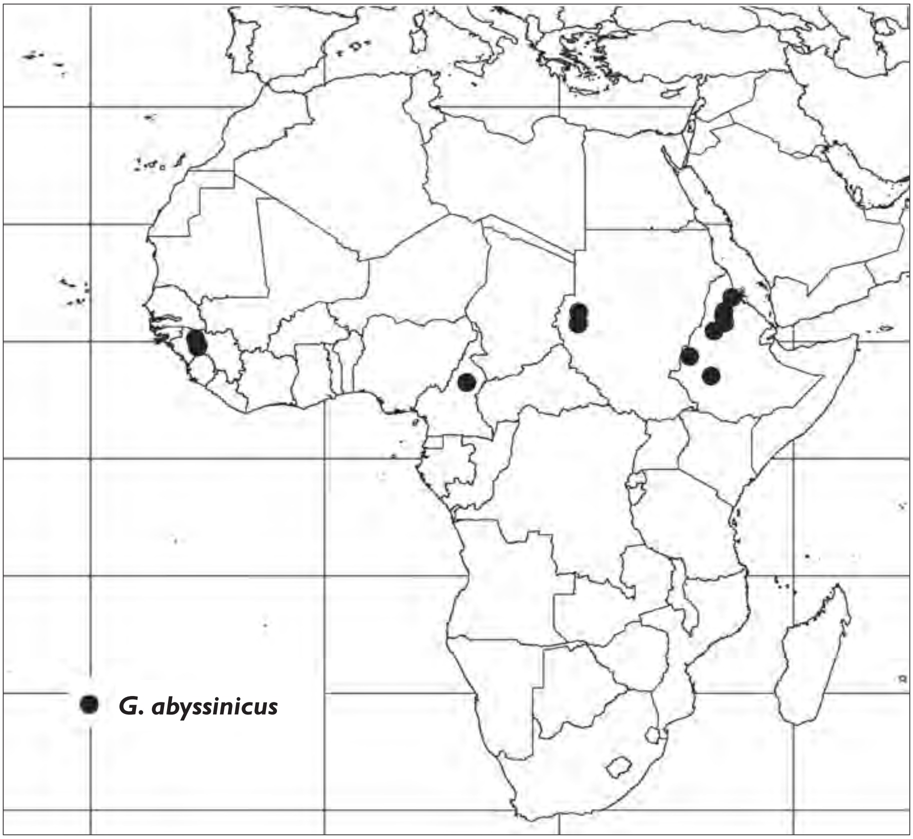

FIG. 3. Distribution of *Gomphocarpus abyssinicus* Decne (Asclepiadaceae). Data from herbarium material at ETH and K.

basins to the West African highlands of the border region between the Guinean Republic, Liberia and Ivory Coast.

It is still difficult to explain why these disjunctions exist, but Clayton (1969) and Wickens (1976) have speculated on the existence of Pleistocene barriers in the large river basins of the Nile and the river Niger. Prichard (1979) has argued for the existence of three major Pleistocene lakes, which more or less agree with the disjunctions demonstrated here. These Pleistocene lakes are: Lake Arouâne in the western part of the Niger basin, Lake Mega-Chad in the border area between Chad, Cameroon, Niger and Nigeria, and Lake Sudd in the upper Nile basin. These past geographical features may be reflected in the present distribution patterns.

However, we should like to caution that the Sudanian region is not everywhere equally well collected and more specimens may be collected in the intervening areas, thus reducing the gaps in the distributions for some of these taxa.

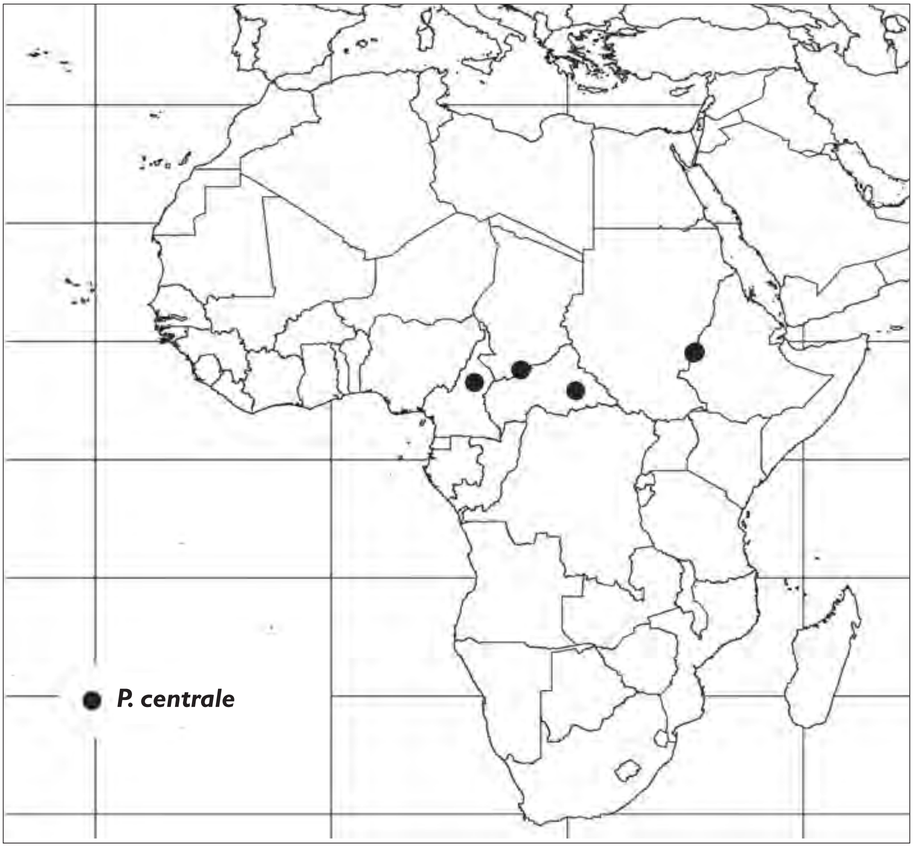

FIG. 4. Distribution of *Pancratium centrale* (A.Chev.) Taub. (Amaryllidaceae). Data from herbarium material at ETH and K.

2 Conclusion

The disjunctions in the Flora of Ethiopia and Eritrea represent both well-known patterns with accepted explanations and completely new ones, for which we can only propose tentative explanations or no explanation at all. We hope that this little review will result in the discovery of more examples of disjunctions in the Flora of Ethiopia and Eritrea, and in further discussion about possible theories that may explain them.

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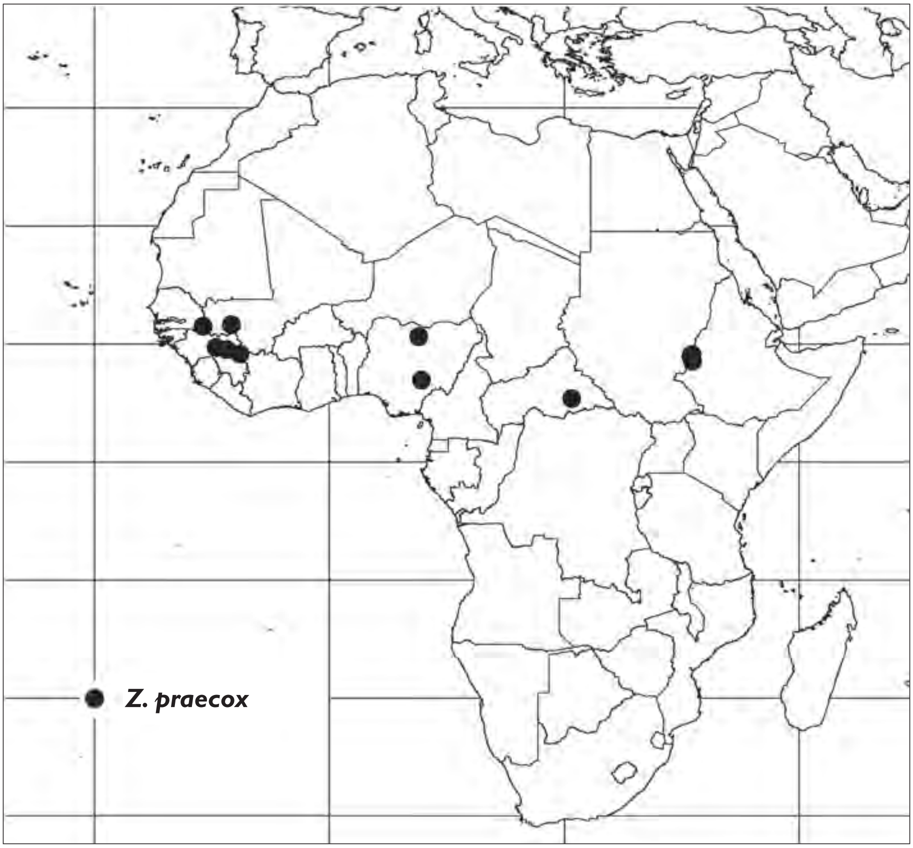

FIG. 5. Distribution of *Zygotritonia praecox* Stapf (Iridaceae). Data from herbarium material at ETH and K.

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FLORISTICS OF GABON'S BATÉKÉ PLATEAUX: GUINEO-CONGOLIAN PLANTS ON KALAHARI SANDS

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Abstract

The grasslands of southeastern Gabon's Plateaux Batéké are maintained by regular anthropogenic fire and are located on the northernmost extension of the Kalahari sands. Fire and substrate are important for species composition on southern areas of the Kalahari sands, but the influence of these two factors on vegetation composition has never been explored for the northern region. Through the analysis of a subset of taxa and their distributions, the floristic affinities and influence of fire and substrate are explored. Although over 50% of the flora is classified as Guineo-Congolian, another 20% of the species have extended distributions into the Zambesian or Sudanian phytochoria. Forest endemics were high, grassland endemics were absent supporting the anthropogenic nature of the grasslands. Twenty per cent of the flora consists of successional species present primarily at the grassland-forest interface. Twenty-four percent of grassland species were arenicolous (sand obligates), but these were also pantropical and pan African species. Pyrophytes were poorly represented. Fire and substrate do not seem to have influenced speciation like they have on the southern Kalahari sands where pyrophytic and arenicolous endemics are abundant. However, ecologically, these fire and sand specialist species are important: fire maintains the grassland which is in turn colonized and stabilized by arenicolous and pyrophytic species. The preservation of this region of Gabon as a national park is noteworthy in that it not only preserves the genetic diversity of the forest grassland mosaic, but also conserves the fire-mediated landscape located on these northernmost Kalahari sand deposits.

Résumé

Floristique des Plateaux Batéké au Gabon: plantes guinéo-congolaises sur sables du Kalahari. Les savanes des Plateaux Batéké, au sud-est du Gabon, sont maintenues par les feux réguliers d'origine anthropique et sont localisés à l'extrême nord de la zone d'extension des sables du Kalahari. Le feu et le substrat jouent un rôle important dans la composition spécifique des régions australes des sables du Kalahari mais l'influence de ces deux facteurs sur la composition végétale n'a jamais été étudiée dans cette région. A travers l'analyse d'un ensemble de taxons et de leur distribution, les affinités floristiques et l'influence du feu et du substrat sont envisagées. Bien que 50% de la flore soit considérée comme guinéo-congolaise, 20% des espèces ont des distributions qui s'étendent jusque dans les phytochories zambézienne et soudanaise. Les espèces forestières endémiques sont nombreuses alors qu'il n'y a pas d'endémiques des savanes, ce qui corrobore la nature anthropogénique de ces dernières. Vingt pour cent de la flore consiste en espèces de succession présentes principalement à l'interface savane-forêt. Vingt-quatre pour cent des espèces de savanes sont arénicoles (poussant obligatoirement sur le sable) mais aussi pantropicales et panafricaines. Les pyrophytes sont faiblement représentées. Le feu et le substrat ne semblent pas avoir influencé la spéciation comme ce fut le cas sur les sables du Kalahari au sud où les endémiques pyrophytes et arénicoles sont abondantes. Néanmoins, ces espèces spécialistes du feu et du sable sont écologiquement importantes: le feu maintient la savane qui est tour à tour colonisée et stabilisée par des espèces arénicoles et pyrophytes. La préservation de cette région du Gabon en tant que parc national est importante car c'est non seulement la diversité génétique de la mosaïque forêt-savane qui est conservée mais également le paysage maintenu par le feu et qui est situé sur la partie la plus septentrionale des dépôts de sables du Kalahari.

Key words: Gabon, Guineo-Congolian, Kalahari sands, fire, grassland

1 Introduction

The vegetation of Gabon is classified as Guineo-Congolian (White, 1993). Forest naturally accounts for only 85% of the land surface (Saint Aubin, 1963) with most of this being still intact (Collomb *et al.*, 2000). The other 15% comprises coastal and interior grasslands (Koechlin, 1962), which can be either edaphic or secondary herbaceous formations (White, 1993). The largest interior grassland in Gabon is on the Batéké Plateaux, an extension of the vast grasslands of the Republic of Congo (Koechlin, 1962).

Anthropogenic fire greatly affects the landscape of the Batéké Plateaux whose grasslands are secondary and anthropogenic (White, 1993; Lock, 1998). Many grasslands have evolved with fire throughout the world (Pyne, 1995) with the fragmentation of the landscape encouraging speciation (Lock, 1998). Substrate is another consideration for the Plateaux. This area of Gabon is on the northernmost reaches of the Kalahari sands which extend all the way from southern Africa. In the southern portion of the Kalahari sands, endemism is high with both fire and sand playing a role (White, 1976).

Saint Aubin (1963) proposed that anthropogenic factors were the major force shaping the Batéké Plateaux vegetation and that soil was “indifferent”. Neither the arenicolous (here defined as sand obligate) nor the pyrophytic components and related endemism of the vegetation of the Batéké Plateaux have been explored. This study uses species distributions from the Batéké Plateaux in order to determine floristic affinities and the effect that fire and substrate have upon species composition.

2 Methods

2.1 Study Site

The study site is located in the Haut Ogooué Province of southeastern Gabon (2°7' south and 14°4' east) and constitutes the Mpassa River drainage, which flows into the Ogooué River (Fig. 1). Elevation is approximately 400 m. There are two rainy seasons between October and March in which there is a total of 1500 mm of rain. The entire area is covered with several hundred feet of Kalahari sand with only a litter layer of a few centimeters over the sand existing in gallery forests. These sands have both fluvial and

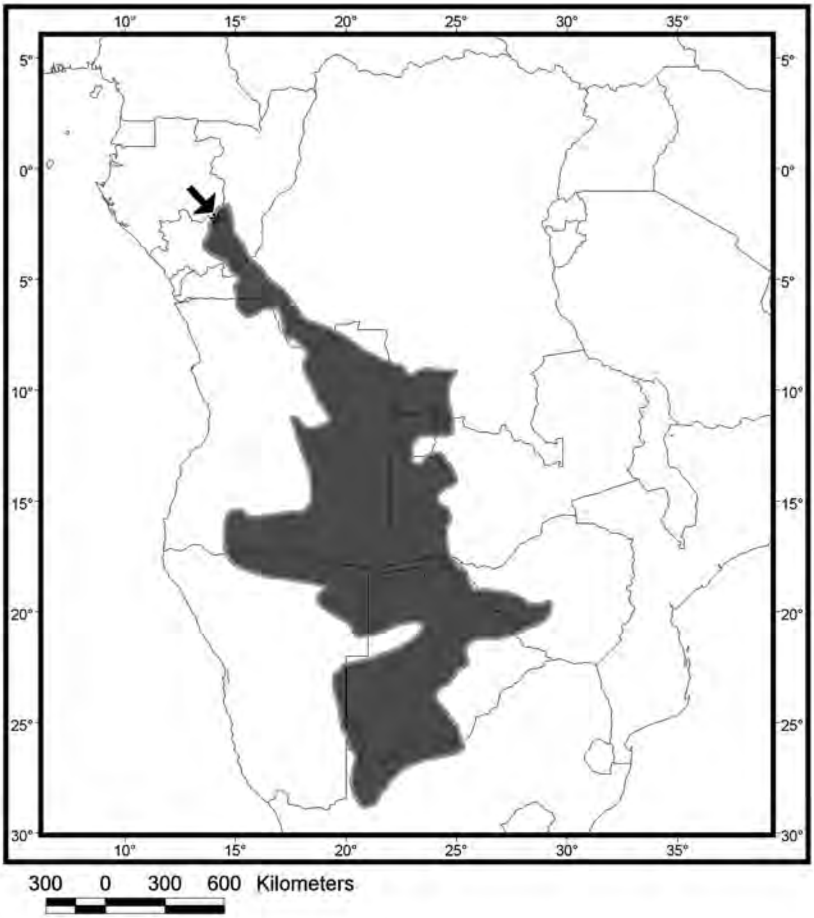

FIG. 1. The Kalahari sands reach their northern limits in Republic of Congo and Gabon. The Plateaux Batéké National Park is indicated by a star and arrow.

aeolian origins (Haddon, 2000) and are divided between the Kalahari and Congo basins. The former is primarily drained by the Zambezi and Okavango rivers and contains the limit of the Kalahari Desert (Thomas & Shaw, 1991). The northern Kalahari sands lie almost entirely within the Congo Basin; however, in Gabon, these sands exist in the Lékoni region of southeastern Gabon, and are part of the Ogooué River basin.

In the Plateaux Batéké, several habitats exist from grassland to forest (White, 1993). All streams and rivers are bordered by gallery forest containing *Ancistrophyllum* and *Eremospatha* (Arecaceae), *Palisota* (Commelinaceae), and *Anonidium mannii* (Oliv.) Engl. & Diels (Annonaceae), though sometimes with only dense monocultures of *Aframomum* spp. (Zingiberaceae) and *Cyrtosperma senegalense* (Schott) Engl. between the river and the forest. The forest extends into swamp forest with *Uapaca* spp. (Euphorbiaceae), *Carapa* sp. (Meliaceae), and various Marantaceae spp. As the forest increases in elevation away from the streams and rivers, it becomes drier, with

Memecylon spp. in the understory (Melastomataceae) eventually transitioning into grassland. Wooded grassland abuts the edge of the forest and is dominated by *Hymenocardia acida* Tul. (Euphorbiaceae) and *Annona senegalensis* Pers. (Annonaceae). Most hills (only an occasional hilltop is capped in a small bosque) are grassland. Recently burned grasslands are often populated by numerous Cyperaceae species and *Melinis nerviglumis* (Franch.) Zizka (Poaceae). Some hills form catchments where wet grasslands or peat bogs form (Makany, 1972). These are dominated by *Xyris* (Xyridaceae), *Utricularia* (Lentibulariaceae), Eriocaulaceae, and *Loudetia phragmatoides* Hochst. (Poaceae) species.

The Batéké Plateaux area was declared a national park in September 2002 (by Presidential declaration) and includes a western lowland gorilla sanctuary; prior to 2001, the area had never been visited by botanists.

We visited the Mpassa River drainage of Plateaux Batéké National Park five times since November 2001, primarily during the rainy seasons. More than 1100 specimens have been collected in sets of six and are planned to be deposited at BR, K, LBV, MO, P and WAG. From these collections, 184 species, two subspecies, five varieties, and one form were fully identified and had published habitat and distributional data; these specimens were databased and used in this analysis. All fully identified plants were categorized into one or more of White's phytochoria (1993) according to geographic distribution. Several plants occurred in the Guineo-Congolian regions, but extended into the Zambesian and Sudanian regions as well. In this study, these species were lumped into a single category since both transition zones contain similar mosaics of Guineo-Congolian riverine forest and secondary grasslands (White, 1993). Taxa were further categorized by habitat, growth form (woody or herbaceous), whether a plant was successional (secondary), arenicolous, and/or pyrophytic (fire dependent). All the information for this study was taken from the most recent taxonomic treatments, including regional floras.

3 Results

Of the 192 taxa in the data set, 51% were strictly Guineo-Congolian, followed by 27% having wide distributions from tropical Africa, the Old World tropics, or the tropics in general. Twenty percent had distributions extending into Sudanian or Zambesian regions (Fig. 2). Less than 2% were introduced. Woody species comprised 64% of all Guineo-Congolian species and 44% of the species extending into Sudanian or Zambezian zones such as *Sesamum parviflorum* Seidentst. Grassland species comprised 52% of the pantropical, tropical African, or Old World species, for example, *Setaria sphacelata* (Schumach.) M.B.Moss ex Stapf & C.E.Hubb. and *Ctenium newtonii* Hack.

Of the taxa in the dataset, 19% were classified as secondary species and 9% were arenicolous. When partitioned by habitat, the grassland showed the highest component of arenicolous vegetation at 24%. Pyrophytes were poorly represented in this vegetation, with only 3% being listed as fire dependent in regional floras including *Annona senegalensis, Bridelia ferruginea* Benth. (Euphorbiaceae), *Hymenocardia acida, Psorospermum febrifugum* Spach (Clusiaceae), and *Maprounea africana* Müll. Arg. (Euphorbiaceae).

Secondary vegetation was examined by habitat (forest, grassland, or edge). Secondary vegetation was characterized most strongly in forest edge habitats, with 38% of these species being secondary (Fig. 3). Grassland-forest transition species include: *Vernonia conferta* Benth. (Asteraceae), *Chaetocarpus africana* Pax (Euphorbiaceae), and *Harungana madagascariensis* Lam. ex Poir. (Clusiaceae). Secondary vegetation is here defined as consisting of successional species that are common in areas with a high frequency of disturbance, such as forest edges subject to fire.

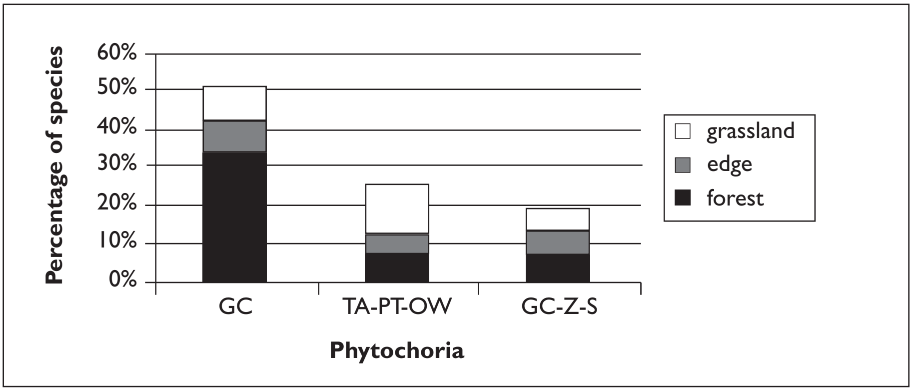

FIG. 2. Guineo-Congolian elements were best represented in the flora, however, the majority of grassland species were tropical African in distribution. GC = Guineo Congolian; TA-PT-OW = tropical African, pantropical, old world; GC-Z-S = Guineo-Congolian-Zambezian, Sudanian.

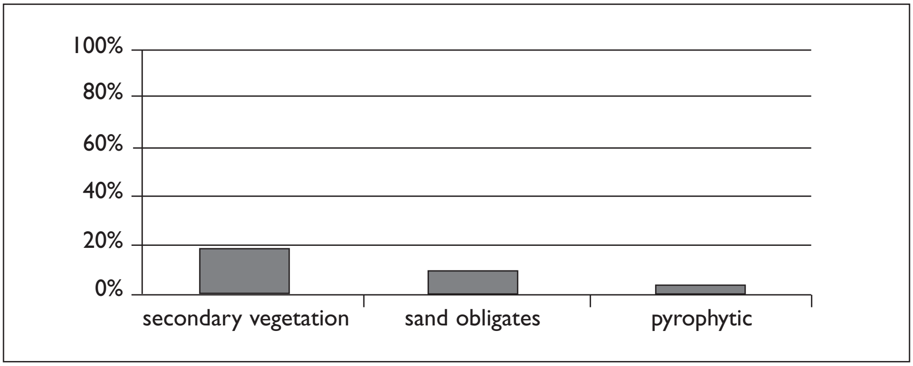

FIG. 3. Almost 20% of the flora was classified as secondary. Sand obligates and pyrophytes were not dominant.

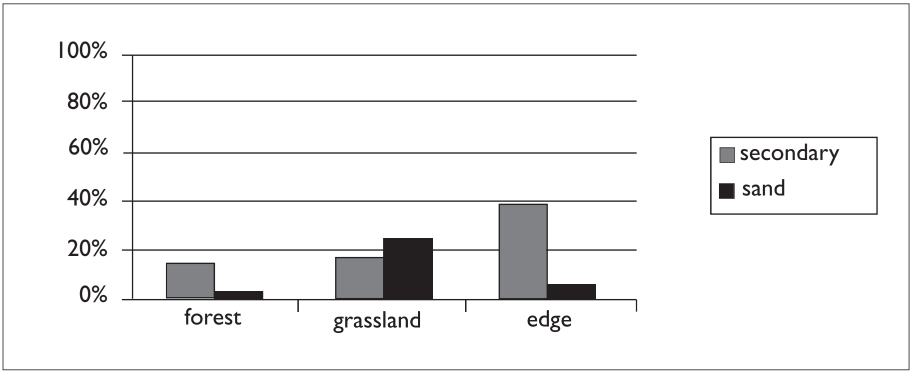

FIG. 4. Almost 40% of all secondary species were edge species. Sand played the largest role in grasslands where more than 20% of the species were sand obligates.

4 Discussion

Fire is a major factor in shaping grassland ecosystems around the world including those of North America (Knapp *et al.*, 1999), Madagascar (Lowry *et al.*, 1997), the South African veld (Pyne, 1995), and the Brazilian cerrado (Pyne, 1995). This is also the case in Central Africa and throughout much of the Sudano-Zambezian grasslands where forest regeneration is curbed by regular anthropogenic fires covering up to 80% of the landscape (Lock, 1998). Elsewhere in Gabon, there is evidence that prehistoric fire maintained grasslands (Oslisly, 2001), but no such data has been researched for the Batéké Plateaux. Present day fire practices in this landscape continue to shape the vegetation with large expanses of rolling wooded grassland dominated by fire resistant shrubs. Almost 40% percent of the forest edge vegetation are secondary species meaning that fire largely maintains the forest-grassland interface, though also aided by a longer dry season (Schnell, 1976) and edaphic conditions (White, 1993). In Lopé National Park, Gabon, another grassland-forest mosaic, Marantaceae forest has been suggested to represent a transition from grassland to forest (White, 2001), but other than in swamp forest, these forests have not been extensively noted in the Mpassa River watershed of the Plateaux Batéké, perhaps indicating that the forest-grassland boundaries have been stable for some time. This is reinforced by the presence of geoxylic suffrutices which are only present on long established grasslands (White, 1976). Fire obviously is essential in maintaining the grasslands ecosystem.

Endemism is radically different between the forest and grassland floras. There are no grassland endemics, while 64% of the forest flora is endemic to the Guineo-Congolian region. The grassland species were primarily pantropical or pan African in distribution. This disparity in endemism between grassland and forest species supports the idea that the grassland is secondary or anthropogenic in nature (White, 1993; Lowry *et al.*, 1997). A brief comparison of plants from the Léfini Reserve, Republic of Congo, also located on Kalahari sands, indicate that there are shared floristic affinities (pers. comm. F. Koubouana). However, in southern Congo, endemicity increases moving south of Gabon along the sands. In the Kalahari sands grasslands of southern Republic of Congo, 12% of the grassland species were endemic and 55% were “Sudano-Angolan” in distribution (Koechlin, 1961). The Zambian Kalahari sands contain the greatest concentration of geoxylic suffrutices with 109 woody grassland species with massive underground stems (White, 1976) which are pyrophytic (Wildman, 1940; Vollesen, 1981). However, only a few occur in the Batéké Plateaux including *Annona, Anisophyllea* (Anisophylleaceae)*,* and *Syzygium* (Myrtaceae) species. In South Africa, a cursory look at a plant list from the southern extreme of the Kalahari sands reveals at least 54 woody endemics to the area (pers. comm. Paul Smith). The lack of a strong pyrophytic component to the vegetation potentially indicates that fire has not been a diversifying force in the vegetation. It appears that the northern reaches of the Kalahari sands did not develop or maintain as rich of an endemic flora on the sands and may not have played a refugia role as was proposed for the central and southern limits (Lock, 1998).

Sand is an important ecological factor in this ecosystem. There are many plants that are arenicolous and some that have evolved specialized water transport systems in the Kalahari sands (Schulze *et al.*, 1998). Across the species surveyed, only 9% were sand obligate. However, when partitioned by habitat, 24% of the grassland species were arenicolous thus demonstrating the ecological importance of these species in grassland areas. Without these arenicolous species, stabilizing the former sand dunes after fire would be difficult. Even now, steep areas of these dunes succumb to severe erosion. Once forest has recovered an area, the arenicolous species are nearly absent.

It is uncertain if the Kalahari sands act as a conduit for bringing southern species into the Guineo-Congolian flora. More than 50% of the Batéké Plateaux flora is Guineo-Congolian, with a large portion being forest flora. However, 20% of all species had distributions extending into Sudanian or Zambesian regions. Even though the Batéké Plateaux contains fewer southern species than do Kalahari sands grasslands in south Congo, the phytogeographic affinity for the south is still notable. Data from non Kalahari sand areas in southern Gabon would be needed to conclusively determine if the southern species in the Batéké Plateaux are due to substrate, climate, and/or latitude.

It may be that Saint Aubin (1963) was correct in saying that soil did not affect the vegetation. From an evolutionary standpoint, the current vegetation does not seem to have the endemism (especially for the pyrophytic and arenicolous components) that its sister locations in the south exhibit and thus fire and sand do not seem to have been an important factor in the area. However, ecologically, fire and sand are paramount: fire maintains the grasslands and sand-loving species colonize after disturbance. It is expected that with future identifications, the Guineo-Congolian component of the flora will become dominant, though the secondary, arenicolous, pyrophytic, and Zambesian-Sudanian components will continue to be reinforced. The preservation of this region of Gabon as a national park is noteworthy in that it not only preserves the genetic diversity of the forest/grassland mosaic (Smith, 1997; Lock, 1998), but also conserves the fire-mediated landscape located on these northernmost Kalahari sand deposits.

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ENDEMIC PLANT SPECIES OF THE EASTERN ARC MOUNTAINS OF KENYA AND TANZANIA: ANALYSIS AND REFINEMENT OF DISTRIBUTIONAL PATTERNS

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Abstract

The Eastern Arc Mountains of Tanzania and Kenya are known for their high level of endemism. GIS analysis of locality data for 32 endemic species and subspecies in 14 flowering plant families refines previously reported distributional patterns among the floristic subregions and mountain blocs of the Eastern Arc. The phytogeographic affinities of the Usambara and South Pare Mountains with the Uluguru and Nguru Mountains are much stronger than previously apparent. *Coffea fadenii* and *Millettia oblata* subsp. *teitensis*, heretofore thought endemic to the Taita Hills in Kenya, are reported from Tanzania for the first time.

Résumé

Espèces végétales endémiques des montagnes de l'arc oriental des montagnes, Kenya et Tanzanie: analyse et amélioration des modèles de distribution. L'arc oriental des montagnes de Kenya et Tanzanie est connu pour un haut taux d'endemisme. Des analyses SIG de données relatives aux localités pour 32 espèces et sous-espèces endémiques au sein de 14 familles d'angiospermes améliorent les modèles de distribution jusqu'alors envisagés parmi les sous-régions floristiques et les massifs montagneux de l'arc oriental. Les affinités phytogéographiques des Monts Usambara et South Pare avec les Monts Uluguru et Nguru sont beaucoup plus fortes qu'il ne paraissait jusqu'ici. *Coffea fadenii* et *Millettia oblata* subsp. *teitensis*, auparavant considérées comme endémiques des Monts Taita au Kenya, sont pour la première fois signalées en Tanzanie.

Key words: Eastern Arc, GIS, Kenya, phytogeography, Tanzania

1 Introduction

The Eastern Arc Mountains of Tanzania and Kenya (Fig. 1) are well known as a regional center of endemism for vascular plants (Lovett, 1985, 1988, 1990; Lovett & Friis, 1996). White (1983, 1993) treated this area as part of his continent-wide "Afromontane Archipelago-like Regional Center of Endemism", but Lovett (1988) documented it as a separate floristic region comprising areas above 1500 m in the ancient igneous mountains of southeastern Kenya (Taita Hills) through southern

Tanzania (Udzungwa Mountains). These mountains lie in the climatic influence of the Indian Ocean, and comprise dry montane forests, wet submontane forests, moist montane forests, cloud forests, heaths, and upland grasslands. Lovett & Friis (1996) attributed the high species richness and endemism of this region to its long history of geological and climatic stability, and Lovett (1998) has noted that the Eastern Arc is an area of conservation priority.

Recently Lovett (1998) analyzed the distributions of 223 tree species and subspecies from the Eastern Arc Mountains, finding 77.5% of them restricted to this floristic region and subdividing it into three subregions (Fig. 1): Northern, comprising the Taita Hills, North and South Pare Mountains and East and West Usambaras; Central, comprising the Nguu, Nguru, Ukaguru, Uluguru, and Rubeho Mountains; and Southern, comprising the Udzungwa and Mahenge Mountains. He presented detailed distributional data for a subset of 66 large trees restricted to the Eastern Arc and Tanzanian coastal forests.

2 Methods

Here, Lovett's subregions are evaluated based on recent botanical exploration of the Eastern Arc region. We analyze the distributions of 32 flowering plant species and subspecies (Table 1) that have new range extensions. These are all strictly endemic to the Eastern Arc and encompass a variety of life forms: small and large trees, understory shrubs, suffrutices, terrestrial and epiphytic herbs, herbaceous and woody climbers, and parasites. The newly documented ranges of these taxa are here used to analyze the patterns of endemism on the more fine-grained scale provided by the subregions noted by Lovett (1998).

Distributions of the 32 study taxa were compiled based on published records (e.g. Flora of Tropical East Africa, 1952–present; Iversen 1991) and new collections. Specimen records were compiled in the TROPICOS database (www.mobot.mobot.org/W3T/Search/vast.html) and mapped using ArcView. Only two of the 32 taxa analyzed here (*Polyscias stuhlmannii* and *Placodiscus amaniensis*) were included by Lovett (1998) in his sublist of 66 large trees; the range of one of these is modified here.

3 Results

The distitributions of these 32 taxa within the Eastern Arc region are summarized by floristic subregion and mountain bloc in Table 1. The following distributional patterns can be seen:

3.1 Widespread Eastern Arc

Ten of our 32 taxa are found in all three floristic subregions (Fig. 2), corresponding to the Eastern Arc floristic region delimited by Lovett (1988). Lovett reported this distribution for 23 or 35% of his large trees, vs. 31% of our taxa with varied habits. The most widespread of our taxa are *Chassalia discolor* subsp. *discolor, Parapentas silvatica, Dicranolepis usambarica*, and *Cynorkis buchwaldiana* subsp. *braunii*, which are known from 8, 8, 8, and 6 mountain blocs respectively. *Sorindeia calantha*, previously considered endemic to the Ngurus, is now known from 4 mountain blocs and all 3 subregions; and *Psychotria brucei* and *Psychotria pandurata* are each known from 1 mountain bloc in each of the 3 floristic subregions. Surprisingly, in the Northern subregion each of the latter two taxa has been collected from the South Pare Mountains but not in the floristically similar West Usambaras (see discussion under "Single Eastern Arc Subregion" below).

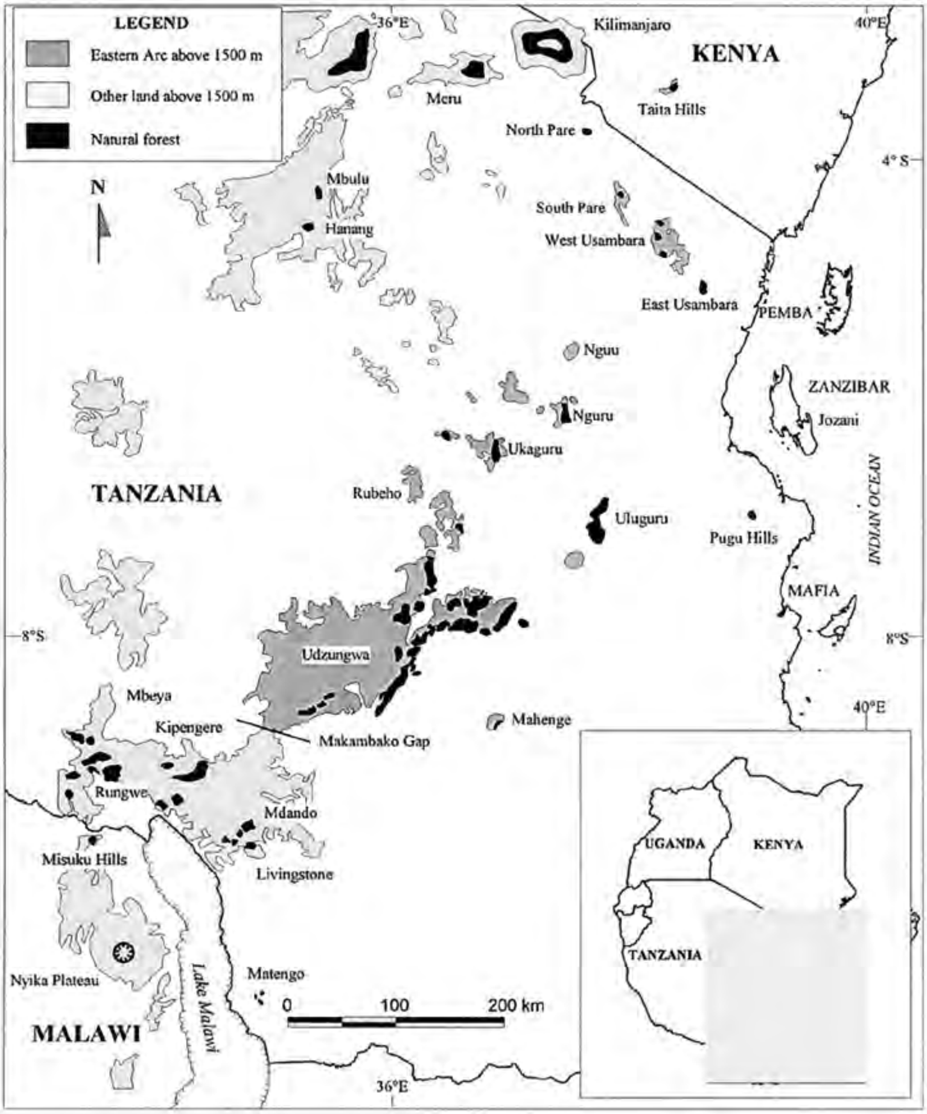

FIG. 1. Map showing highlands (above 1500 m elevation) of Tanzania and southeastern Kenya, their forested portions, and the Eastern Arc floristic region as delimited by Lovett (1998).

TABLE 1. Distributions of Eastern Arc endemic plant taxa by floristic subregion (Lovett, 1998) and by mountain bloc: TA = Taita, NP = North Pare, SP = South Pare, WU = West Usambara, EU = East Usambara, NU = Nguu, NG = Nguru, UK = Ukaguru, UL = Uluguru, RU = Rubeho, UD = Udzungwa, MA = Mahenge. 12 mountain blocs are noted here, 5 in the Northern subregion, 5 in the Central subregion, and 2 in the Southern subregion.

	Northern					**Central**					**Southern**	
ANACARDIACEAE												
Sorindeia calantha Mildbr.	TA		SP				NG				UD	
APIACEAE												
Cryptotaenia calycina C.C.Towns.				WU			NG		UL		UD	
ARALIACEAE												
Polyscias stuhlmannii Harms	TA		SP	WU	EU				UL			
ASTERACEAE												
Bothriocline argentea (O.Hoffm.) Wild & G.V.Pope	TA	NP	SP				NG	UK				
BALSAMINACEAE												
Impatiens engleri Gilg subsp. *engleri*				WU	EU		NG		UL			
DIOSCOREACEAE												
Dioscorea longicuspis R.Knuth				WU	EU				UL			MA
FABACEAE												
Millettia oblata Dunn subsp. *teitensis* J.B.Gillett	TA		SP	WU								
MELASTOMATACEAE												
Lijndenia procteri (A. & R.Fern.) Borhidi			SP	WU								
Medinilla engleri Gilg				WU	EU		NG		UL		UD	
Memecylon cogniauxii Gilg			SP	WU	EU		NG		UL			
Memecylon deminutum Brenan			SP	WU								
ORCHIDACEAE												
Cynorkis buchwaldiana Kraenzl. subsp. *braunii* (Kraenzl.) Summerh.	TA			WU			NG	UK	UL		UD	
Neobenthamia gracilis Rolfe						NU	NG		UL	RU		
Polystachya caespitifica Kraenzl. subsp. *caespitifica*				WU					UL			
RANUNCULACEAE												
Clematis dolichopoda Brenan	TA		SP	WU	EU							
RUBIACEAE												
Chassalia albiflora K.Krause			SP	WU	EU		NG					
Chassalia discolor K.Schum. subsp. *discolor*			SP	WU	EU		NG	UK	UL		UD	MA
Coffea fadenii Bridson	TA		SP									
Mitriostigma usambarense Verdc.			SP	WU								
Mussaenda microdonta Wernham subsp. *microdonta*				WU			NG		UL			

TABLE 1. continued

	Northern					**Central**					**Southern**	
Parapentas silvatica (K.Schum.) Bremek.			SP	WU	EU		NG	UK	UL		UD	MA
Pavetta diversicalyx Bridson			SP	WU								
Pavetta mazumbaiensis Bridson			SP	WU								
Pentas longituba K.Schum.				WU			NG	UK	UL	RU		
Psychotria brucei Verdc.			SP						UL		UD	
Psychotria griseola K.Schum.				WU	EU		NG					
Psychotria pandurata Verdc.					EU				UL		UD	
Rytigynia longicaudata Verdc.			SP	WU								
Rytigynia xanthotricha (K.Schum.) Verdc.					EU				UL			
SAPINDACEAE												
Placodiscus amaniensis Radlk.					EU						UD	
THYMELAEACEAE												
Dicranolepis usambarica Gilg	TA		SP	WU	EU		NG		UL		UD	MA
TURNERACEAE												
Stapfiella usambarica J.Lewis			SP	WU								
TOTAL	9	1	22	27	15	1	17	6	19	2	8	4

3.2 Partial Eastern Arc

Ten of our 32 taxa are restricted to the Northern and Central floristic subregions (Fig. 3). Lovett (1998) reported this distribution for 6 or 9% of his large trees, vs. 31% of our taxa with varied habits. The most widespread of our taxa are *Bothriocline argentea* and *Chassalia albiflora*, which are known from 5 and 4 mountain blocs respectively. Of more restricted distribution are *Psychotria griseola*, only in the West and East Usambaras and the Ngurus; *Rytigynia xanthotricha*, only in the East Usambaras and the Ulugurus; and *Polystachya caespitifica* subsp. *caespitifica*, only in the West Usambaras and the Ulugurus. The Usambaras and Ulugurus probably share more floristic elements than has previously been reported, and further examples of this disjunction can confidently be expected.

None of our 32 taxa studied were shared between the Central and Southern subregions. Lovett (1998) did document this distribution for 5 or 8% of his large trees. This may in part be an artifact the recent concentration of collecting activities in the Northern subregion by Missouri Botanical Garden staff and associates.

Only one of our taxa, *Placodiscus amaniensis* (Fig. 4), showed a disjunct distribution between the Northern and Southern floristic subregions. This species is only known from its type locality in the East Usambaras and a single collection from the Udzungwas. Lovett (1998) documented 3 additional taxa with this disjunct distribution: *Isolona heinsenii*, subsequently reported by Q. Luke from the Ngurus in the Central subregion; *Pterocarpus mildbraedii* subsp. *usambarensis*; and *Diospyros occulta*. However in this same study he reported *Placodiscus amaniensis* only from the Northern subregion. In view of the inadequacy of biodiversity inventories to date in parts of the Central subregion, especially the Nguu and Rubeho Mountains, it seems likely that all of these taxa will eventually be found in all three subregions.

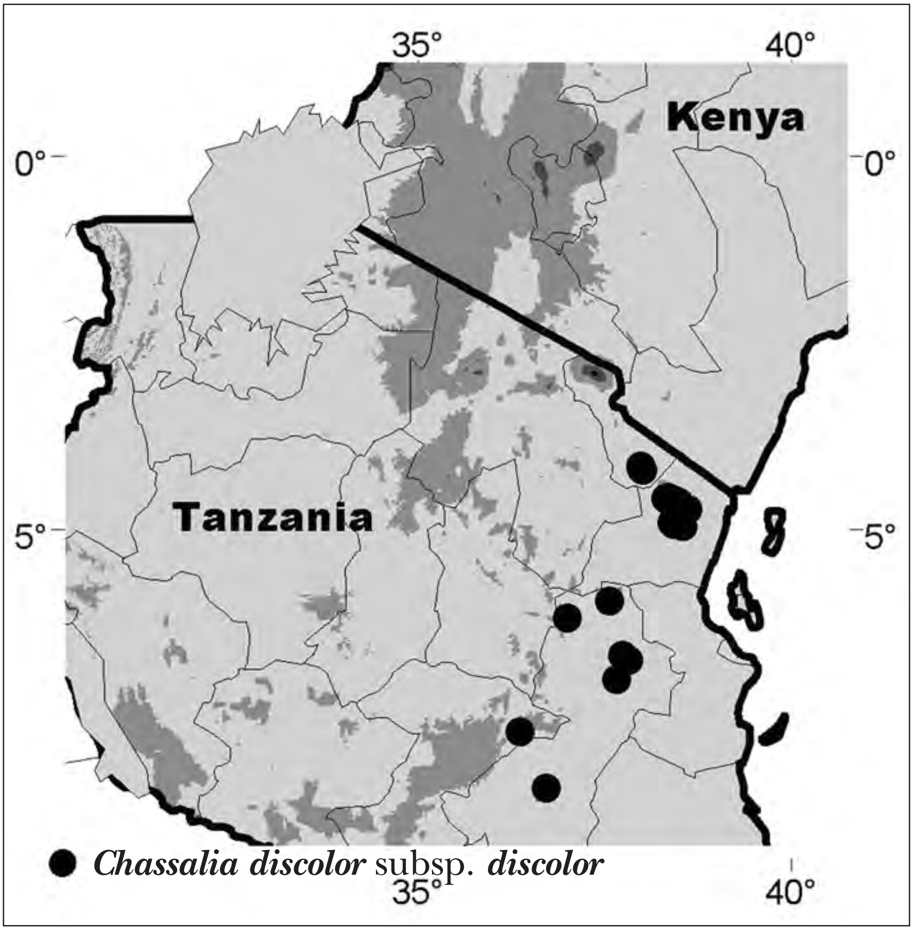

FIG. 2. Widespread Eastern Arc distribution: *Chassalia discolor* subsp. *discolor* is found in 8 of the 12 Eastern Arc mountain blocs and all 3 of Lovett's subregions.

3.3 Single Eastern Arc Subregion

Ten of our 32 taxa are restricted to the Northern floristic subregion (Fig. 5). The most widespread is *Clematis dolichopoda*, which is known from 4 of its 5 mountain blocs. Lovett (1998) reported this distribution for 21% or 32% of his 66 large trees, although *Placodiscus amaniensis* is now known from the Southern subregion as well, vs. 31% of our taxa with varied habits. Recent exploration has expanded the range within this subregion of several taxa: *Lijndenia procteri*, *Mitriostigma usambarense*, and *Stapfiella usambarica* were all previously thought endemic to the West Usambaras but are now known from the South Pares. This South Pare-West Usambara distribution is shared by *Memecylon deminutum*, *Pavetta diversicalyx*, *Pavetta mazumbaiensis*, and *Rytigynia longicaudata*. *Coffea fadenii* and *Millettia oblata* subsp. *teitensis* (Fig. 5), previously considered endemic to the Taita Hills, are now known from the South Pares, and *Millettia oblata* subsp. *teitensis* is additionally known from the West Usambaras.

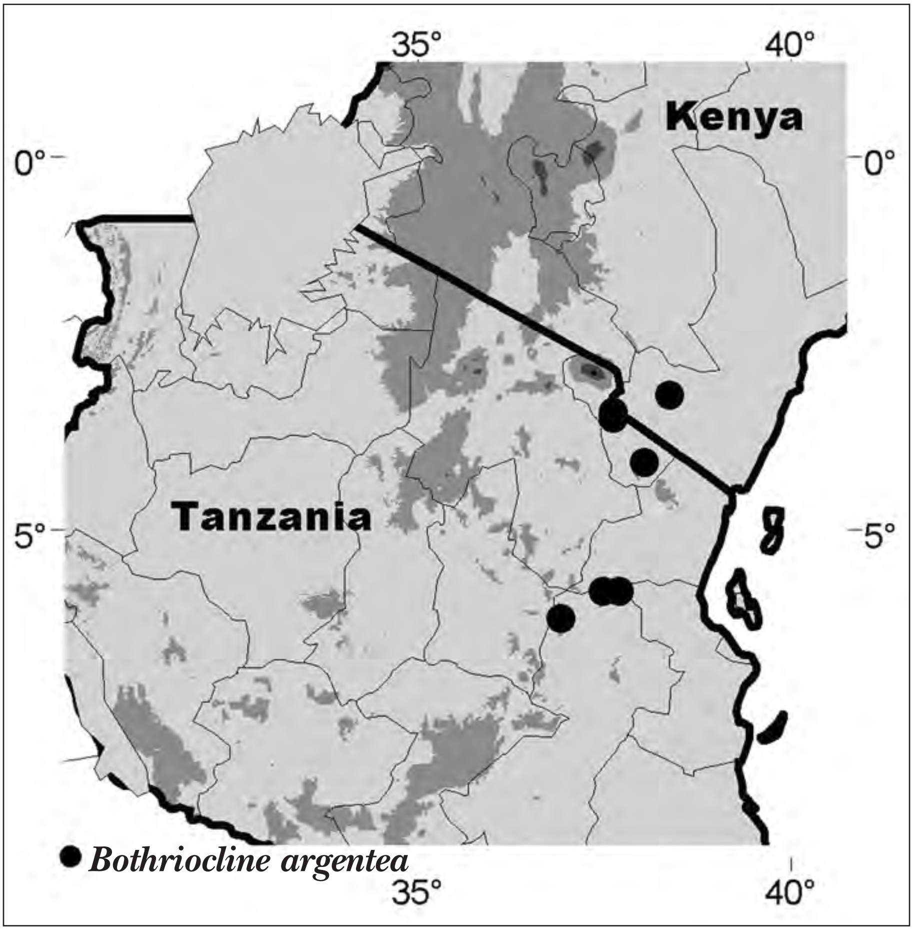

FIG. 3. Partial Eastern Arc distribution: *Bothriocline argentea* is found in both the Northern and Central subregions, in 3 mountain blocs in the former and 2 in the latter subregion.

Neobenthamia gracilis is the only one of our 32 taxa that is restricted to the Central subregion, where it is known from 4 of the 5 mountain blocs (Fig. 6). Similarly Lovett (1998) found only one of his 66 taxa of large trees to be restricted to this subregion. Thus this subregion does not appear to be rich in narrow endemics. However, our sampling is directed at floristic relations among the various mountain blocs, thus we excluded taxa known from only 1 mountain bloc; a more representative sample including, e.g. endemic species of *Lasianthus* (Rubiaceae) from the Ulugurus would modify this result.

None of our 32 taxa is restricted to the Southern subregion. Lovett (1998) reported this distribution for 5% or 8% of his 66 taxa of large trees. Thus similarly to the Central subregion, the Southern subregion does not appear to be rich in narrowly endemic species. Although a more complete sample might modify this result in some measure, the Southern subregion flora appears to be characterized by an admixture of widespread Eastern Arc endemics and floristic elements shared with areas outside the Eastern Arc, rather than by a coherent set of endemic species of its own.

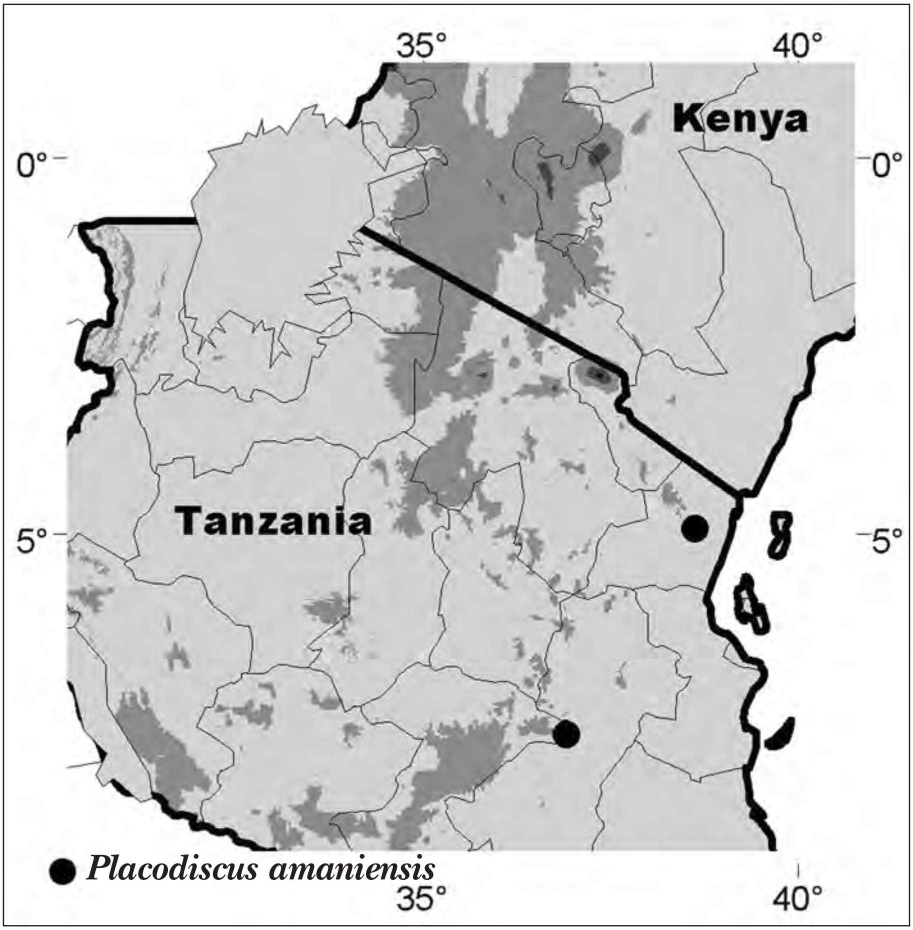

FIG. 4. Partial Eastern Arc distribution: *Placodiscus amaniensis* is the only species found in the disjunct Northern and Southern subregions, in 1 mountain bloc in each region.

4 Conclusions

Plants endemic to the Eastern Arc floristic region are more widespread within this region than previously known, and future exploration will find range extensions for many more. Of the subregions recognized by Lovett, the Northern has notable endemism of its own, but narrow endemism is less in the Central subregion and relatively low in the Southern subregion. The distribution of several taxa in the Northern and Southern but not Central subregions is notable but unexplained. Both Lovett's and our data sets are incomplete; a more thorough understanding of Eastern Arc phytogeography awaits distributional analysis of all its endemic taxa.

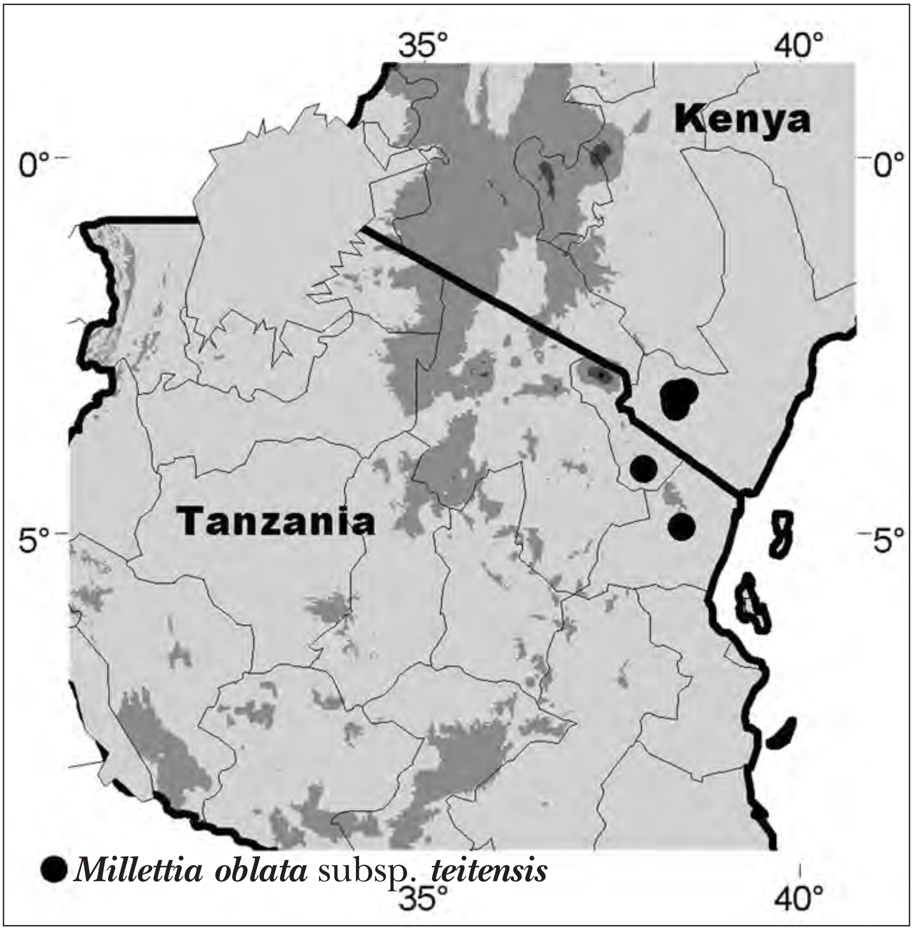

FIG. 5. Single Eastern Arc Subregion distribution: *Millettia oblata* subsp. *teitensis* is found in 3 mountain blocs in the Northern subregion; it is here newly reported from Tanzania, in the South Pares and the West Usambaras.

Although in general the flora of East Africa is reasonably well known, its detailed floristic patterns are still being delimited. Accurate and reliable distributional data are a prerequisite to both elucidation of floristic affinities and assessment of conservation priorities. The most inadequately explored parts of the Eastern Arc (Nguu, Nguru, Ukaguru, and Rubeho) need intensive inventory, and the conservation status of all endemic and near-endemic Eastern Arc plant taxa needs assessment.

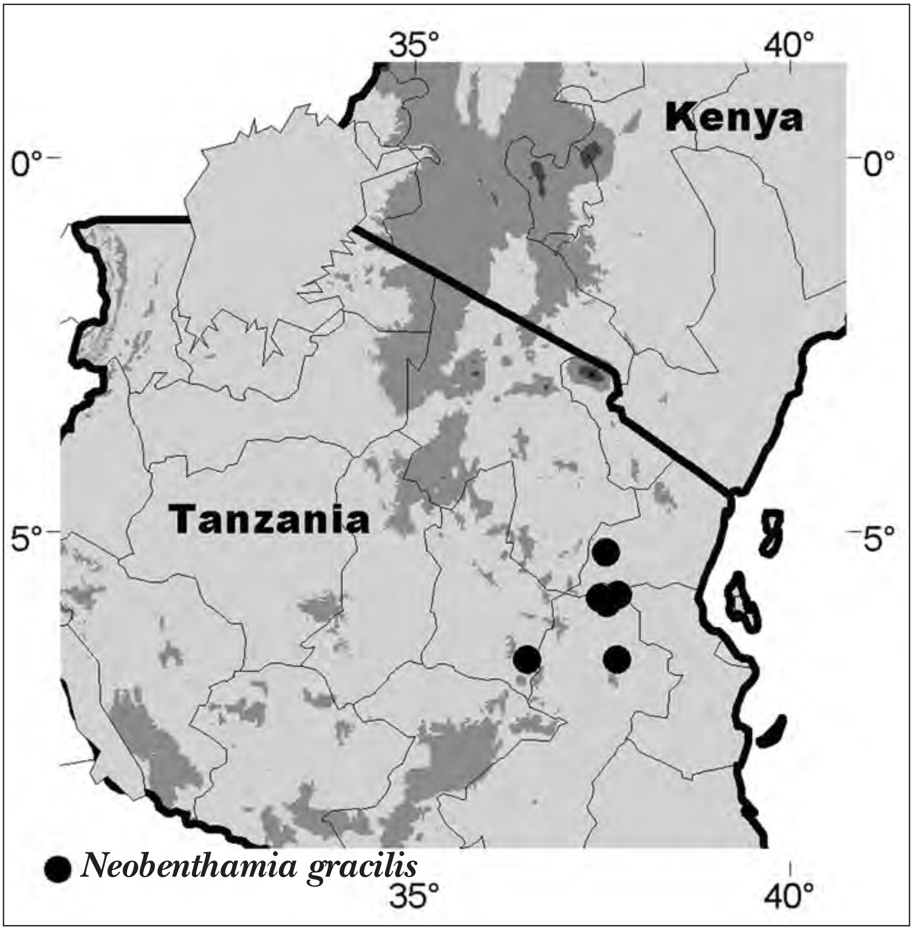

FIG. 6. Single Eastern Arc Subregion distribution: *Neobenthamia gracilis* is found in 4 mountain blocs of the Central subregion.

Acknowledgments

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DISTRIBUTION PATTERNS OF *SOLANUM* IN THE HORN OF AFRICA

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Abstract

Distribution maps for phytogeographically interesting species of *Solanum* in the Horn of Africa are presented. The maps confirm for the Horn of Africa the previously made general prediction that most species of *Solanum* show distributions and patterns of endemism that agree with White's phytochoria. The wild *Solanum* species of the Horn of Africa have centres of endemism in the Afromontane and the Somalia-Masai regions. The distribution of the Somalia-Masai species agrees best with the view that the Red Sea lowlands and Afar should be included with the Somalia-Masai region. The Ethiopian Rift Valley should also be included. Within the Horn of Africa, the Afromontane species are mostly widely distributed, while only few Somalia-Masai species are widespread within the entire Somalia-Masai part of the Horn.

Résumé

Modèles de distribution d'espèces indigenes de *Solanum* dans la corne de l'Afrique. Les cartes de distribution, dans la corne de l'Afrique, d'espèces de *Solanum* intéressantes d'un point de vue phytogéographique, sont présentées. Elles confirment l'hypothèse selon laquelle la plupart des espèces de *Solanum*, dans la corne de l'Afrique, montrent des distributions et des modèles d'endémisme qui corroborent les phytochories de White. Les espèces sauvages de *Solanum* de la corne de l'Afrique ont des centres d'endémisme dans les régions afromontagnarde et Somali-Masai. La distribution des espèces Somali-Masai concorde au mieux avec l'opinion selon laquelle les terres basses de la Mer Rouge et de l'Afar devraient être incluses dans la région Somali-Masai. La vallée du Rift éthiopien devrait également y être adjointe. A l'intérieur de la corne de l'Afrique, les espèces afromontagnardes sont, pour la plupart, largement distribuées alors que peu d'espèces Somali-Masai sont fréquentes dans l'ensemble de la partie Somali-Masai de la corne de l'Afrique.

Key words: Afromontane, distribution, endemism, Horn of Africa, phytogeography, *Solanum*

1 Introduction

This paper is based on my revision of the genus *Solanum* (Solanaceae) for the Flora of Ethiopia and Eritrea and the Flora of Somalia, the two modern flora works that together cover most of the Horn of Africa (here defined to include Eritrea, Ethiopia, Djibouti and Somalia). The revision does not cover sect. Solanum, which has been studied by Dr. Jennifer Edmonds, Leeds, United Kingdom.

The family Solanaceae has rarely been treated for the major African floras, but Wood (1997) has covered the family for Yemen. In the latest published review of *Solanum* for the Horn of Africa Cufodontis (1963) enumerated 84 species. This number has been reduced to about 50 in my unpublished treatment, of which ± 25 are indigenous. But the Horn of Africa and the southern part of the Arabian Peninsula have, according to my treatment, a rich and singular flora of *Solanum* species, and many taxa are endemic or near-endemic (i.e. occur mainly in the Horn of Africa, but with single or a few records in adjacent parts of neighbouring countries).

Hepper & Jaeger (1986) presented a critical review of the sections of *Solanum* in Africa and compared broad distribution patterns of *Solanum* with the phytogeographical regions of White (1976). The sections of *Solanum* accepted and used by Hepper & Jaeger are the ones of an unpublished thesis by P. Jaeger. Most of Hepper & Jaeger's sections have been accepted since the classical works of M.F. Dunal (1789–1856) and F.A.G. Bitter (1873–1927). Hepper & Jaeger (1986) pointed out as one of their conclusions that several of the sections of *Solanum* have their main distribution or have speciated within a single of White's phytogeographical regions. White (1976) divided the Horn of Africa on the following phytochoria: The western lowlands of Eritrea and Ethiopia as far south as c. 5°N belong to the Sudanian Regional Centre of Endemism. Djibouti and Somalia and the eastern lowlands of Eritrea and Ethiopia as far north as c. 15°N on the eastern side of the mountains and as far as about 5°N on the south-western side of the mountains belong to the Somalia-Masai Regional Centre of Endemism; it meets the Sudanian region in SW Ethiopia. The mountains of Eritrea, Ethiopia, Djibouti and Somalia belong to the Afromontane Archipelago-like centre of endemism. The coastal zone of southern Somalia belongs to the Zanzibar-Inhambane Regional mosaic, and the north-western lowlands of Eritrea belongs to the Sahel Regional transition zone. This pattern is largely unchanged in the main publication of the phytogeographical classification (White, 1983), except that the northern limit of the Somalia-Masai region in the Red Sea coastal zone has been pushed up to the border with the Sudan and the south-eastern border of the Sahel transition zone has moved out of Eritrea. Later, White & Léonard (1991, 1994) maintained the latter position of the border of the Somalia-Masai region in the Horn of Africa, but included also the coastal zone of tropical Arabia.

Friis *et al.* (2005) have analysed biodiversity and endemism within the Horn of Africa, using the flora-regions from the Flora of Ethiopia and Eritrea, Flora of Somalia and Flore du Djibouti as their basal units. They found that there is a high concentration of narrowly distributed endemic taxa (taxa with their distribution restricted to one or two flora-regions) in north-eastern Somalia, while endemics in the mountain regions tend to occur in several flora-regions and hence are more widespread.

This paper intends to use detailed distribution maps of the species of the genus *Solanum* to test, at least within the Horn of Africa, the statements of Hepper & Jaeger (1986) that several of the sections of *Solanum* and the majority of the species have their main distribution or have speciated within a single of the phytogeographical regions of White. The paper will also try to test a statement by Friis *et al.* (2005), according to which the species in the Somalia-Masai Region of the Horn, particularly near the tip of the Horn, tend to be more narrowly distributed than those in other parts, particularly those in the Afromontane region.

2 Materials and methods

The Horn of Africa material of *Solanum* (excl. sect. Solanum) kept in the herbaria C, ETH, FT, K, and P has been identified and the geographical information recorded. Together, these herbaria contain a representative sample of *Solanum* material (± 1250 collections) from the study area. All species dealt with in the revision have also been seen in the field in Ethiopia and Somalia, with the exception of *S. cymbalarifolium*. The data was entered in the specimen management system BRAHMS 5, from which files were generated for producing the maps. These were produced with ArcView 3.2 and projected on Global Land One-km Base Elevation (GLOBE) 1.0, a digital altitude model of the Earth. The base map shows altitudes with 305 m intervals and the flora-regions used to indicate distributions in the Flora of Ethiopia and Eritrea, Flora of Somalia and Flore du Djibouti.

3 Observations

Sect. Oliganthes (Dunal) Bitter – (Fig. 1 [Afromontane] & 2 [Somalia-Masai])

This is a group of small to medium-sized spiny shrubs with two subgroups of contrasting habitat preferences: (1) species preferring moist habitats with forest and evergreen bushland, and (2) species preferring arid habitats with deciduous bushland. According to my revision, both groups have speciated in the Horn of Africa.

The first group (Fig. 1) includes the very widespread palaeotropical species *S. anguivi* Lam., which in the Horn of Africa occurs throughout the humid parts of the mountains. There are also two Afromontane endemics in the highlands of Ethiopia: (1) The newly re-established and redefined *S. macracanthum* A.Rich., which occurs in the mountains of southern Ethiopia, except for a northern outpost just south of Lake Tana. (2) The somewhat poorly defined endemic *S. adoense* Hochst. ex A.Rich., which is mainly restricted to the mountains of northern Ethiopia, apart from a few southern outposts in the southern central highlands.

The second group (Fig. 2) includes a number of endemics or near-endemics in the lowlands of Eritrea, Ethiopia and Somalia: (1) *S. hastifolium* Hochst. ex Dunal, a Somalia-Masai endemic in the dry lowlands of the Horn of Africa and in Kenya. In the Horn of Africa it is restricted to the eastern and southern lowlands. (2) *S. cordatum* Forssk., distributed in the arid parts of the Horn of Africa, in Yemen and in the arid parts of Pakistan and India. In the Horn of Africa it occurs in southern Somalia, the Ogaden region and in the southern part of the Afar region. However, the scarcity of this species in the northern part of its range may be due to under collection, as there are records from western and north-western parts of Afar. (3) *S. glabratum* Dunal, distributed in the arid parts of the Horn of Africa and in Yemen. In the Horn of Africa it seems associated with the eastern escarpment of Eritrea and the Ethiopian highlands and the mountains of northern Somalia. There is, however, one (two?) record from southern Ethiopia. (4) *S. lanzae* J.Lebrun & Stork, distributed in the southern part the Horn of Africa and in the dry lowland parts of Uganda, Kenya and Tanzania. In the Horn it is fairly closely associated with the Ethiopian Rift

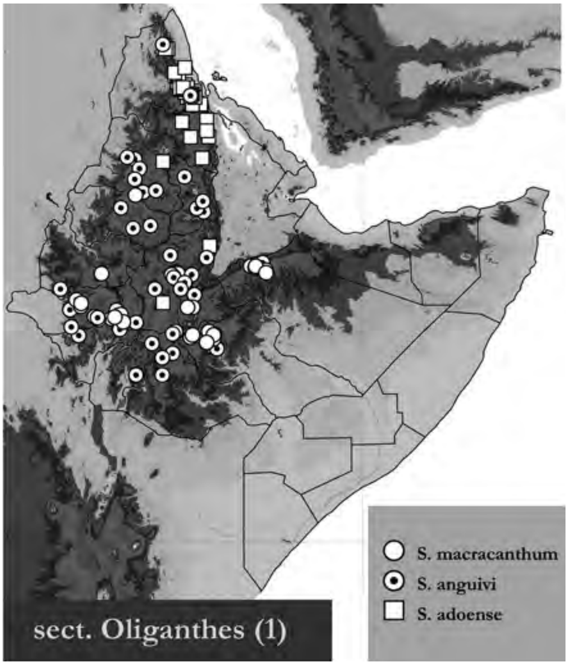

FIG. 1. The distribution in the Horn of Africa of the montane species of sect. **Oliganthes**.

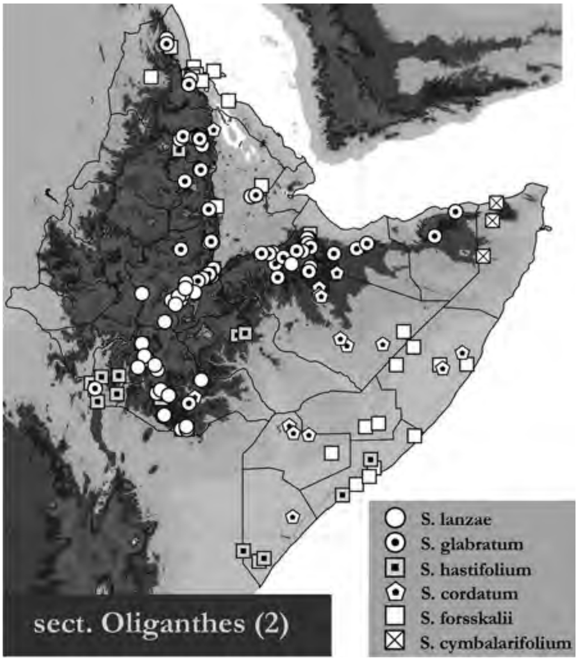

FIG. 2. The distribution in the Horn of Africa of the lowland species of sect. **Oliganthes.**

Valley. (5) *S. forskalii* Dunal, distributed in the arid lowlands of the Horn of Africa and in the coastal zone of tropical Arabia. In the Horn of Africa it is widespread in the eastern lowlands from Eritrea to southern Somalia. It has rarely been collected from Afar and seems to be absent from northern Somalia. (6) *S. cymbalarifolium* Chiov., a narrow endemic in north-eastern Somalia.

Sect. Ischyracanthum Bitter – (Fig. 3 [Somalia-Masai])

This group, which is near-endemic to White's Somalia-Masai region, consists of large, very spiny shrubs characterised by their fruits with a hard or tough yellow pericarp. The two species in this group are: (1) *S. dennekense* Dammer, distributed in the arid lowlands of the Horn of Africa and in similar habitats in Uganda, Kenya and Tanzania. In the Horn of Africa it is restricted to the lower parts of the eastern escarpment of the Ethiopian Highlands south of Afar and the immediately adjacent parts of the Borana region and the Ogaden. (2) *S. arundo* Mattei, restricted to the narrow coastal dune region in southern Somalia, but apparently distributed over a wider range of dryland habitats in the lowland parts of Kenya and Tanzania.

Sect. Monodolichopus Bitter – (Fig. 4 [Somalia-Masai])

This is a group of subshrubs or perennial herbs. It contains two taxa that are both restricted to the Somalia-Masai region in the wide sense (including the southern, coastal parts of tropical Arabia): (1) *S. coagulans* Forssk., which occurs in the southern and south-eastern arid part of the Horn of Africa and in Yemen and Saudi Arabia. In the Horn it is found from the eastern lowlands of Eritrea to southern Somalia, but seems to be absent from the driest parts of Afar. 2) *S. melastomoides* C.H.Wright, a strict Horn of Africa endemic; it is restricted to the Borana region, Ogaden and northern and central Somalia.

Sect. Afrosolanum Bitter – (Fig. 5 [Afromontane]).

This group contains two closely related climbing species, which have sometimes been united as subspecies of the same taxon: (1) *S. terminale* Forssk., which is widely distributed in forests and woodlands at medium altitudes (1200–2200 m) from Nigeria and Cameroon through eastern Africa south to Angola and South Africa. In the Horn of Africa it occurs widely in the Ethiopian highlands but avoids the wettest and the driest parts. (2) *S. welwitschii* C.H.Wright, which occurs in the lowland and intermediate forests of West and East Africa, south to Angola. Hepper & Jaeger (1986) consider it a slightly transgressing Guineo-Congolian species. In the Horn of Africa it is restricted to the humid, altitudinal transitional forests of south-western Ethiopia.

Sect. Benderianum Bitter – (Fig. 6 [Afromontane])

This group includes the near-endemic climbing species *S. benderianum* Schimper ex Dammer, which, in the strict sense, outside the Horn of Africa only occurs in the mountains of northern Kenya. It is restricted to Afromontane forests and *Erica* bushland at high altitudes and is widespread in the mountains of Ethiopia, avoiding only the drier forests of the northern part of the highlands. It is absent from Eritrea and the mountains of northern Somalia. A closely related species, *S. runsoriense* C.H.Wright, occurs in Uganda and western Kenya. Hepper & Jaeger (1986) suggested that the two are subspecies of the same taxon, but the appropriate combination does not seem to have been made.

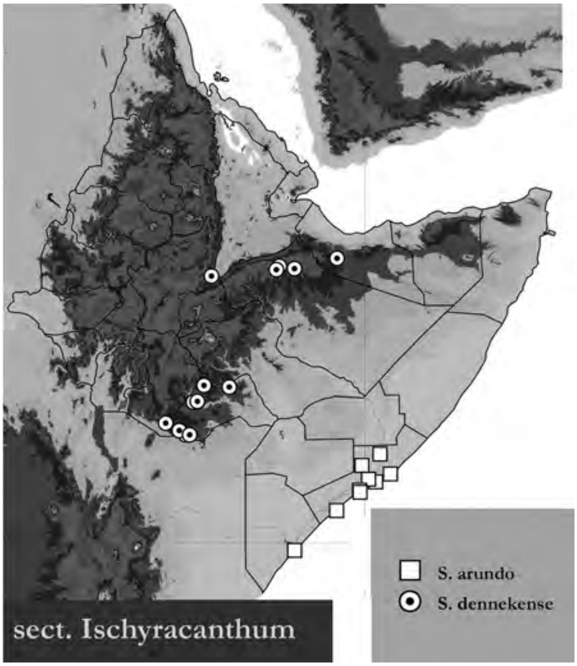

FIG. 3. The distribution in the Horn of Africa of the lowland species of sect. **Ischyracanthum**.

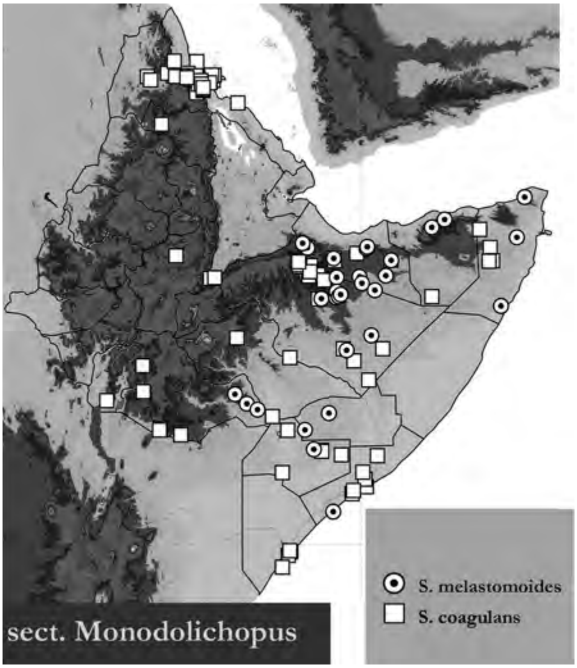

FIG. 4. The distribution in the Horn of Africa of the lowland species of sect. **Monodolichopus**.

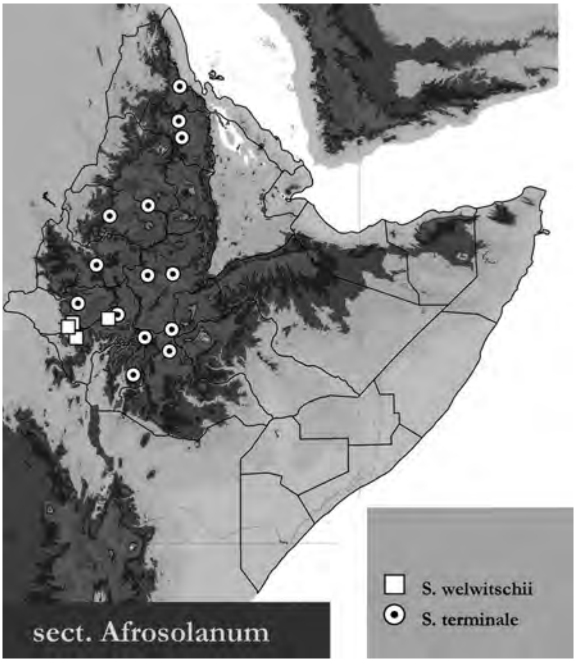

FIG. 5. The distribution in the Horn of Africa of the submontane (*S. welwitschii*) and the montane species (*S. terminale*) of sect. **Afrosolanum**.

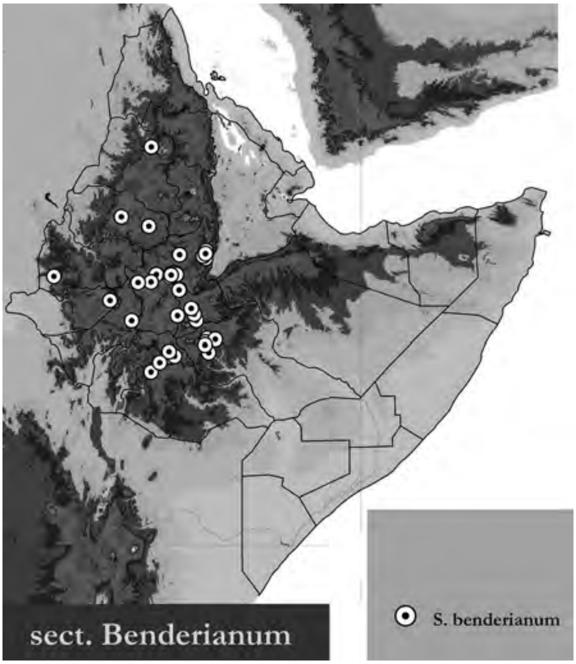

FIG. 6. The distribution in the Horn of Africa of the montane species (*S. benderianum*) of sect. **Benderianum**.

Sect. Somalanum Bitter – (Fig. 7 [Somalia-Masai])

Three rather narrow endemics occur in the this section, which is near-endemic to the Horn of Africa: (1) *S. jubae* Bitter, which outside the Horn occurs only in the most adjacent parts of north-eastern Kenya. In the Horn of Africa it occurs in the eastern lowlands of Ethiopia and southern Somalia. (2) *S. benadirense* Chiov., a Horn of Africa endemic which occurs in central and southern Somalia and the adjacent part of eastern Ethiopia. (3) *S. pampaninii* Chiov., a species with spectacularly large flowers; it is a Horn of Africa endemic, restricted to the large sand dunes of southern Somalia.

Sect. Torva Nees – (Fig. 8 [species either Afromontane or Somalia-Masai])

This section, which is widespread in Africa and other continents, contains three species in the Horn of Africa. (1) *S. giganteum* Jacq., a forest species probably indigenous in South Africa, but now widely naturalised in the humid parts of Ethiopia and elsewhere in the mountains of eastern Africa. It has not been mapped here. (2) *S. tettense* Klotzsch (syn.: *S. renschii* Vatke), which occurs widely in eastern Africa from the Horn of Africa southwards to Botswana, Namibia and South Africa. In the Horn of Africa it occurs in the drier lowlands of southern Ethiopia and in southern Somalia. (3) *S. schimperianum* Hochst ex A.Rich., a near-endemic species with some localities in the coastal mountains of Sudan (and Gebel Elba in SE Egypt) and Yemen. In the Horn of Africa it is restricted to the northern part of the mountains.

Sect. Anisantherum Bitter – (Fig. 9 [Somalia-Masai])

Only one species, *S. somalense* Franch., occurs in the Horn of Africa; the only other species in the section, *S. pubescens* Willd., is not African. *S. somalense* is a near-endemic of the Horn of Africa, but is also known from the adjacent parts of Kenya. In the Horn it occurs in the eastern lowlands from central Afar to southern Ethiopia and Somalia.

Sect. Melongena Dunal – (Fig. 9 [only the least weedy species mapped, taxa either Afromontane or Sudanian])

The species in this section are all more or less weedy herbs and subshrubs. *S. dasyphyllum* Schumach. is a very weedy species restricted to the high rainfall areas, while the *S. incanum* complex consists of weedy, poorly differentiated species or subspecies that could be referred to as *S. incanum* L., *S. campylacanthum* Hochst ex A.Rich., and a taxon sometimes named *S. benguelense* Waw. & Peyr. *S. marginatum* is a somewhat weedy species, which is now widely cultivated in South America, but is believed to have been originally endemic to the Ethiopian highlands, where it must be considered to have an Afromontane distribution. As pointed out by Hepper & Jaeger (1986), *S. ceraciferum* Dunal seems to be an example of a Sudanian endemic species.

Sect. Acanthophora Dunal (not mapped)

In the Horn of Africa this section contains only the two very closely related, introduced species, *S. capsicoides* Allioni and *S. aculeatissimum* Jacq.; these are not mapped here.

Sect. Solanum (not mapped)

In the Horn of Africa this section contains mainly weedy species. *S. hirtulum* Steud. ex A.Rich. is possibly indigenous, having perhaps originated in disturbed Afroalpine habitats and should possibly be considered an Afromontane endemic of the Horn. The section is not dealt with here further.

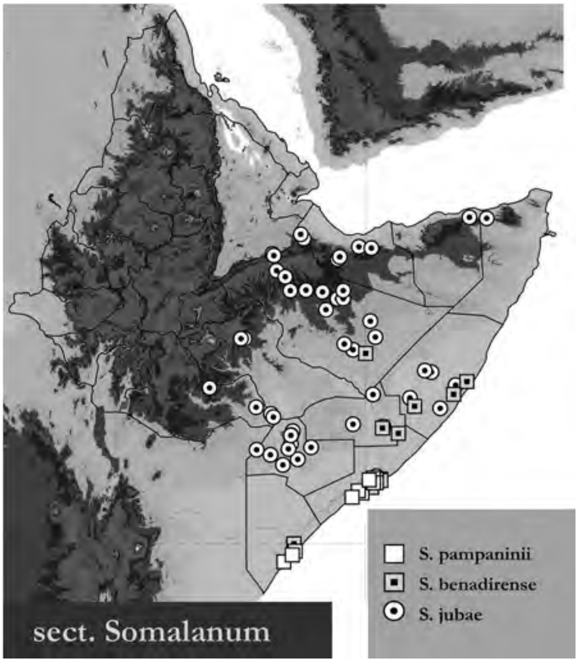

FIG. 7. The distribution in the Horn of Africa of the three lowland species of sect. **Somalanum.**

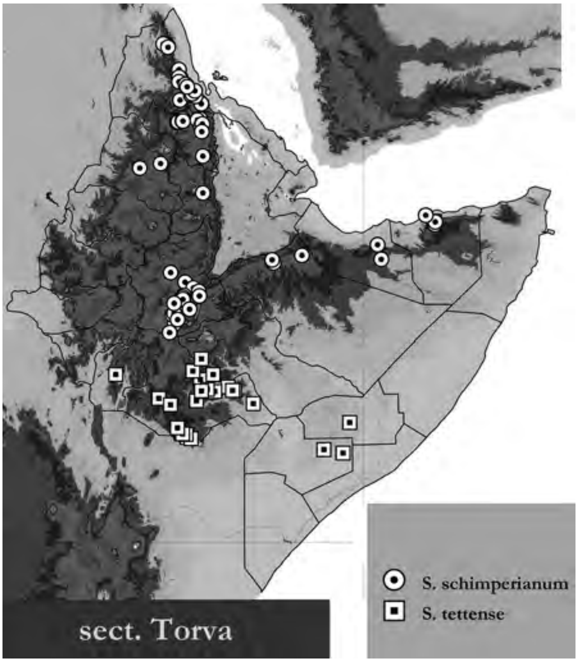

FIG. 8. The distribution in the Horn of Africa of the lowland (*S. tettense*) and submontane species (*S. schimperianum*) of sect. **Torva**.

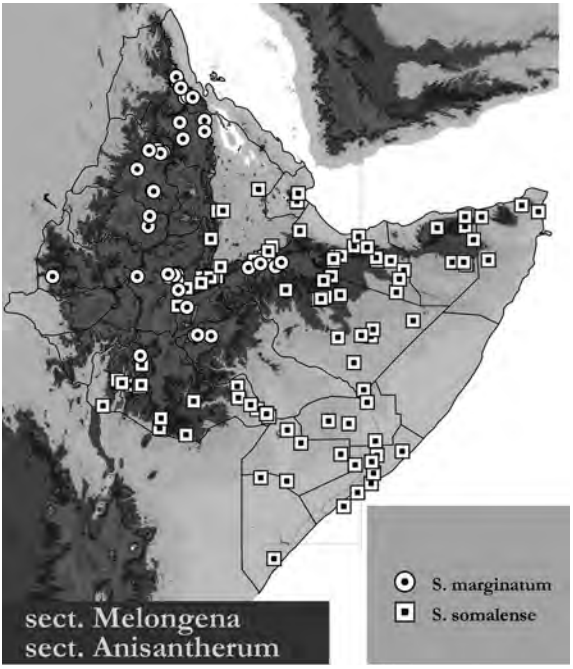

FIG. 9. The distribution in the Horn of Africa of the montane species (S. *marginatum*) of sect. **Melongena** and of the lowland species (*S. somalense*) of sect. **Anisantherum**.

4 Conclusion

This study shows that the distribution patterns in the Horn of Africa of the indigenous species of the genus *Solanum* agree with the phytochoria of White (1983) and only weedy species (species in sect. Solanum and the poorly defined species in the *S. incanum* complex) transgress the border between the lowland Sudanian, the Somalia-Masai and the Afromontane regions. This is consistent with Hepper & Jaeger (1986), who concluded that the majority of the African species of *Solanum* agreed in their distribution patterns with the phytochoria of White (1976), except for some of the weedy species. Also, with regard to the endemism of the sections, the present study confirms the finding of Hepper & Jaeger (1986). The most striking finding in this study is that the sections Monodolichopus and Ischyrachantum and several species of sect. Oliganthes are restricted to the Somalia-Masai region when this is taken in the broader sense of White & Léonard (1991, 1994). However, it is important to note that according to these findings, parts of the Ethiopian Rift Valley should also be included within the Somalia-Masai region.

The species that occur in the Somalia-Masai region have very varied distribution patterns: (1) restricted to the tip of the Horn (*S. cymbalarifolium*), (2) restricted to the Rift Valley (*S. lanzae*), (3) restricted to the coastal southern Somalia (*S. pampaninii*), (4) restricted to the transition zone between lowland and highland in the Borana region and the Ogaden (*S. dennekense*; a similar pattern is also found in trees of dry evergreen forest (Friis, 1992)), (5)? restricted to central Somalia and adjacent parts of the Ogaden (*S. benadirense*), (6) widespread in southern Somalia and eastern Ethiopia, but avoiding the tip of the Horn, Afar and the coastal lowlands of Eritrea (*S. jubae*), (7) widespread in Somalia, in southern Ethiopia, in the Ethiopian Rift Valley and in southern Afar, but absent further north (*S. somalense*, *S. melastomoides*), and (8) widespread in the eastern lowlands of the Horn, but absent from certain parts (*S. coagulans*, *S. forskalii*). Some lowland distributions have outposts and are probably still not completely known (*S. glabratum*, *S. hastifolium*).

Solanum benderianum (sect. Benderianum), *S. terminale* (sect. Afrosolanum) and *S. marginatum* (sect. Melongena) are restricted to the Afromontane region, while *S. welwitschii* (sect. Afrosolanum), which Hepper & Jaeger (1986) place as a slightly transgressing Guineo-Congolian species, occurs into the humid highlands of southwestern Ethiopia, an area to which Guineo-Congolian species of forest trees also reach (Friis, 1992). The Afromontane species of *Solanum* have rather wide distributions in the Horn, occurring either in the southern (*S. macracanthum*) or northern highlands (*S. adoense*, *S. marginatum*) or both, avoiding only the driest parts of the highlands north of Lake Tana (*S. benderianum*).

The general conclusions are that the patterns of endemism in the genus *Solanum* in the Horn of Africa agrees well with the phytochoria of White in that part of Africa, if a wide definition of the Somalia-Masai region is accepted, and that the Somalia-Masai species in the Horn have a more varied set of distribution patterns than the rather widely distributed Afromontane species, as predicted by Friis *et al.* (2005).

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AFRICAN SPECIES OF *LEPIDIUM* (BRASSICACEAE) CONTRIBUTED VIA HYBRIDIZATION TO THE ORIGIN OF AUSTRALIAN/NEW ZEALAND SPECIES

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Abstract

Lepidium sensu stricto (Brassicaceae) (± 150 species) is distributed world-wide with endemic species on every continent. It is represented in Australia and New Zealand by 19 and 7 native species respectively. In the present study we used a nuclear ribosomal ITS phylogeny in comparison with a *cp*DNA phylogeny to unravel the origin of Australian/New Zealand species. The *cp*DNA data indicate a Californian origin of *Lepidium* species from Australia/New Zealand. With respect to the Australian/New Zealand taxa, strongly conflicting signals between the *cp*- and nuclear DNA phylogenetic analysis clearly indicated hybridogenous genomic constitution of Australian *Lepidium* s.s. species: all 18 studied Australian/New Zealand *Lepidium* s.s. species examined shared a Californian *cp*DNA type. While eleven Australian/New Zealand taxa appeared to harbor a Californian ITS type, a group of seven species shared a South African ITS type. This pattern is most likely explained by two trans-oceanic dispersals of *Lepidium* from California and Africa to Australia/New Zealand and subsequent hybridization followed by homogenization of the ribosomal DNA either to the Californian or South African ITS type in the two different lineages. Calibration of our molecular trees indicates a Pliocene/Pleistocene origin of *Lepidium* in Australia/New Zealand. Low levels of *cp*DNA- and ITS sequence divergence and unresolved topologies within Australian/New Zealand species suggest a rapid and recent radiation of *Lepidium* after the hybridization event. This coincides with dramatic climatic changes in that geological epoch shaping the composition of the vegetation.

Résumé

Des espèces africaines de *Lepidium* (Brassicaceae) ont contribué, par hybridation, à l'origine d'espèces australiennes/néo-zélandaises. Le genre *Lepidium* sensu stricto (Brassicaceae) (± 150 espèces) est distribué à travers le monde et est constitué d'espèces endémiques sur chaque continent. Il est représenté en Australie et en Nouvelle-Zélande par 19 et 7 espèces natives, respectivement. Dans le cadre de la présente étude, nous avons utilisé une phylogénie basée sur l'ITS de l'ADN ribosomique (non codant) et nous l'avons comparée à une phylogénie du *cp*DNA afin de trouver l'origine des espèces australiennes/néo-zélandaises. En ce qui concerne les taxons australiens/néo-zélandais, des signaux fortement conflictuels sont apparus entre les analyses du *cp*- et de l'ADN nucléaire. Ils prouvaient clairement la constitution génomique hybridogène des espèces de *Lepidium* s.s. australiens. Les 18 espèces étudiées de *Lepidium* s.s. australiens/néo-zélandais avaient en commun un *cp*DNA de type californien, 11 taxons australiens/néo-zélandais avaient un type d'ITS californien et un groupe de sept espèces montrait un type d'ITS sud-africain. Cette situation peut vraisemblablement être expliquée par deux dispersions transocéaniques de *Lepidium* à partir de la Californie et de l'Afrique vers l'Australie/Nouvelle Zélande, suivies par une hybridation et par l'homogénéisation de l'ADN ribosomique en deux lignées, l'une avec un type d'ITS californien, l'autre sud-africain. Le calibrage de nos arbres moléculaires indique une origine Pliocène/Pleistocène de *Lepidium* en Australie/Nouvelle Zélande. Une faible divergence des séquences *cp*DNA et ITS et des topologies non résolues entre les espèces australiennes/néo-zélandaises suggèrent une radiation rapide et récente de *Lepidium* après l'événement d'hybridation. Celui-ci coïncide avec les changements climatiques drastiques de cette époque géologique qui ont conditionné la composition de la végétation.

Key words: biogeography, Brassicaceae, hybridization, *Lepidium*, long-distance dispersal

1 Introduction

Lepidium L. is one of the largest genera in the Brassicaceae, consisting of ± 175 species worldwide. Recent molecular studies of *Lepidium* phylogeny utilizing the nuclear *r*DNA internal transcribed spacer (ITS), noncoding *cp*DNA and single copy nuclear DNA sequences (an intron of PISTILLATA, PI), respectively, clarified some relationships within the genus (Bowman *et al.*, 1999; Mummenhoff *et al.*, 2001; Lee *et al.*, 2002). However, an important unanswered question concerns the evolutionary history, i.e., the biogeographic context and time of origin, of Australian/New Zealand *Lepidium* s.s. species (for a definition of *Lepidium* s.s. see Mummenhoff *et al.*, 2001). Based on morphological differences among native Australian taxa, H. Hewson (personal communication, CSIRO, Canberra) suggested independent introductions of *Lepidium* in Australia from South America, South Africa, and Southeast Asia.

In the present study we clarify the evolutionary history of *Lepidium* s.s. in Australia/New Zealand by comparing noncoding *cp*DNA and ITS sequences from 18 Australian/New Zealand species along with 38 species from the other continents. This represents the whole spectrum of variation in *Lepidium* s.s. Molecular footprints in Australian/New Zealand *Lepidium* revealed that these species arose through hybridization with Californian and South African *Lepidium* species being involved.

2 Materials and methods

2.1 Taxon sampling

Fifty-six taxa were chosen to represent the whole spectrum of variation in the *Lepidium* s.s lineage and cover all major geographic distributions areas: Europe/Asia, Africa, North and South America, and Australia/New Zealand. Australia and New

Zealand harbor 19 and nine native taxa, respectively; our sampling of ten Australian and eight New Zealand taxa comprises representatives of all taxonomic entities and thus represents the full range of variation of *Lepidium* s.s. in Australia and New Zealand. As an outgroup, species of section *Lepia* s.l., i.e., *L. campestre* and *L. hirtum* subsp. *hirtum*, were used. In previous analyses section *Lepia* appeared as sister to *Lepidium* s.s. (Bowman *et al.*, 1999, Mummenhoff *et al.*, 2001). GenBank accession numbers and collection data are given in Table 1.

2.2 Molecular methods

Methods for DNA extraction, PCR and direct sequencing of ITS and noncoding *cp*DNA (*trn*T/*trn*L spacer, *trn*L intron, *trn*L/*trn*F spacer) are given elsewhere (Bowman *et al.*, 1999, Mummenhoff *et al.*, 2001). To study the parental ITS units in presumed hybridogenous Australian *Lepidium*, the PCR (Polymerase Chain Reaction) products of selected Australian/New Zealand polyploids (*L. fasciculatum*, *L. pseudohyssopifolium, L. pseudotasmanicum, L. muelleri-ferdinandi, L. oleraceum*, *L. banksii*) were cloned and 2–8 clones were sequenced. The same primers as for the PCR amplification were used for sequencing. Compilation of the information obtained from direct sequencing and from clone sequencing reveals one nucleotide polymorphism in *L. oleraceum* and *L. fasciculatum*, respectively, two polymorphic sites in *L. pseudohyssopifolium*, and three in *L. muelleri-ferdinandi*. Thus, we treated these nucleotide sites as polymorphic character states in the ITS data set used for subsequent phylogenetic analyses. DNA sequences were aligned by hand. Regions of ambiguous alignment were eliminated.

2.3 Phylogenetic analysis

Parsimony analysis of ITS and *cp*DNA assumed unordered and unweighted character states (i.e., Fitch parsimony) and used the heuristic search strategy in PAUP (version 4.0b10; Swofford, 2000) with TBR (tree bisection-reconnection) branch swapping, and 100 random taxon additions. Up to 10,000 trees were kept from each random addition sequence replicate. Bootstrap support values were obtained from 100 replicates by using a heuristic search and simple addition.

2.4 Sequence divergence and relative rate test

Pairwise distance divergences were calculated in PAUP under Kimura's two parameter model (K2P) by using the pairwise-deletion option for gaps and ambiguous data. Rate heterogeneity among lineages in the *cp*DNA and ITS trees was examined by using a tree-wide likelihood ratio (LR) test (Modeltest 3.04; Posada & Crandall, 1998). This test compares the log likelihoods (determined in 4.0b10) of constrained and unconstrained hypotheses (constrained: DNA substitution rates are equal among lineages; unconstrained: rates are allowed to vary among lineages) under the most adequate substitution model that best fits the data (Huelsenbeck & Rannala, 1997).

3 Results

3.1 *cp*DNA- and ITS sequence variation

Details on the characterization of noncoding *cp*DNA regions (*trn*T/*trn*L spacer, *trn*L intron, *trn*L/*trn*F spacer) are given in Mummenhoff *et al.* (2001). After eliminating regions with ambiguous alignment, 1435 positions were available for phylogenetic analysis. Of the 220 variable characters, 89 were potentially parsimony informative.

TABLE 1. Collection data and GenBank accession numbers of *Lepidium* species studied.

Species	**Origin**	**Provenance/Source [a]/Collector**	**GenBank accession number**				
			***trn*T/*trn*L spacer [b]**	***trn*L *intron***	***trn*L/*trn*F spacer [c]**	**ITS1**	**ITS2**
L. africanum (Burm.f.) DC.	Africa	South Africa, Cape Province, Williston District/PRE, 95056-102/ G. Germishuizen	AY015703 AY015704	AY015833	AY015921	AJ582441	AJ582498
L. alluaudii Maire	Africa	Morocco, near Tazenakh/ ETSIA, 418-1483-68	AY015705 AY015706	AY015834	AY015922	AJ582436	AJ582493
L. apetalum Willd.	Asia	China, Beijing/ B.G. Beijing, China, s.n.	AY015823	AY015835	AY015923	AJ582466	AJ582514
L. arbuscula Hillebr.	Hawaii	Hawaii, Oahu , Makua Valley, Ohikilolo Ridge/National Tropical B.G. Lawai, Kauaii, Hawaii, 945176/ S. P. Pearlman	AY015707 AY015708	AY015836	AY015924	AJ582451	AJ582517
L. armoracia Fisch. & Mey.	Africa	Arabian Republic Yemen, Shibam/ K, MWC 2307/A. G. Miller	AY015709 AY015710	AY015837	AY015925	AJ582454	AJ582502
L. aschersonii Thell.	Australia	Australia, Victoria, Lake Omeo/ La Trobe Univ., Australia, s.n./ N. H. Scarlett	AY015711 AY015712	AY015838	AY015926	AJ582426	AJ582483
L. aucheri Boiss.	Asia	Jordania, Wadi Araba/Orient Herbarium, FU Berlin, Germany, s.n./ H. U. Baierle & C. Prime	AY015713 AY015714	AY015839	AY015927	AJ582443	AJ582525
L. austrinum Small	North America	USA, Texas, Hidalgo Co./Tucker Herbarium, Univ. of California, Davis, 17451/L. H. Shinners	AY015715 AY015716	AY015840	AY015928	AJ582467	AJ582515
L. banksii Kirk	New Zealand	New Zealand, Abel Tasman National Park, Totaranui/P. de Lange, Dept. Conservation, Auckland Conservancy, New Zealand, 942179	AY015717 AY015718	AY015841	AY015929	AJ582433	AJ582490
L. bidentatum Montin	Hawaii	Hawaii, Kauaii, Haupu/National Tropical B.G. Lawai, Kauaii, Hawaii, 905054/S. P. Pearlman	AY015719 AY015720	AY015842	AY015930	AJ582468	AJ582516

TABLE 1. continued

Species	Origin	Provenance/Source [a]/Collector	GenBank accession number				
			*trn*T/*trn*L spacer [b]	*trn*L *intron*	*trn*L/*trn*F spacer [c]	ITS1	ITS2
L. bipinnatifidum Desv.	South America	Bolivia, La Paz , railway station/ Univ. Osnabrück, Germany, 451/ K. Mummenhoff & H. Brüggemann	AY015721 AY015722	AY015843	AY015931	AJ582446	AJ582522
L. bonariense L.	South America	Chile, Prov. Atacama, Dept. Valle Iorquera/CETYBO, 3078/O. Zöllner	AY015723 AY015724	AY015844	AY015932	AJ582458	AJ582506
L. campestre (L.) R.Br.	Europe	France, Meurthe-et-Moselle, Villers-les-Nancy/B.G. Nancy, France, s.n.	AY015725 AY015726	AY015845	AY015906 AY015907	AJ582412	AJ582469
L. capense Thunb.	Africa	South Africa, Cape Province/ PRE, 95056/49/H. C. Taylor	AY015727 AY015728	AY015846	AY015933	AJ582452	AJ582500
L. desertorum Eckl. & Zeyh.	Africa	South Africa, Cape Province/ PRE, 95056/68/M. B. Bayer	AY015729 AY015730	AY015847	AY015934	AJ582453	AJ582501
L. desvauxii Thell.	Australia	Australia, Victoria, Townsend/ La Trobe Univ., Australia , s.n./ N. H. Scarlett	AY015731 AY015732	AY015848	AY015935	AJ582429	AJ582486
L. dictyotum A.Gray	North America	USA, California, San Luis Obispo Co./ Tucker Herbarium, Univ. of California, Davis, 32057/E. C. Twisselmann	AY015733 AY015734	AY015849	AY015936	AJ582415	AJ582472
L. divaricatum Ait.	Africa	South Africa, Cape Province, Williston District/PRE, 95056/134/ P. Germishuizen	Sequence data not available	AJ582565	AJ582566	AJ582437	AJ582494
L. fasciculatum Thell.	Australia	Australia, Victoria, river road near Lake Walla Walla/La Trobe Univ., Australia, s.n./J. H. Browne	AJ582562	AJ582563	AJ582564	AJ582428	AJ582485
L. ferganense Korsh.	Asia	Russia, Moscow/B.G. Moscow, Russia, s.n.	AY015737 AY015738	AY015851	AY015938	AJ582449	AJ582519
L. flavum Torr.	North America	USA, Nevada, Churchill Co., Slate Mountain/MO/A. Tiehm & P. Lott, 4011	AY015739 AY015740	AY015852	AY015908 AY015909	AJ582444	AJ582524

TABLE 1. continued

Species	Origin	Provenance/Source [a]/Collector	GenBank accession number				
			*trn*T/*trn*L spacer [b]	*trn*L *intron*	*trn*L/*trn*F spacer [c]	ITS1	ITS2
L. flexicaule Kirk	New Zealand	New Zealand/Auckland B. G., cultivated plants, 950769	AY015741 AY015742	AY015853	AY015939	AJ582430	AJ582487
L. fremontii S.Wats.	North America	USA, California, Joshua Tree Desert/ Univ. Osnabrück, Germany/ H. Hurka, s.n.	AY015815	AY015854	AY015940	AJ582456	AJ582504
L. hirtum (L.) Sm. ssp. *hirtum*	Europe	France, Dept. Aude, Montagne de Tauch/B.G. Univ. Liege, Belgium, 85-3863	AY015819	AY015858	AY015944	AJ582413	AJ582470
L. hyssopifolium Desv.	Australia	Australia, Victoria, Beveridge/ La Trobe Univ., Australia, 70-296-940/ N. H. Scarlett	AY015743 AY015744	AY015861	AY015947	AJ582435	AJ582492
L. lasiocarpum Nutt.	North America	USA, California, Joshua Tree Desert/ ETSIA, 430-1738-69	AY015745 AY015746	AY015862	AY015948	AJ582455	AJ582503
L. latifolium L.	Europe	Germany, Leipzig, garbage dump/ B.G. Leipzig, Germany/P. Gutte	AY015747 AY015748	AY015863	AY015949	AJ582447	AJ582521
L. latipes Hook.	North America	USA, California, Solano Co./Tucker Herbarium, Univ. of California, Davis, 37209/J. M. Tucker	AY015749 AY015750	AY015864	AY015950	AJ582416	AJ582473
L. lyratum L.	Asia	Iran, mountains near Abadeh/ ETSIA, 433-3758-75	AY015755 AY015756	AY015867	AY015953	AJ582448	AJ582520
L. meyenii Walpers	South America	Peru, Dept. Junin, Huayre/ M. Hermann, Intern. Potato Center, Quito, Ecuador, JTA-106/J. Anco	AY015757 AY015758	AY015868	AY015954	AJ582445	AJ582523
L. montanum Nutt.	North America	USA, Arizona, Shonto/B.G. Univ. Liege, Belgium, s.n.	AY015759 AY015760	AY015869	AY015955	AJ582457	AJ582505
L. muelleriferdinandi Thell.	Australia	Australia, New South Wales, Menindee Lakes/La Trobe Univ., Australia, s.n./J. H. Browne	AY015761 AY015762	AY015870	AY015956	AJ582427	AJ582484

TABLE 1. continued

Species	Origin	Provenance/Source [a]/Collector	GenBank accession number				
			*trn*T/*trn*L spacer [b]	*trn*L *intron*	*trn*L/*trn*F spacer [c]	ITS1	ITS2
L. myriocarpum Sond.	Africa	South Africa, Cape Province, Vaalbos National Park/PRE, 95056/53/P. C. Zietsman	AY015763 AY015764	AY015871	AY015957	AJ582442	AJ582499
L. naufragorum Garnock-Jones & D.A.Norton	New Zealand	New Zealand/P. de Lange, cultivated plants, Dept. Conserv., Auckland Conservancy, New Zealand, 950771	AY015765 AY015766	AY015872	AY015958	AJ582422	AJ582479
L. nitidum Nutt.	North America	USA, California , Table Mountains/Univ. Osnabrück, Germany, 338/H. Hurka	AY015767 AY015768	AY015873	AY015959	AJ582414	AJ582471
L. oblongum Small	North America	Cultivated plants/B.G. Copenhagen, Denmark, s.n.	AY015769 AY015770	AY015874	AY015960	AJ582462	AJ582510
L. oleraceum Sparrm.	New Zealand	New Zealand, Port Waikato, Ngatutura Point/Dept. Conserv., Auckland Conservancy, New Zealand, 941265/P. de Lange	AY015771 AY015772	AY015875	AY015961	AJ582434	AJ582491
L. oxycarpum Torrey & A.Gray	North America	USA, California, Merced Co./Tucker Herbarium, Univ. of California, Davis, 115743/C. A. & L. P. Janeway	AY015773 AY015774	AY015876	AY015962	AJ582417	AJ582474
L. oxytrichum Sprague	Australia	Australia, Northern Territorium/National B.G. Canberra, Australia, s.n.	AY015775 AY015776	AY015877	AY015963	AJ582424	AJ582481
L. papillosum F.Muell.	Australia	Australia, Victoria, Red Cliffs, Bottle Bend River/T.H. Browne, Australia, s.n.	AY015777 AY015778	AY015878	AY015964	AJ582425	AJ582482
L. pinnatifidum Ledeb.	Asia	USA, California, Yolo Co./Tucker Herbarium, Univ. of California, Davis, 96441/A. M. Shapiro	AY015787 AY015788	AY015883	AY015968	AJ582464	AJ582512
L. pinnatum Thunb.	Africa	South Africa, Cape Province, Drinkriver farm/PRE, 95056/45/K. A. Dahlstrand	AY015827	AY015884	AY015969	AJ582439	AJ582496

TABLE 1. continued

Species	**Origin**	**Provenance/Source [a]/Collector**	**GenBank accession number**				
			***trn*T/*trn*L spacer [b]**	***trn*L *intron***	***trn*L/*trn*F spacer [c]**	**ITS1**	**ITS2**
L. pseudohyssopifolium Hewson	Australia	Australia, Victoria, Mitre Rock, near Mt. Arapiles/La Trobe Univ., Australia, s.n./N. H. Scarlett	AY015789 AY015790	AY015885	AY015970	AJ582431	AJ582488
L. pseudopapillosum Thell.	Australia	Australia, Victoria, Kamarooka Forest/La Trobe Univ., Australia, s.n./N. H. Scarlett *et al.*	AY015791 AY015792	AY015886	AY015971	AJ582423	AJ582480
L. pseudotasmanicum Thell.	Australia	Australia, Victoria, George National Park/La Trobe Univ., Australia s.n./N. H. Scarlett *et al.*	AY015826	AY015887	AY015972	AJ582432	AJ582489
L. quitense Turcz.	South America	Ecuador, Prov. Tungurakua, road from Pillaro to Ambato/MO, 3792042/C. E. & M. Ceron	AY015793 AY015794	AY015888	AY015973	AJ582463	AJ582511
L. ruderale L.	Europe	Germany, Borgholzberg near Oldenburg/B.G. Oldenburg, Germany, s.n.	AY015795 AY015796	AY015890	AY015975	AJ582465	AJ582513
L. sativum L.	Europe	Denmark, Jersie/B.G. Copenhagen, Denmark, s.n.	AY015828	AY015891	AY015912 AY015913	AJ582459	AJ582507
L. schinzii Thell.	Africa	South Africa, Orange Free State Excelsior, Korannaberg/PRE, 95056/6/J. du Perez	AY015797 AY015798	AY015892	AY015976	AJ582440	AJ582497
L. serra H.Mann	Hawaii	Hawaii, Kauai, Kalalau valley near Puu O Kila/National Tropical B.G. Lawai, Hawaii, Kauaii, 915398/S.P. Pearlman	AY015799 AY015800	AY015893	AY015977	AJ582450	AJ582518
L. sisymbrioides ssp. *kawarau* (Petrie) Thell.	New Zealand	New Zealand, Central Otago, Slapjack Creek/P. de Lange, Dept. Conserv., Auckland Conservancy, New Zealand, 950766/R. B. Allen	AY015801 AY015802	AY015894	AY015978	AJ582419	AJ582476

Table 1. continued

Species	Origin	Provenance/Source [a]/Collector	GenBank accession number				
			*trn*T/*trn*L spacer [b]	*trn*L *intron*	*trn*L/*trn*F spacer [c]	ITS1	ITS2
L. sisymbrioides ssp. *matau* (Petrie) Thell.	New Zealand	New Zealand, Central Otago, Galloway/P. de Lange, Dept. Conserv., Auckland Conservancy, New Zealand , 950767/R. B. Allen	AY015803 AY015804	AY015895	AY015979	AJ582418	AJ582475
L. sisymbrioides Hook.f. ssp. *sisymbrioides*	New Zealand	New Zealand, Central Otago, Pisa Flats/P. de Lange, Dept. Conserv., Auckland Conservancy, New Zealand , 950768/R. B. Allen	AY015805 AY015806	AY015896	AY015980	AJ582420	AJ582477
L. spinescens DC.	Asia	Israel, Upper Galilee/B.G. Univ. Tel Aviv, Israel, s.n.	AY015807 AY015808	AY015897	AY015981	AJ582461	AJ582509
L. spinosum Ard.	Asia, Europe	Turkey, Central Anatolia, near Gaziantep/ETSIA, 436-6229-83	AY015824	AY015898	AY015914 AY015915	AJ582460	AJ582508
L. tenuicaule Kirk	New Zealand	New Zealand, Kakanui, Shag Point/ P. de Lange, Dept. Conserv., Auckland Conservancy, New Zealand, 950191/P. de Lange	AY015809 AY015810	AY015899	AY015982	AJ582421	AJ582478
L. trifurcum (Sond.) Marais	Africa	South Africa, Cape Province, SW slopes of Pakhuispiek, cedarberg/ PRE, 95056-111/H. C. Taylor	AY015811 AY015812	AY015900	AY015983	AJ582438	AJ582495
L. virginicum L.	North America	Mexico, Carrizal Chico, riverbed/ Univ. of Osnabrück, Germany/ R. Stöckmann & K. Bosbach, s.n.	AY015813 AY015814	AY015902	AY015984	AF283496	AF283497

[a] ETSIA = Escuela Tecnica Superior de Ingenieros Agronomos, Madrid, Spain; B.G. = Botanical Garden; CETYBO = Centro de Estudios Farmacologicos y Botanicos, Buenos Aires, Argentina; DAV = Davis Herbarium, Deptartment of Botany, University of California, Davis, USA; K = Herbarium, Royal Botanic Gardens, Kew, UK; MO = Herbarium, Missouri Botanical Garden, St. Louis, USA; PRE = National Herbarium, Botanical Research Institute, Pretoria, South Africa.

[b] Species with two GenBank accession numbers refer to sequences starting from the 5´ and 3´ end, respectively. In these species presence of poly-A/T tracts caused premature termination of sequencing reactions.

[c] Species with two GenBank accession numbers refer to sequences starting from the 5´ and 3´ end, respectively. For these species overlapping sequencing could not be achieved due to extreme length of spacer regions.

	`ITS1          ITS2`
	`    1111111112233344`
	`67880013446775936933`
	`83478965680241795402`
Californian taxa, clade C	
dic (4x), lat (4x), nit (4x), oxyc	`CATTAGCCCGTCATCGG-TA`
Australian/New Zealand taxa, clade C	
nau (4x), oxyt (3x), pap, sis (3 ssp., 4x), ten	`CATTACCCCGTCATCGG-TA`
fasc (4x)	`CATTATCCCGTCATCGG-TA`
pseup	`CGTTACCCCGTCATCGG-TA`
asch	`CATTATCCCGTCATCGG-TW`
muel (6x)	`CATTRCCCCGTCATCGG-TA`
Australian/New Zealand taxa, clade A	
ban (4x), des, fle (4x), hys (4x), ole (4x), pseut (4x)	`TTCGGCGTGCAACCTA-TCT`
pseuh (4x)	`TTCGGCGTGCAACCYA-TCT`
South African taxa, clade A	
afr (2x), dese, div, myr, pin, schi, tri	`TTCGGCGTGCAACCTA-TCT`
cap	`TTCGGCGTGCAACCAA-TCT`

FIG. 1. Composition of the ITS sequences of Californian, Australian/New Zealand and South African *Lepidium* s.s. species. This data matrix contains only those positions of a complete alignment (not shown) that distinguish Californian from South African *Lepidium* taxa. Californian and South African species are extant members of two different lineages suggested to have been involved in the hybridogenous origin of Australian/New Zealand *Lepidium*. Clade A and clade C refer to the ITS tree in Fig. 2. Site numbers are those of the complete alignment. R = A and G; W = A and T; Y = C and T. Taxon abbreviations; Californian taxa: dic = *L. dictyotum*; lat = *L. latipes*; nit = *L. nitidum*; oxyc = *L. oxycarpum*; Australian/New Zealand clade C taxa: nau = *L. naufragorum*; oxyt = *L. oxytrichum*; pap = *L. papillosum*; sis (3 ssp.) = *L. sisymbrioides* ssp. *kawarau*, ssp. *sisymbrioides*, ssp. *matau*; ten = *L. tenuicaule*; fasc = *L. fasciculatum*; pseup = *L. pseudopapillosum*; asch = *L. aschersonii*; muel = *L. muelleri-ferdinandi*; Australian/New Zealand clade A taxa: ban = *L. banksii*; des = *L. desvauxii*; fle = *L. flexicaule*; hys = *L. hyssopifolium*; ole = *L. oleraceaum*; pseut = *L. pseudotasmanicum*; pseuh = *L. pseudohyssopifolium*; South African taxa: afr = *L. africanum*; dese = *L. desertorum*; div = *L. divaricatum*; myr = *L. myriocarpum*; pin = *L. pinnatum*; schi = *L. schinzii*; tri = *L. trifurcum*; cap = *L. capense*. Ploidy levels (2x–6x) are based on own chromosome counts.

Averaged over the three regions K2P pairwise sequence divergence among the *Lepidium* s.s. taxa varied between 0 and 2.5% and within Australian/New Zealand taxa between 0 and 1.5%.

The ITS regions were sequenced for 56 species and 34 clones of selected Australian *Lepidium* species. The alignment generated a matrix of 456 characters, of which 87 are potentially informative in parsimony analysis. K2P pairwise sequence divergence among the *Lepidium* s.s. taxa ranged between 0 and 7.9%, and within Australian/New Zealand taxa between 0 and 1.5%.

3.2 ITS sequence polymorphism in Australian/New Zealand *Lepidium* and presumed progenitors

Eighteen Australian *Lepidium* s.s. taxa were analyzed by direct sequencing. Known polyploids (*L. fasciculatum, L. pseudohyssopifolium, L. pseudotasmanicum, L. muelleri-ferdinandi, L. oleraceum, L. banksii;* ploidy level see Fig.1) were also analyzed by cloning amplified ITS sequences. Three species (*L. aschersonii, L. muelleri-ferdinandii, L. pseudohyssopifolium*) show additivity at one nucleotide position that is variable between the Californian (clade C) and South African (clade A) species group (Fig. 1, sites 108, 297, 432). This indicates that the Australian/New Zealand species may have originated by hybridization. With respect to those sites that are variable between the California and South Africa species group (Fig. 1) the Australian species of clade C and A show exactly those character states of the Californian (clade C) or South African (clade A) species, respectively. However, at site 109 most Australian/New Zealand taxa including those of clade C (related to Californian species) are characterized by the nucleotide found in the South African species (clade A).

3.4 Phylogenetic position of Australian/New Zealand *Lepidium*

We analyzed noncoding *cp*DNA regions and nuclear ITS regions from 56 *Lepidium* s.s. taxa of all major geographic distributions to unravel the origin of Australian/New Zealand *Lepidium* in this lineage. Comparison of the phylogenetic trees (strict consensus of most parsimonious trees) generated from the two data sets is illustrated in Fig. 2. Several nodes are reasonably well supported (>70% bootstrap values), while other nodes are less so, due to low numbers of nucleotide substitutions. This is not surprising in view of a Pliocene/Pleistocene origin of *Lepidium* s.s. (Mummenhoff *et al.*, 2001). In the current study of *Lepidium* s.s. both phylogenies agree in grouping geographically related species, but there are strongly conflicting signals between the *cp*DNA and ITS topologies (Fig. 2). In the *cp*DNA strict consensus tree all Australian/New Zealand species are grouped into a monophyletic assemblage arising from a polytomy. However, in 60% of all maximally parsimonious trees (clade B, *cp*DNA, Fig. 2) four coastal Californian species are found as sister to the Australian/New Zealand clade. Within clade B species relationships are not well resolved due to lack of characters. However, within this clade two distinct groups may be recognized composed of New Zealand species, i.e., *L. sisymbrioides* with three subspecies (100% bootstrap support) and *L. naufragorum, L. flexicaule, L. banksii,* and *L. oleraceum* (53% bootstrap support), respectively. In the ITS tree Australian species are distributed among two different lineages. One group shares common ancestry with the same four Californian species mentioned above (clade C). The remaining species are nested within an unresolved clade A along with South African species and one East African species.

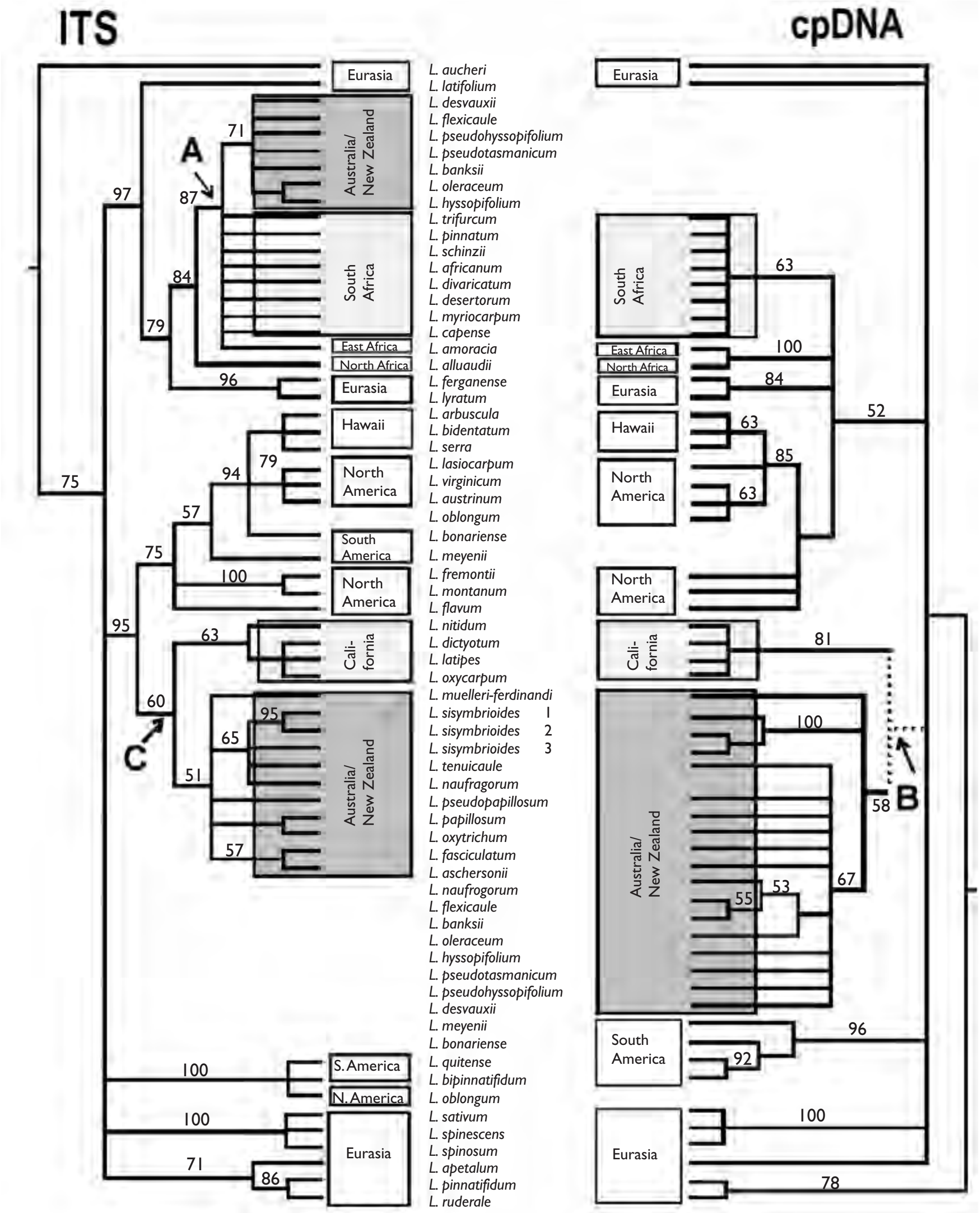

FIG. 2. Comparison of nuclear and chloroplast phylogeny of Australian/New Zealand *Lepidium* s.s. species and continental relatives based on sequence analysis of ribosomal ITS and three noncoding *cp*DNA regions (*trn*T/*trn*L spacer, *trn*L intron, *trn*L/*trn*F spacer), respectively. Shown is the strict consensus each of 1369 most parsimonious ITS and 990 001 *cp*DNA trees with 202 and 275 steps and a consistency index (autapomorpies excluded) of 0.80 and 0.71, respectively. Dashed line in the *cp*DNA tree indicates a branch present in 60% of the minimum length trees. Arrows indicate clades involving *Lepidium* species of South Africa, Australia/New Zealand (clade A), and California, Australia/New Zealand (clade C), and Australia/New Zealand solely (clade B). Bootstrap values >50% are given above branches. *Lepidium sisymbrioides* 1 through 3 refer to subspecies *sisymbrioides*, *kawarau*, and *matau*. Trees were rooted by outgroup comparison.

3.5 Relative-rate-test and molecular clock calibration

Rate heterogeneity among lineages in the *cp*DNA and ITS trees, respectively, was examined by using a tree-wide likelihood ratio (LR) test (Modeltest 3.04; Posada & Crandall, 1998). Rate constancy across lineages throughout the ITS and *cp*DNA tree was rejected. So we followed the recommendations given in Sanderson (1998) to perform localized LR tests on subclades of the phylogenies. As we have focussed in the present study on the origin of Australian/New Zealand *Lepidium* species we tested for rate constancy within those clades containing Australian/New Zealand species (Fig. 2: ITS tree, clade A, C; *cp*DNA tree, clade B). Substitution rate constancy was rejected for clade B in the *cp*DNA tree, but rate constancy within clades A and C of the ITS phylogeny cannot be rejected at the $\alpha = 0.01$ level.

We used fossil data (Mai, 1995) of *Rorippa* (Brassicaceae) to calibrate mutation rates in *Lepidium. Rorippa* was found sister to *Cardamine* in recent phylogenetic analyses (Franzke *et al.*, 1998; Mitchell and Heenan, 2000). Assuming a correct dating for the *Rorippa* fossil, a minimum of K2P sequence divergences of 1.8% (*trn*T/L spacer, *trn*L intron) and 4.4% (ITS), respectively, observed between *Rorippa* and *Cardamine* taxa analyzed (Franzke *et al.*, 1998), might then correspond to 2.5–5 million years ago (mya), as a rough estimate for divergence time between *Rorippa* and *Cardamine.* Thus, 1% sequence divergence corresponds to 0.6–1.1 my (million years) for the ITS regions and 1.3–2.8 my for the *cp*DNA. Our calibrated ITS rates are in the same order of magnitude as recently published ITS rates, e.g., *Gossypium*: ca 1% = 1 my (Wendel *et al.*, 1995b), *Gentianella* 1% = 0.6–1.1 my (Hagen & Kadereit 2001), *Soldanella* 1% = 0.6–1.3 my (Zhang *et al.*, 2001), *Robinsonia* 1% = 0.6 my (Sang *et al.*, 1995b), and are thus reasonable.

Sequence divergence among the Australian/New Zealand species ranged from 0% to 1.2% (0.5% mean) for the *trn*T/L spacer and *trn*L intron. ITS divergence ranged from 0.2 to 3.4% (1.2% mean) and from 0 to 1.1% (0.5% mean) among the Australian/New Zealand species of lineage A and C (Fig. 2), respectively. By using the ITS substitution rate calibrated with *Cardamine/Rorippa* (see above), we roughly estimated an age of 0.7–1.3 my and 0.3–0.55 my for the Australian/New Zealand species of lineage C and A, respectively. As we had to reject a tree-wide constant rate of ITS, the deviating divergence values of these two lineages might result from rate heterogeneity and reticulation between basal lineages. Although noncoding *cp*DNA evolution (even within the Australia/New Zealand clade) was not clocklike, the estimated age for the Australian/New Zealand lineage ranges from 0.6 to 1.4 my. Our time estimates based on ITS and *cp*DNA data are in the same order of magnitude indicating a Quaternary origin of Australian/New Zealand *Lepidium* species.

4 Discussion

4.1 Reticulate evolution in *Lepidium* s.s.

Lepidium s.s. includes species from all continents. Most of the species are characterized by reduced flowers, an autogamous breeding system and polyploidy, all these being typical features of colonizing plants (Al-Shehbaz 1986, Bowman *et al.*, 1999). Our recent phylogenetic analysis of the *PISTILLATA* (PI) intron, a member of the MADS-box gene family involved in stamen and petal specification, indicates that many species have originated from alloploidization (Lee *et al.*, 2002). The present ITS- and *cp*DNA data reinforces this hypothesis. Strongly conflicting signals between the different genome phylogenies are easily observed throughout the trees. Although incongruence among gene trees can result from a variety of factors, including sampling error, evolutionary rate heterogeneity, and phylogenetic sorting, the most common source of such phylogenetic discordance in plants appeared to reticulation events (Rieseberg *et al.*, 1996; Barrier *et al.*, 1999). Although reticulate evolution seems to have played an important role in the phylogeny of *Lepidium* s.s. world-wide, the current study focuses on the origin of Australian/New Zealand *Lepidium* s.s. species.

4.2 Two nuclear genomes in Australian/New Zealand *Lepidium*

Judged from the *cp*DNA phylogeny all Australian/New Zealand species harbor a *cp*DNA type most closely related to that of Californian species, and they are grouped into Clade B in 60% of maximally parsimonious trees (Fig. 2). The *cp*DNA mean sequence divergence values of 0.48% between species from California and Australia/New Zealand compared to the 0.92% sequence divergence observed between Australian/New Zealand species of clade B and South American species, i.e., *L. bonariense*, *L. meyenii*, and *L. quitense*, also supports this close relationship between Californian and Australian/New Zealand species. However, the ITS data provides strong evidence that some Australian/New Zealand *Lepidium* species contain the nuclear genome of the Californian species (clade C), while others have the nuclear genome of the South African lineage (clade A). The predominance of a distinct ITS type within each Australian lineage (clade C and A), respectively, may be explained by rapid bidirectional concerted evolution, following ancient hybridization between species from California and South Africa. The *cp*DNA data indicates that species of a Californian lineage represented by e.g., *L. dictyotum* was the most probable maternal parent of the Australian/New Zealand species, both groups sharing a similar *cp*-genome. The ITS data confirms this Californian lineage to be among the parental taxa but indicates that South African species (e.g., *L. africanum* etc.) were also involved. The hybridogenous genomic constitution of Australian/New Zealand *Lepidium* species can also be observed directly in ITS sequences. Nucleotide additivity at three nucleotide sites (Fig. 1) in the ITS regions Australian/New Zealand *Lepidium* s.s. species indicates that reticulate evolution has occurred as has been demonstrated in *Paeonia* (Sang *et al.*, 1995a) and that parental taxa of both continents were involved. The Australian/New Zealand species of clade C and A show with one exception exactly those character states of the Californian or South African species, respectively (Fig. 1). Thus, concerted evolution via gene conversion or unequal crossing-over is apparently operating. The observation of (nearly) homogenous ITS sequences (Fig. 1) indicates (nearly) complete uni- or bidirectional homogenization or transition stages in the homogenization process of the ITS region in the alloploids, respectively (Wendel *et al.*, 1995a, Campbell *et al.*, 1997).

Based on PI intron sequences(Lee *et al.*, 2002) demonstrated that many polyploid taxa harbored two or more phylogenetically distinct sequences, confirming a hybrid nature of Australian/New Zealand taxa.

4.3 Bicontinental hybrid origin of Australian/New Zealand *Lepidium* s.s.

We suggest that Australian *Lepidium* s.s. species are hybrids derived from a cross between colonizing species of the Californian and South African lineages C and A, respectively. Uniform/similar *cp*DNA and ITS sequences within the lineages containing Australian/New Zealand *Lepidium* taxa indicate that this ancient hybridization scenario predated the rapid speciation within these lineages. These speciation events probably also include later hybridization events as evidenced from grouping of species in the *cp*DNA tree (i.e., *L. naufragorum*, *L. banksii*, *L. flexicaule*, *L. oleraceum*) that are distributed among the two different clades A and C in the ITS tree (Fig. 2). The question whether polyploid Australian/New Zealand *Lepidium* are homoploid or alloploid hybrids cannot be answered from our data. The very few South African and Californian species from which chromosome numbers are known are *L. africanum* (2n = 2x = 16) and *L. dictyotum*, *L. latipes*, *L. nitidum*, (all 2n = 4x = 32), respectively. We generally used herbarium specimens in the current study and thus the ploidy level of Californian and South African *Lepidium* could not be analyzed. Until this point is clarified, one may suggest that the parental species were perhaps polyploid as polyploidy may have facilitated the establishment of the colonizing taxa from California and South Africa prior to hybridization. This is an attractive hypothesis because polyploidy may confer various characteristics appropriate to colonizing organisms including self-compatibility and buffering the effects of selfing (i.e., inbreeding depression), better vigor, and broader ecological tolerance (Barrier *et al.*, 1999; Miller & Venables, 2000). Indeed, based on PI intron sequences, *L. nitidum* is suggested to be an allopolyploid (Lee *et al.*, 2002).

An attractive hypothesis is that the ancient hybridization event occurred in Australia. This implies one dispersal from South Africa and California, respectively. Dispersal from California to South Africa and subsequent hybridization with an endemic taxon (or vice versa) followed by transoceanic migration of the hybrid (that retained the two different parental ITS copies) to Australia is equally parsimonious. But this scenario may be less likely because to our knowledge there are no sea birds migrating from California to South Africa (or vice versa) potentially having transported seeds. Whereas well documented sea bird migration pathways between coastal California and Australia/New Zealand (Lincoln *et al.*, 1998) are compatible with the former colonization scenario.

The origin of *Lepidium* and of the Brassicaceae as a whole presumably occurred in an area encompassing the Mediterranean and the Irano-Turanian territory, a region extremely diverse ecologically, altitudinally, and geologically (Thellung, 1906; Mummenhoff *et al.*, 2001). Fossil data, easy dispersible mucilaginous seeds, widespread autogamy and polyploidy, and low levels of *cp*DNA divergence between species from different continents or islands suggest a rapid radiation of *Lepidium* by long distance dispersal in the Pliocene/Pleistocene (Mummenhoff *et al.*, 2001). As a consequence of climatic changes in this geological epoch, arid/semiarid regions were established, providing favorable conditions for the radiation of *Lepidium* worldwide. South Africa was reached by the “arid corridor”, a belt of dry country that stretched from the Horn of Africa to Namibia (Hedge, 1976; Jürgens, 1997), and immigration of *Lepidium* into North and subsequently South America in Quaternary times is compatible with our estimates of divergence times, based on *cp*DNA sequence data (Mummenhoff *et al.,* 2001).

There are several genera centred in southern Africa with a few species in Australia, e.g., *Bulbine* (Asphodeliaceae), *Wurmbea* (Colchicaceae), *Caesia* (Hemerocallidaceae), *Spiloxene* (Hypoxidaceae), and *Dietes* (Iridaceae). In a phylogenetic analysis of *Pelargonium* (Geraniaceae) the close relationship between the South African and Australian species is caused by long distance dispersal to Australia, probably as recent as the late Pliocene (Bakker *et al.,* 1998). In the other cases mentioned above the possibility of recent dispersal across the Indian Ocean has not been confirmed, but it seems unlikely that the distributions date to the Jurassic, which is when the continents were last physically connected via Antarctica.

Our data provide evidence that Australian/New Zealand *Lepidium* are polyploid descendants of two different continental ancestors, one probably immigrating from California, and the other from South Africa. Long distance dispersal of colonizing species from California and South Africa to Australia/New Zealand seems unlikely given that these areas are currently separated by more than 10,000 km, respectively. Carlquist (1983) however, demonstrated intercontinental dispersal (California to Chile) of mucilaginous *Lepidium* seeds adhering to birds (Mummenhoff *et al.*, 1992; Norton *et al.*, 1997) and sea bird migration pathways between coastal California and Australia/New Zealand and between South Africa and Australia/New Zealand (Lincoln *et al.*, 1998) are compatible with the proposed colonization scenario.

4.4 Time of origin

Calibration of our molecular trees by using *Rorippa* fossil data yield ages of approximately 0.7–1.3 my and 0.3–0.55 my for the Australian/New Zealand species of clade C and A, respectively. These age differences might slightly modify our hypothesis that the hybridization of more or less concurrently arriving Californian and South African ancestors predates the radiation of Australian/New Zealand species. Different estimates of time of origin of Australian/New Zealand representatives of clades A and C, respectively might indicate that the diversification of Californian ancestors in Australia predates a chloroplast transfer into a later arriving South African colonizing species. The evidence against this scenario are the additive sequences in *L. aschersonii* and *L. muelleri-ferdinandi* (Fig. 1). Of course, another possibility is that the A-clade nucleotides in these two species were acquired later by secondary hybridization between clades A and C in Australia and are not relicts of an original hybridization. This would be more consistent with the dating analyses. However this discrepancy in time estimations may simply be explained by the observed rate heterogeneity between these two lineages and across the whole ITS tree. The low levels of *cp*DNA and ITS sequence divergence and unresolved topologies within Australian/New Zealand species (due to low numbers of nucleotide substitutions) suggest a rapid and recent radiation of *Lepidium* after the hybridization event. This coincides with dramatic climatic fluctuations of the Quaternary when a cooling climate and the formation of a more mountainous landscape in New Zealand, and a drying trend in Australia may have created novel habitats and thus highly invasible terrain (Markgraf *et al.*, 1995; McGlone *et al.*, 2001). This could have provided the necessary ecological space into which *Lepidium* could have radiated.

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ECOLOGY AND ALTITUDINAL ZONATION OF PTERIDOPHYTES ON MT KILIMANJARO

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Abstract

Based on the analysis of 1450 vegetation plots along 34 transects using the method of Braun-Blanquet (1964) the vegetation of Mt Kilimanjaro was analysed with respect to pteridophytes. Along an altitudinal range of over 5000 m their distribution on the northern and southern slope of the mountain is discussed focussing on altitudinal zonation, habitat requirements, diversity, life forms, and ecological factors. Due to its high precipitation Mt Kilimanjaro is very rich in pteridophytes, especially in filmy ferns and epiphytic ferns. Altogether 151 taxa, including 11 filmy ferns and 28 holo-epiphytic pteridophytes were found on this mountain. Flora and vegetation on Mt Kilimanjaro show distinct altitudinal discontinuities; pteridophytes are excellent tools to investigate this zonation. In respect of fern diversity and biomass forests and rocks are the main habitat for pteridophytes. Beside habitat diversity, precipitation is the main factor for the altitudinal distribution of pteridophytes. This is indicated by major differences in species numbers and composition of the dry northern and wet southern slope and the altitudinal distribution of forest ferns in general and tree ferns, filmy ferns and epiphytes in particular. Another important factor are fires, influencing the distribution of deciduous species, and the lower borderline of frost, controlling the occurrence of tree ferns.

Résumé

Basée sur l'analyse de 1450 quadrats de la végétation le long de 34 transects utilisant la méthode de Braun-Blanquet (1964) la végétation des ptéridophytes du Mt Kilimandjaro fut analysée. Selon une échelle altitudinale de plus de 5000 m leur distribution sur l'adret et l'ubac des montagnes fût analysée par rapport á la zonation altitudinale, l'habitat, la diversité, le type biologique et les facteurs écologiques. Grâce a son importante pluviométrie le Mont Kilimandjaro est riche en ptéridophytes, principalement en hyménophyllum et fougères épiphytes. 151 taxa, comprenant 11 hyménophyllum et 28 ptéridophytes holo-épiphytes furent trouvées dans ces montagnes. La flore et végétation du Mont Kilimandjaro montrent une distincte discontinuité altitudinale. Les ptéridophytes sont d'excellentes indicatrices pour démontrer cette zonation. Avec la diversité en habitat, la pluviométrie est le principal facteur pour la distribution altitudinale des ptéridophytes. Ceci est indiquée par des différences majeurs en nombre d'espèces et en composition sur les pentes sèches de l'ubac et humide de l'adret et par la distribution altitudinale générale des forêts riches en fougères, fougères arborescentes, hyménophyllum et épiphytes en particulier. Un

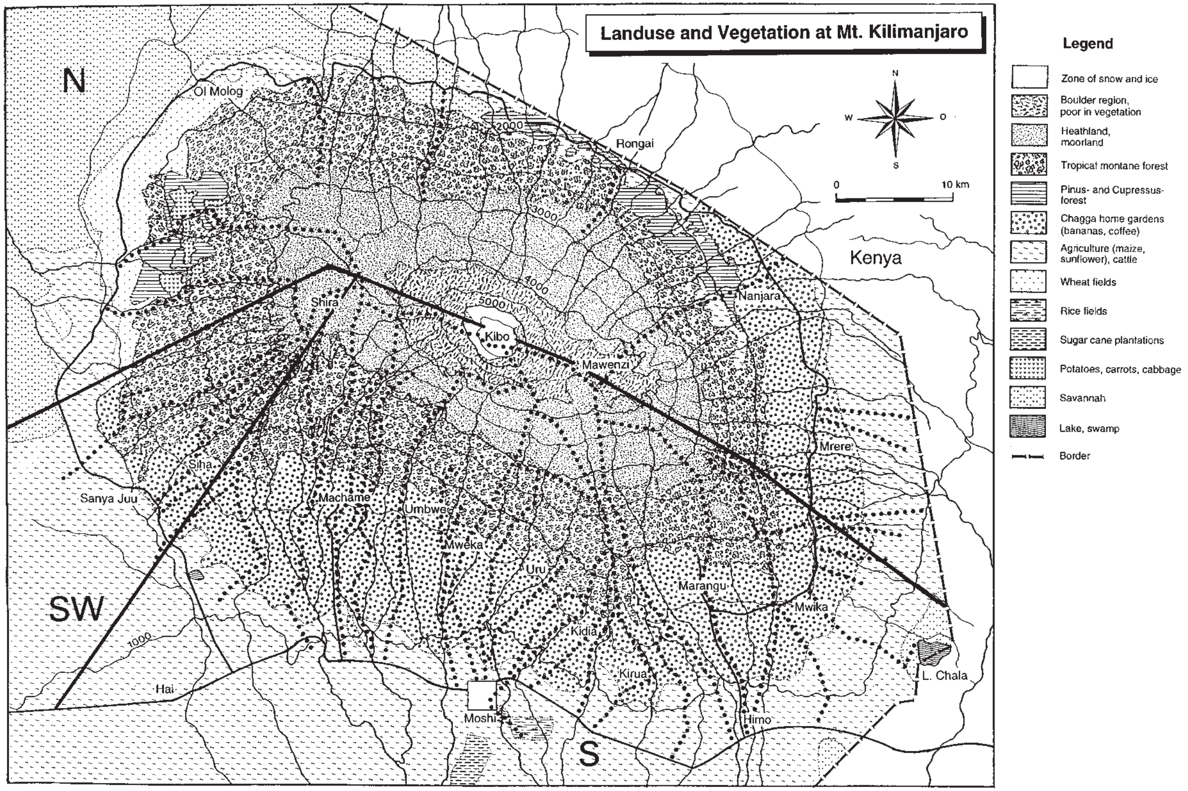

FIG. 1. Vegetation and land use of the study area with location of transects (dotted lines) and division into northern, southern and south western slopes.

autre important facteur sont les incendies, ayant une influence sur la distribution des espèces caduques et par la limite inférieure du gel, contrôlant la présence des fougères arborescentes.

Key words: altitudinal zonation, epiphytes, ferns, tropical montane forest, Mt Kilimanjaro

1 Introduction

Tropical mountains are exceptionally rich in pteridophyte species (Parris *et al.*, 1992; Moran, 1995). Mt Kilimanjaro, one of the highest solitary mountains in the world (750 m to 5895 m asl), overtopping its surrounding area by more than 5000 m, is an outstanding subject for the investigation of the altitudinal distribution and habitat demands of tropical plants.

Altitudinal zonation, the habitat requirements and strategies of the pteridophytes of Mt Kilimanjaro on the southern slope have been described by Hemp, 2001a & b & Hemp, 2002. The aim of the present study is to give a synopsis of the pteridophyte flora of the whole mountain with respect to the taxonomic composition, altitudinal ranges, the fern diversity at different altitudes and habitats, and the main ecological factors that influence the distribution of pteridophytes. As the northern slope differs substantially from the southern slope in climatic conditions, variation in altitudinal zonation and diversity can be reliably attributed to these environmental differences. Distribution patterns of ferns with different life forms are particularly useful in this respect.

2 Study area

2.1 Location and topography

Mt Kilimanjaro is located 300 km south of the equator in Tanzania on the border with Kenya between 2°45' and 3°25' South and 37°0' and 37°43' East. It represents an eroded relic of an ancient volcano with three peaks (Shira, Mawenzi and Kibo) rising from the savanna plains at 700 m elevation to a snow- and ice-clad summit at 5895 m. Its diameter from northwest to southeast is about 90 km.

34 transects were established on the whole mountain (Fig. 1). The study area was dissected into two major climatic and vegetational homogeneous blocks on the southern and northern slope. Because of differences in respect to climatic parameters and vegetation the southern slope was further divided into a central southern and a south-western part (Hemp, in press a). The whole study area covered nearly 3500 km^2.

2.2 Climate

Mt Kilimanjaro is characterized by a typical equatorial day-time climate. The distribution of precipitation over the year follows the intertropical convergence zone and is modified by the respective elevations. Due to its equatorial location, two distinct rainy seasons occur: the long rains from March to June, and the short rains around December. The driest period is from August to October, while April and May are the wettest months. According to the climate classification system of Köppen and Troll/Pfaffen (Müller, 1983) Mt Kilimanjaro belongs to the zone of a seasonal dry tropical climate. However, rainfall and temperature vary with altitude and exposure to the dominant wind from the Indian Ocean. The northern slopes, on the lee side of the mountain, receive much less annual rainfall than the southern slopes. Maximum precipitation occurs at 2200 m asl on the central southern slope with about 3000 mm

(Hemp, 2001a & in press a). The mean annual temperature in Moshi (813 m) is 23.4°C (Walter *et al.*, 1975). It decreases to –7.1°C at the top of Kibo (Thompson *et al.*, 2002). From 2700 m upslope frost occurs (Hemp, in press a).

2.3 Vegetation

A more detailed description of the vegetation types has been presented elsewhere (Hemp, 2001a, 2001b; Hemp & Hemp, 2003), and a vegetation map was published by Lambrechts *et al.* (2002).

On Mt Kilimanjaro several vegetation zones can be differentiated (Hedberg, 1951; Pócs, 1994; Hemp *et al.*, 1999; Hemp, 2002, in press a; Fig. 1). Between 700 and 1000 m a dry and hot savanna zone stretches around the mountain base. Most of this area is used for crop production (maize, beans and sunflowers fields) or as pasture land. Remnants of the former savanna vegetation are encountered only around Lake Chala in the eastern and on the (north-) western foothills of the study area.

Due to the favourable climate the main zone of agriculture and horticulture extends from 1000 to 1800 m on the southern and eastern slopes. Using an agroforestry system, the Chagga people grow bananas, coffee, and vegetables there (Hemp, 2005a). Remnants of the former forests of this zone have survived only in the deepest valleys and gorges.

The forest borders the cultivated zone in the central and eastern parts of the study area between 1600 and 1800 m, in the western parts at 1300 m, and extends to about 3100 m, surrounding the whole mountain. In the western and northern parts of the mountain the comparatively dry submontane forest below 1600 m is dominated by *Olea europaea* subsp. *africana*, *Croton megalocarpus* and *Calodendrum capense*. Above 1600 m *Cassipourea* forests prevail in this area, which are substituted above 2400 m by *Podocarpus* and *Juniperus* forests. On the wet southern slope the most important tree is the camphor-tree *Ocotea usambarensis*. In the lower part it occurs with *Agauria salicifolia*, *Macaranga kilimanjarica* and *Syzygium guineense*. In the upper part it is associated with *Podocarpus latifolius*. Above 2800 m *Erica excelsa* is an important tree species (Hemp & Beck, 2001).

Between 3100 and 3500 m the forests of *Erica excelsa* are gradually replaced by bushy species of *Erica*. In the southeastern parts moorland vegetation, composed of tussock grass and giant lobelias, fringe the forest. At an altitude of about 3900 m the *Erica* heathlands grade into *Helichrysum* cushion vegetation that extends up to 4500 m. The higher altitudes are sparsely vegetated and the top of Kibo is covered with glaciers (for details of the (sub-) alpine vegetation of Mt Kilimanjaro see Hedberg, 1951; Kötzli, 1958; Beck *et al.*, 1983).

3 Methods

3.1 Vegetation analysis

Data have been collected since 1996 along 34 transects (Fig. 1) subdivided in altitudinal intervals of 100 m (for details of the following see Hemp, 2001a & in press a). The altitudinal range of the transects extended from 760 m (Rau forest near Moshi) to 5895 m (Kibo peak). All ferns were recorded at altitudinal steps of 100 m and mapped with reference to the UTM grid, with degree squares of 1 km^2. About 1450 relevés (plots) were produced in all vegetation types using the method of Braun-Blanquet (1964). To encompass all important vegetation types of a given altitudinal interval, sampling intensity varied in accordance with the diversity of habitats in the respective range.

For the detection of altitudinal zonation the method of Sendtner (Gradstein & Frahm, 1987) and the “chronological clustering” (Legendre *et al.*, 1985) of the R package (Legendre & Vaudor, 1991) were used.

To determine the significance and relative importance of pteridophytes and of distinct life forms of pteridophytes in the vegetation types (the ”importance value”, Whittaker, 1972), the relevés were analysed and the so-called ”average percentage cover value” (in German referred to as ”mittlerer Gruppenmengenanteil”) was calculated. For comparison of the fern habitats their life form spectra were evaluated using Raunkiaer's (1905) classification of life forms in plants. In addition the division of Kornaś (1977, 1979, 1985), regarding patterns of growth and dormancy (evergreen, poikilohydrous and deciduous) was also applied to the ferns of Mt Kilimanjaro.

3.2 Nomenclature and floristic problems

Systematics in general follows Johns (1991) and the published fern issues of the Flora of Tropical East Africa (FTEA), except for the Hymenophyllaceae, where the system of Faden (1994) was applied. Since the previous papers about the pteridophytes of Mt Kilimanjaro (Hemp, 2001a, 2002) some changes in taxonomic treatment have taken place: according to Verdcourt (2003) specimens identified as *Cystopteris nivalis* (Pirotta) Pic.Serm. in East Africa are a subspecies of *C. fragilis* (*C. fragilis* subsp. “A”), whereas *C. fragilis* belongs to Verdcourt's subsp. “B”. *Anogramma leptophylla* (L.) Link var. *caespitosa* Pic.Serm. is merely a robust growth form of *A. leptophylla* (Nakazato & Gastony, 2003; Verdcourt, 2002). *Athyrium scandicinum* belongs in East Africa to the subspecies *newtonii* (Verdcourt, 2003). The *Asplenium* species provisionally named “*praegracile* Rosenst.” is *A. decompositum* Peter (Chaerle, pers. comm.). *Pellaea viridis/adiantoides* is *P. viridis*, since *P. adiantoides* (Willd.) J.Sm. is treated by Verdcourt (2002) as a synonym. The *Ophioglossum* species named *O. petiolatum* Hook. (which is probably a New World species, Burrows & Johns, 2001) is *O. vulgatum* subsp. *kilimandscharicum* and subsp. *africanum*; both subspecies were combined in the analysis. Due to the difficulty of differentiation in the field, the same holds for *Elaphoglossum angulatum* and *E. conforme* (Sw.) J.Sm. as well as for *Lepisorus excavatus* and *L. schraderi* (Mett.) Ching, which in East Africa have only questionable differences (Verdcourt, 2001).

Abbreviations of authors names follow Pichi Sermolli (1996). Author's names of each taxon are given in Table 1.

4 Results and discussion

4.1 Floristics

One hundred and fifty-one taxa in 65 genera and 25 families of pteridophytes were found in the study area (Table 1). These are 38% of the 399 known taxa for Tanzania (Schippers, 1993a, b) and 30% of the 510 taxa recorded for East Africa (Johns, 1991). Compared to other volcanoes in East Africa, Mt Kilimanjaro is distinctly richer in fern species in general and in filmy ferns, tree ferns and epiphytic ferns in particular, indicating that the forest belt of the southern slope of Mt Kilimanjaro is wetter than those of other high mountains in East Africa. However, compared with the mountains of the Eastern Arc, the number of pteridophytes on Mt Kilimanjaro is smaller. This can be explained by the widely destroyed submontane (intermediate) forest rather than by the higher age of the Eastern Arc Mts. (Hemp, 2002).

Twenty species were new records for Mt Kilimanjaro (region T2 as in FTEA); *Adiantum reniforme* is a new record for Tanzania (Hemp, 1997, 2000, 2002). *Lellingeria paucipinnata*, (treated as a *Xiphopteris* species by Hemp (1997)) was recently described as a new species known only from Kilimanjari (Parris, 2005) The following are 8 new records for the region T2, not published in FTEA (1999–2003): *Adiantum raddianum*, *Microlepia speluncae*, *Blotiella stipitata*, *Elaphoglossum spatulatum*, *Lomariopsis warneckei*, *Pteris tripartita* and *Vittaria isoetifolia*.

TABLE 1. Altitudinal ranges and main habitats of the pteridophytes of Mt Kilimanjaro.

Name	lf	gp	Altitudinal range (m asl)	Distribution	Main habitat
Actiniopteridaceae					
Actiniopteris dimorpha Pic.Serm	H	d	800–1500	south	dry rocks
Actiniopteris radiata (Sw.) Link	H	p	700–1300	south	dry rocks
Actiniopteris semiflabellata Pic.Serm.	H	p	800–1300	south	dry rocks
Adiantaceae					
Adiantum capillus-veneris L.	H	d	800–2000	north, south	moist rocks near water
Adiantum hispidulum Sw.	H	p	800–1600	south	shady embankments
Adiantum incisum Forssk.	H	p	800–1700	north, south	shady embankments
Adiantum poiretii Wikstr.	H	d	800–2500	north, south	shady embankments
Adiantum raddianum C.Presl	H	d	800–2500	north, south	shady embankments
Adiantum reniforme L. var. *reniforme*	H	d	1300–1700	south	semi-shaded rocks
Anogramma leptophylla (L.) Link	H	d	2500–4000	north, south	wet rocks
Cheilanthes farinosa (Forssk.) Kaulf.	H	d	900–3900	north, south	thicket edges, rocks
Cheilanthes multifida (Sw.) Sw.	H	p	1500–1800	north, south	dry forests and thickets
Coniogramme africana Hieron.	H	e	1200–1900	south	moist forests
Doryopteris kirkii (Hook.) Alston	H	d	800–2000	north, south	roadsides, embankments
Pellaea dura (Willd.) Hook.	H	p	900–1600	south	rocky places in grassland
Pellaea quadripinnata (Forssk.) Prantl	H	e	1300–3100	north, south	meadows, forest edges
Pellaea schippersii Verdc.	H	d	1600–1900	north, south	forests
Pellaea schweinfurthii (Hieron.) Diels	H	p	900–1800	north, south	sunny embankments
Pellaea viridis (Forssk.) Prantl	H	d	800–2200	north, south	banana plantations, roadsides
Pityrogramma aurantiaca (Hieron.) C.Chr.	H	d	2400–3300	south	Erica forests, moorland
Aspleniaceae					
Asplenium abyssinicum Fee	H	e	1400–3200	north, south	moist forests
Asplenium adamsii Alston	H	e	3000–3100	north	wet rocks
Asplenium adiantum-nigrum L.	H	d	1300–4500	north, south	crevices; embankments
Asplenium aethiopicum (Burm.f.) Bech.	E	p	1000–3600	north, south	forests
Asplenium boltonii Hook.	H	e	1400–1700	south	forests

TABLE 1. continued

Name	lf	gp	Altitudinal range (m asl)	Distribution	Main habitat
Asplenium bugoiense Hieron.	H, ge	e	1300–2300	south	moist forests
Asplenium decompositum Peter	H	p	2200–4600	north, south	forests, Erica bushland
Asplenium elliottii C.H.Wright	H, ge	e	1300–3000	north, south	forests
Asplenium erectum Willd. var. *usambarense* Hieron.	H	e	1500–3200	north, south	forests
Asplenium friesiorum C.Chr.	H	p	1300–3100	north, south	forests
Asplenium gemmiferum Schrad.	H, ge	e	1300–2300	north, south	moist forests
Asplenium hypomelas Kuhn	E	e	1500–2700	south	moist forests
Asplenium inaequilaterale Willd.	H	e	1000–1700	south	moist forests
Asplenium linckii Kuhn	H	e	1600–2700	north, south	forests
Asplenium lividum Kuhn	H	e	1300–1900	north, south	moist forests
Asplenium loxoscaphoides Baker	H	e	2100–3600	north, south	forests
Asplenium mannii Hook.	E, ge	p	1600–1800	south	forests
Asplenium megalura Hieron.	E	p	1400–2000	south	forests
Asplenium monanthes L.	H	e	1900–3100	north, south	forests
Asplenium normale D.Don	H, ge	e	1600–3000	north, south	forests
Asplenium protensum Schrad.	H, ge	e	1100–3000	north, south	forests
Asplenium sandersonii Hook.	E, ge	p	1200–2700	north, south	forests
Asplenium smedsii Pic.Serm.	H	e	1500–3000	north, south	forests
Asplenium strangeanum Pic.Serm.	H	p	900–1900	north, south	forests
Asplenium theciferum (Kunth) Mett.	E	p	900–2700	north, south	(dry) forests
Asplenium uhligii Hieron.	H	p	3300–4200	north, south	rocks
Asplenium unilaterale Lam.	H	e	900–1900	south	wet rocks
Asplenium varians Hook. & Grev.	H	e	1900–2000	north	rocks
Asplenium volkensii Hieron.	H	e	1900–3300	north, south	forests
Azollaceae					
Azolla africana R.Br. var. *africana* (Desv.) Baker	Hy	d	700–1100	south	water
Azolla nilotica Decne.	Hy	d	700–900	south	water

TABLE 1. continued

Name	lf	gp	Altitudinal range (m asl)	Distribution	Main habitat
Blechnaceae					
Blechnum attenuatum (Sw.) Mett.	E	e	1500–2800	north, south	moist forests
Blechnum australe L.	H	e	1300–2500	north, south	forest edges
Blechnum ivohibense C.Chr.	H	e	1600–2300	south	moist forests
Cyatheaceae					
Cyathea dregei Kunze	P	e	1400–1600	north	riverine forest
Cyathea humilis Hieron.	P	e	2000–2200	south	moist forests
Cyathea manniana Hook.	P	e	1200–2900	south	moist forests
Dennstaedtiaceae					
Blotiella glabra (Bory) Tryon	H	e	1800–3000	south	forests
Blotiella stipitata (Alston) Faden	H	e	1700–2800	south	forests
Histiopteris incisa (Thunb.) J.Sm.	H	e	1900–3400	south	forests, forest clearings
Hypolepis goetzei Reimers	H	d	2200–3600	north, south	forests
Hypolepis sparsisora (Schrad.) Kuhn	H	e	800–2800	north, south	forest clearings
Microlepia speluncae (L.) Moore	H	e	900–1400	south	riverine forest
Pteridium aquilinum (L.) Kuhn ssp. *aquilinum*	G	d	1000–3600	north, south	forest clearings
Dryopteridaceae					
Arachnoides foliosa (C.Chr.) Schelpe	H	e	1300–3000	north, south	moist forests
Didymochlaena truncatula (Sw.) J.Sm.	C	e	1300–2200	south	moist forests
Dryopteris antarctica (Baker) C.Chr.	H	d	2500–3600	south	Erica forests and bushlands
Dryopteris fadenii Pic.Serm.	H	e	1300–3300	north, south	forests
Dryopteris kilemensis (Kuhn) Kuntze	H	e	1600–3300	north, south	forests
Dryopteris pentheri (Krasser) C.Chr.	H	d	1200–3900	north, south	forests
Megalastrum lanuginosum (Kaulf.) Holttum	C	e	1200–2100	south	moist forests
Nothoperanema squamiseta (Hook.) Ching	H	e	1800–3200	south	forests
Phanerophlebia caryotidea (Hook. & Grev.) Copel.	H	e	1100–2000	north, south	forests
Polystichum kilimanjaricum Pic.Serm.	H, ge	e	2100–3000	south	moist forests

TABLE 1. continued

Name	**lf**	**gp**	**Altitudinal range (m asl)**	**Distribution**	**Main habitat**
Polystichum transvaalense N.C.Anthony	H	e	1300–2800	north, south	forests
Polystichum volkensii (Hieron.) C.Chr.	H, ge	d	2500–3400	north, south	moist forests
Polystichum wilsonii Christ	H	e	2400–4500	north, south	forests
Tectaria gemmifera (Fee) Alston	H, ge	e	900–2300	north, south	forests
Equisetaceae					
Equisetum ramosissimum Desf.	G	e	900–1100	south	riverine forests
Gleicheniaceae					
Dicranopteris linearis (Burm.f.) Underw.	C	e	1200–1800	north, south	roadsides, forest edges
Gleichenia elongata Baker	C	e	2600–2800	south	forest clearings
Sticherus flagellaris (Willd.) Ching	C	e	1800–2000	south	moist forests
Grammitidaceae					
Melpomene flabelliformis (Poir.) A.R.Smith & R.C.Moran	E	p	1900–4300	north, south	epiphytic in forests; in the alpine zone lithophytic
Lellingeria paucipinnata Parris	H	p	1900–2400	south	epiphytic and lithophytic in forests
Hymenophyllaceae					
Hymenophyllum capillare Desv. var. *capillare*	E	p	1700–3300	north, south	forests
Hymenophyllum kuhnii C.Chr.	E	p	1600–3100	south	forests
Hymenophyllum splendidum Bosch	H	p	1700–2500	south	forests
Hymenophyllum tunbrigense (L.) Sm.	E	p	1800–3000	south	forests
Trichomanes borbonicum Bosch	H	p	1400–2500	south	forests
Trichomanes chevalieri Christ	E	p	1300–2000	south	forests
Trichomanes erosum Willd.	H	p	1500–2300	south	lithophytic near water in forests
Trichomanes melanotrichum Schltdl.	E	p	1200–2800	north, south	epiphytic and lithophytic in forests
Trichomanes radicans Sw.	L	p	1600–1700	south	moist forests, wet rocks
Trichomanes ramitrichum Faden	E	p	1600–2000	south	epiphytic in forests
Trichomanes rigidum Sw.	H	p	1900–2100	south	moist forests

TABLE 1. continued

Name	lf	gp	Altitudinal range (m asl)	Distribution	Main habitat
Lomariopsidaceae					
Elaphoglossum acrostichoides (Hook. & Grev.) Schelpe	E	p	1500–2800	south	forests
Elaphoglossum angulatum (Blume) Moore	E	e	1800–3200	south	forests
Elaphoglossum aubertii (Desv.) Moore	H	e	1500–3000	south	forests
Elaphoglossum deckenii (Kuhn) C.Chr.	E	e	1800–3600	north, south	forests
Elaphoglossum hybridum (Bory) Brack.	H	e	1500–3300	north, south	epiphytic and epilithic in forests
Elaphoglossum lastii (Baker) C.Chr.	E	e	1600–2400	south	(dry) forests
Elaphoglossum spathulatum (Bory) Moore	H	p	1500–1800	south	on rocks in stream bed
Elaphoglossum subcinnamomeum (Christ) Hieron	H	d	2600–3600	north, south	moist rocks
Lomariopsis warneckei (Hieron.) Alston	L	e	1500–2100	north, south	moist forests
Lycopodiaceae					
Huperzia dacrydioides (Baker) Pic.Serm.	E	e	1400–2800	south	forests
Huperzia ophioglossoides (Lam.) Rothm.	E	e	1800–3000	south	forests
Huperzia saururus (Lam.) Trevis.	C	e	3100–3700	south	Erica forests and bushlands
Lycopodiella cernua (L.) Pic.Serm.	C	e	1200–1800	north, south	forest clearings on open soil
Lycopodium clavatum L.	C	e	1600–3300	south	forest clearings; Erica forests
Marattiaceae					
Marattia fraxinea Sm.	C	e	1200–2300	south	moist forests
Marsileaceae					
Marsilea minuta L.	Hy	d	700–1100	south	waterholes
Oleandraceae					
Arthropteris orientalis (J.F.Gmel.) Posth.	H	d	1000–2200	north, south	dry forests and thickets
Nephrolepis biserrata (Sw.) Schott	H	d	900–1100	south	swamp forests, swamps
Oleandra distenta Kunze	E	d	1600–2500	south	forests

TABLE 1. continued

Name	lf	gp	Altitudinal range (m asl)	Distribution	Main habitat
Ophioglossaceae					
Ophioglossum polyphyllum A.Braun	G	d	900–1000	south	grassland
Ophioglossum vulgatum L. agg. (ssp. *africanum* Burrows + ssp. *kilimandscharicum* (Hieron.) Burrows)	G	e	1400–2100	south	grassland
Polypodiaceae					
Drynaria volkensii Hieron.	E	d	1100–2600	north, south	forests
Lepisorus excavatus (Willd.) Moore	E	d	1300–3500	north, south	forests
Loxogramme abyssinica (Baker) M.G.Price	E	p	900–2900	north, south	forests
Pleopeltis macrocarpa (Willd.) Kaulf.	E	p	900–3300	north, south	epiphytic in forests; in the alpine zone lithophytic
Pyrrosia schimperiana (Kuhn) Alston	E	p	1300	south	banana plantation
Pteridaceae					
Pteris albersii Hieron.	H	e	1100–1300	south	riverine/gorge forests
Pteris bavazzanoi Pic.Serm.	H	e	2600–3300	north, south	forests
Pteris catoptera Kunze	H	e	700–3100	north, south	forests
Pteris cretica L.	H	d	1800–2800	north	forests
Pteris dentata Forssk.	H	e	1000–2800	north, south	forests
Pteris tripartita Sw.	C	e	1500–1700	south	riverine forests
Pteris vittata L.	H	d	900–1600	south	swampy places
Schizaeaceae					
Mohria vestita Baker	H	p	1300–1900	north, south	dry grassland
Selaginellaceae					
Selaginella goudotiana Spring var. *abyssinica* (Spring) Bizzarri	H	d	1000–2600	south	moist rocks
Selaginella kraussiana (Kunze) A.Br.	H	e	1300–3200	north, south	forests
Selaginella mittenii Bak.	H	e	1000–1300	south	riverine forests

TABLE 1. continued

Name	lf	gp	Altitudinal range (m asl)	Distribution	Main habitat
Thelypteridaceae					
Amauropelta bergiana (Schltdl.) Holttum	H	e	800–3200	north, south	moist forests
Amauropelta oppositiformis (C.Chr.) Holttum	H	e	1800–2900	south	riverine forests
Ampelopteris prolifera (Retz.) Copel.	C, ge	e	800–1300	south	swampy places near rivers
Christella dentata (Forssk.) Brownsey & Jermy	H	e	700–2100	north, south	shady roadsides
Christella hispidula (Decne.) Holttum	H	e	700–1000	south	swampy places in forests
Christella microbasis (Bak.) Holttum	H	e	900–1100	south	riverine forests
Cyclosorus interruptus (Willd.) H.Ito	Hy	e	700–1300	south	swamps, swamp forests
Pneumatopteris unita (Kunze) Holttum	H, ge	e	1300–2500	south	moist forests
Pseudocyclosorus pulcher (Willd.) Holttum	H	e	1000–2400	north, south	moist forests
Sphaerostephanus unitus (L.) Holttum	H	e	1000–1500	south	swampy places
Stegnogramma pozoi (Lag.) K.Iwats.	H	e	1700–3200	north, south	moist forests and rocks
Thelypteris confluens (Thunb.) Morton	Hy	e	900–1800	south	swamps
Vittariaceae					
Vittaria isoetifolia Bory	E	p	2200–2300	south	forests
Vittaria volkensii Hieron.	E	p	1500–2100	south	forests
Woodsiaceae					
Athyrium scandicinum (Willd.) C.Presl ssp. *newtonii* (Bak.) Verdc.	H	e	1300–3100	north, south	moist forests
Cystopteris fragilis (L.) Bernh. ssp. A Verdc.	H	d	2600–4400	north, south	moist rocks
Cystopteris fragilis (L.) Bernh. ssp. B Verdc.	H	d	1500–3900	north, south	moist rocks near water
Deparia boryana (Willd.) M.Kato	C	e	900–2900	north, south	moist forests
Diplazium zanzibaricum (Baker) C.Chr.	C	e	1400–2800	north, south	moist forests

Lf=Lifeform (C= Chamaephyte, E= Epiphyte, G= Geophyte, ge= gemmiferous, H= Hemicryptophyte, Hy= Helophyte, Hydrophyte, L=Lianas, P= Phanerophyte), gp=growth pattern (d deciduous, e evergreen, p poikilohydrous)

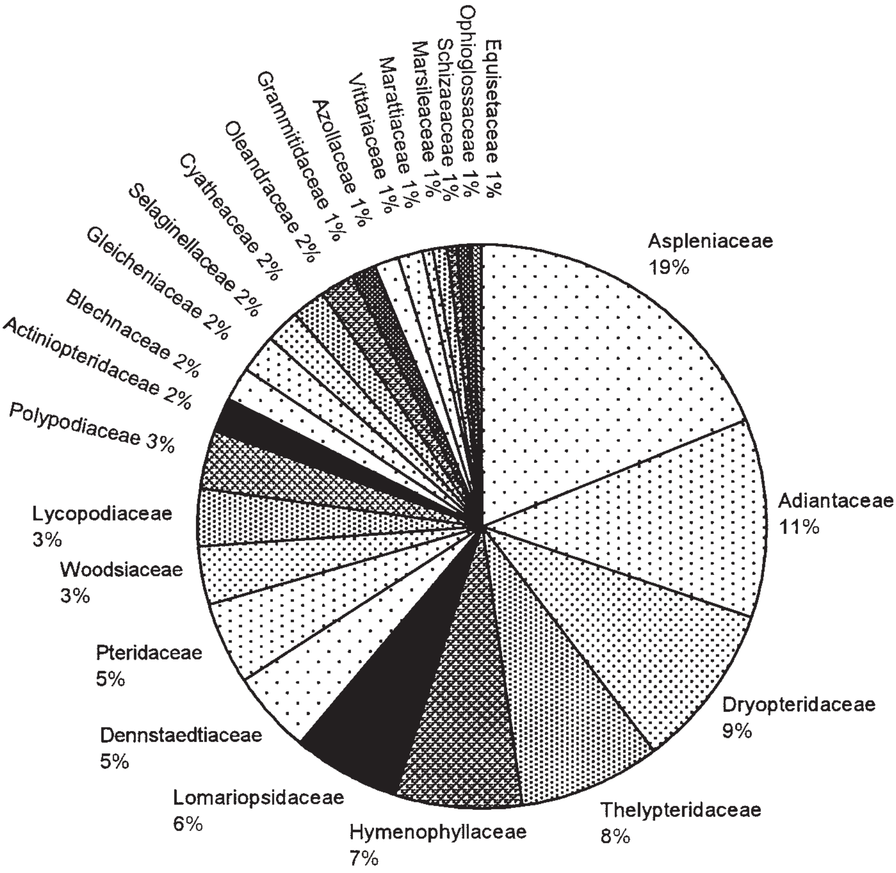

FIG. 2. Percentage composition of the pteridophyte families on Mt Kilimanjaro.

The 10 most common ferns of the study area are: *Asplenium aethiopicum, Lepisorus excavatus, Pteris catoptera, Asplenium decompositum, Polystichum wilsonii, Pleopeltis macrocarpa, Amauropelta bergiana, Dryopteris kilemensis, Asplenium elliottii* and *Dryopteris fadenii.*

The families most rich in species are Aspleniaceae with 29 species, Adiantaceae with 17 species, Dryopteridaceae with 14 species, Thelypteridaceae with 12 species and Hymenophyllaceae with 11 species (Fig. 2). This is quite typical of montane areas in East Africa except for the high share of filmy ferns reflecting the extremely humid climate in the forest belt of Mt Kilimanjaro.

As on other East African high mountains, endemic pteridophyte species are rare on Mt Kilimanjaro. Only *Pteris bavazzanoi* is endemic to Mt Meru and Kilimanjaro (Verdcourt, 2002), and *Lellingeria paucipinnata* is only known from Kilimanjaro (Parris, 2005). In contrast to the flowering plants a much higher percentage of pteridophytes is either cosmopolitan (6%) or pantropical (4%). Bicontinental palaeotropic species are likewise numerous (6%) and ferns of African-American distribution are also frequent (6%; see Hemp, 2002 for a list of species).

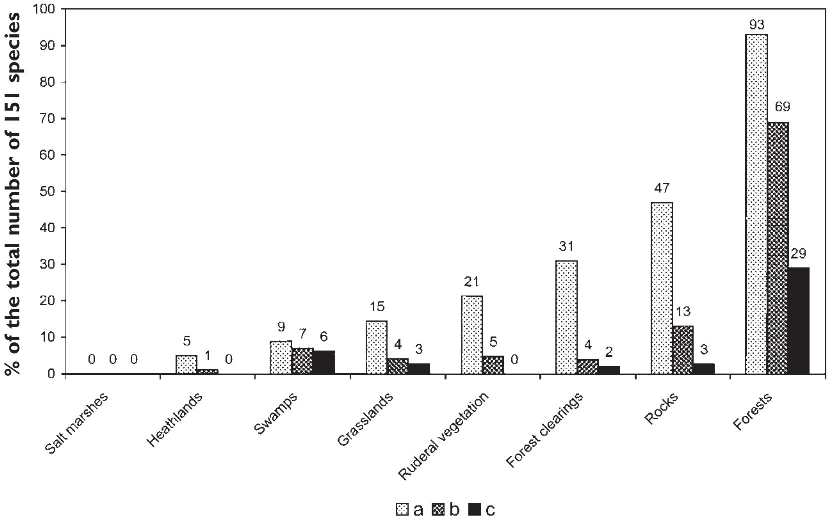

FIG. 3. Pteridophyte diversity in different vegetation formations; a: relative number of pteridophyte species compared to the total number of 151 species occurring on Mt Kilimanjaro, b: relative number of pteridophyte species occurring mainly in the respective formation, c: relative number of pteridophyte species restricted to the formation under consideration.

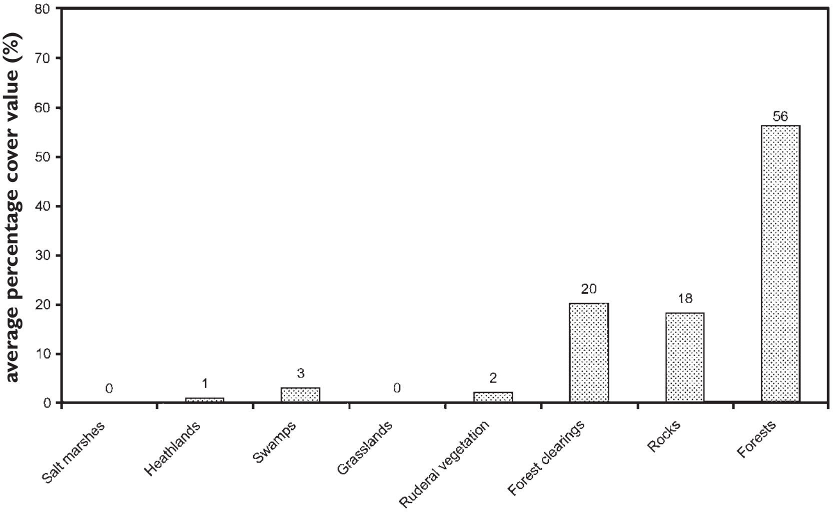

FIG. 4. Ecological importance as expressed by the average percentage cover value of the pteridophytes in different vegetation formations on Mt Kilimanjaro.

Most of these 151 pteridophytes occur on the southern slope (147 taxa), whereas only 78 taxa were found on the northern slope. Only four species, *Cyathea dregei*, *Pteris cretica*, *Asplenium adamsii* and *Asplenium varians* were restricted to the northern part of Kilimanjaro and *Asplenium monanthes* and *Pteris bavazzanoi* had their main distribution in this area of the mountain.

4.2 Habitat preferences

Based on the analysis of about 1450 sampling plots, vegetation types occurring on the southern slopes of Mt Kilimanjaro were united into eight formations: rocks; ruderal vegetation; grasslands; salt marshes; freshwater swamps; forest clearings; forests, and heathlands (constancy tables and descriptions of these vegetation types are presented in Hemp, 2001a, 2005a and Hemp & Hemp, 2003). Fig. 3 compares the diversity of the different habitats with respect to ferns. Fig. 4 shows the average percentage cover value of the pteridophytes providing information on the ecological importance, i.e. the leafy biomass of pteridophytes in different vegetation formations. It is apparent that forests and rocks were the most important habitat for pteridophytes on Mt Kilimanjaro. 138 and 69 species occurred in forests and on rocks respectively. On rocks over half of the vegetation cover was contributed by pteridophytes, in forests nearly one fifth.

4.3 Life forms

Nearly two thirds of all species were hemicryptophytes (Fig. 5). This number is similar to that found in Zambia by Kornaś (1977). Hemicryptophytes were the dominant group in most vegetation formations except swamps. In forests epiphytes were of same importance. Phanerophytes were also restricted to the forest belt. Two tree fern species were found in the forest plots of Mt Kilimanjaro: the widespread *Cyathea manniana* and the rare *C. humilis*. Another tree fern, *C. dregei*, was encountered only once in a riverine forest remnant on the eastern slope; this species is not included in Fig. 5. Chamaephytes were found in several formations. However, large shrub-like chamaephytes such as *Diplazium zanzibaricum*, *Pteris tripartita*, *Deparia boryana* and *Marattia fraxinea*, which sometimes grow like phanerophytes, constituted a characteristic group in the life form spectrum of forests and forest clearings. Only two pteridophytes grew occasionally as lianas on Mt Kilimanjaro: *Lomariopsis warneckei* and the very rare *Trichomanes radicans*. Both ferns have a climbing rhizome (root climber) and were restricted to gorge forests and riverine forests of the lower montane zone below 1800 m. Geophytes with subterranean rhizomes – although of minor importance in the composition of the whole pteridophyte flora and only represented by *Equisetum ramosissimum*, *Pteridium aquilinum*, *Ophioglossum polyphyllum* and *Ophioglossum vulgatum* – were prominent in clearings and grasslands. The five helo- and hydrophytes of the study area occurred exclusively in swamps.

4.4 Seasonal growth and dormancy

Evergreen species formed 54% of the pteridophyte flora on Mt Kilimanjaro (Fig. 6) and were mostly montane forest species. Poikilohydrous species constituted 25% of the pteridophyte flora of Mt Kilimanjaro and were either plants of dry rocky slopes or epiphytes. Their fronds were either tough and xeromorphic (as in *Actiniopteris radiata*) or delicate and hygromorphic (as in the filmy ferns). 21% of the pteridophyte flora of Mt Kilimanjaro were deciduous. These species occupied a wide range of habitats, from seasonal pools (*Marsilea minuta*) and semi-shaded roadsides (*Adiantum poiretii*) to alpine sites (*Dryopteris pentheri*).

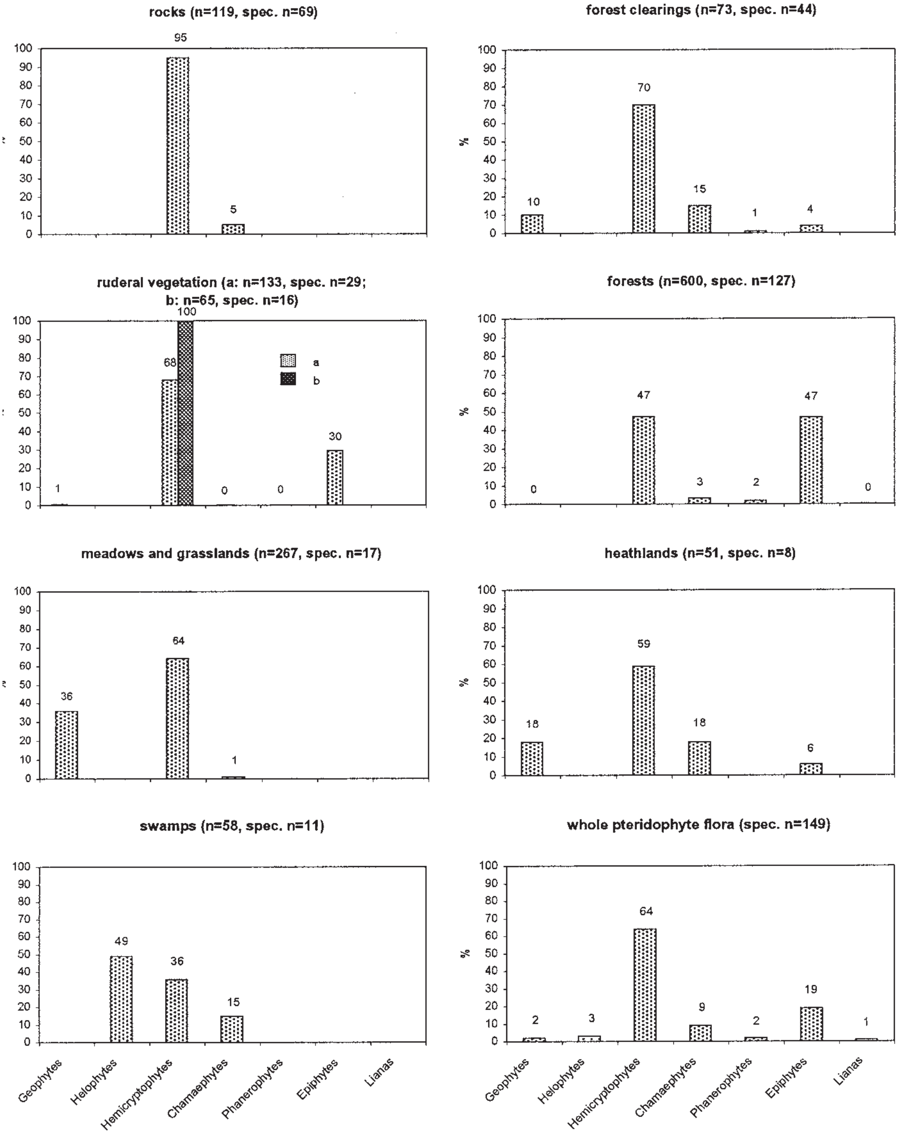

FIG. 5. Life form spectra of the different habitats based on constancy; n=number of sampling plots (relevés), spec. n=number of pteridophyte species, a=ruderal vegetation including the forest-like coffee-banana plantations, b=without coffee-banana plantations.

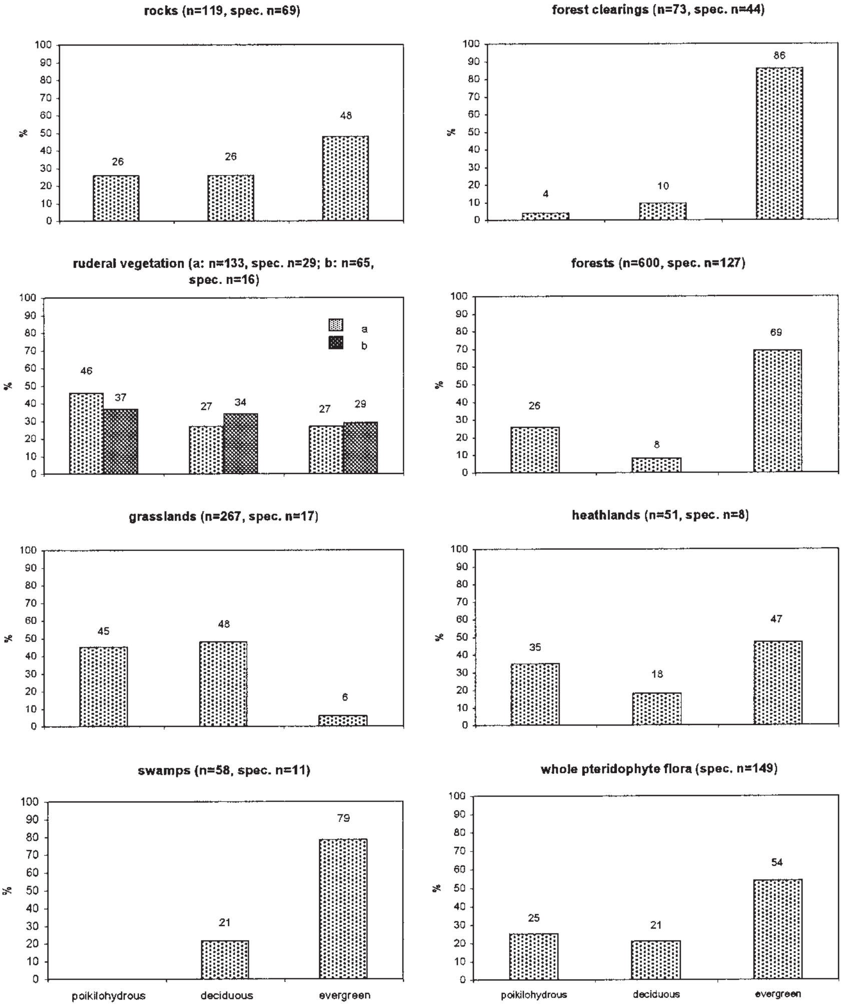

FIG. 6. Growth pattern spectra of the different habitats based on constancy; n=number of sampling plots (relevés), spec. n=number of pteridophyte species, a=ruderal vegetation including the forest-like coffee-banana plantations, b=without coffee-banana plantations.

TABLE 2. Altitudinal zonation based on Pteridophytes on the southern and northern slope of Mt Kilimanjaro.

Southern slope					**Northern slope**		
Altitude (m asl)	**Main vegetation**	**Vegetation zone**		**Fern zone**	**Fern zone**	**Main vegetation**	**Altitude (m asl)**
4400	Helichrysum cushion vegetation	alpine	lower	11	11	Helichrysum cushion vegetation	4400
4300							4300
4200							4200
4100							4100
4000							4000
3900							3900
3800	Erica shrubland, Helichrysum cushion vegetation	(upper montane) subalpine	upper	10	10	Erica shrubland, Helichrysum cushion vegetation	3800
3700							3700
3600							3600
3500	Erica shrubland, *Erica excelsa* forest, Hagenia-forest		lower	9	9	Erica shrubland, *Erica excelsa* forest	3500
3400							3400
3300							3300
3200							3200
3100							3100
3000	*Erica excelsa* forest, Podocarpus forest, moorland		lower	8	8	*Erica excelsa* forest, Juniperus–Podocarpus forest	3000
2900							2900
2800							2800
2700	Podocarpus-Ocotea forest	montane	upper	7	7	Juniperus–Podocarpus forest	2700
2600							2600
2500							2500
2400					6	middle montane Cassipourea forest	2400
2300	Ocotea-Podocarpus forest		middle	6			2300
2200							2200
2100					4/5	lower montane Cassipourea forest	2100
2000	Ocotea–Agauria forest, Ocotea–Syzygium forest, Cassipourea forest (south west)		lower	5			2000
1900					3	Croton–Calodendrum forest	1900
1800							1800
1700	Agauria-Ocotea forest, Cassipourea forest (south west), coffee-banana plantations			4			1700
1600					2	coffee-banana plantations, savanna, agriculture, pasture	1600
1500	coffee-banana plantations, Croton-Calodendrum forest, *Hyparrhenia* meadows	submontane	upper	3			1500
1400							1400
1300					1	coffee-banana plantations, savanna, agriculture, pasture	1300
1200	coffee-banana plantations, savanna, agriculture, pasture		lower	2			1200
1100							1100
1000							1000
900							
800	savanna, agriculture, pasture	coll		1			
700							

4.5 Altitudinal distribution

4.5.i Range

On Mt Kilimanjaro the habitat of ferns extends from the Rau forest (760 m asl) on the foothills up to the alpine zone in 4600 m asl covering an altitudinal range of 3840 m. *Christella hispidula*, *Azolla nilotica*, *Azolla africana* and *Marsilea minuta* are restricted to the foothills, while *Anogramma leptophylla*, *Polystichum wilsonii*, *Cystopteris fragilis* subsp. A, *Asplenium adiantum-nigrum*, *A. decompositum*, *A. uhligii* and *Melpomene flabelliformis* reach to 4,000 m and above.

The fern with the widest altitudinal range (2600 m, Table 1) is *Asplenium aethiopicum*, followed by *Amauropelta bergiana*, *Asplenium decompositum*, *Pleopeltis macrocarpa* and *Melpomene flabelliformis* (all with an altitudinal range of 2400 m) while *Cheilanthes farinosa*, extending from 900 to 3900 m, has a gap of occurrence in the central zone of the forest. Similar is the disjunction of *Asplenium adiantum-nigrum*, which was found between 1300 and 1800 m in the plantation belt of the southern slope but has its main occurrence in altitudes above 3400 m (see distribution maps of many of these ferns on Kilimanjaro in Hemp, 2001a, 2001b, 2002).

4.5.ii Zonation

Table 2 shows the zonation based on significant floristic discontinuities of pteridophytes on the southern slope (from Hemp, 2001a) and on the northern slope in relation to the main vegetation zones. This altitudinal zonation is in agreement with the zonation of the multilayered forests that occurred parallel in all strata (trees, shrubs, herbs, lianas, epiphytes) (Hemp, in press a). In the foothill areas the corresponding altitudinal zones are shifted 400 m higher on the northern slope than on the southern slope but the zonation equals with rising altitude.

Fig. 7 presents the altitudinal zones with the main vegetation types viewed from the western side of the mountain showing the contrast between the dry northern and the wet southern slope. Fig. 8 shows the distribution of four ferns typical of different habitats and altitudinal zones.

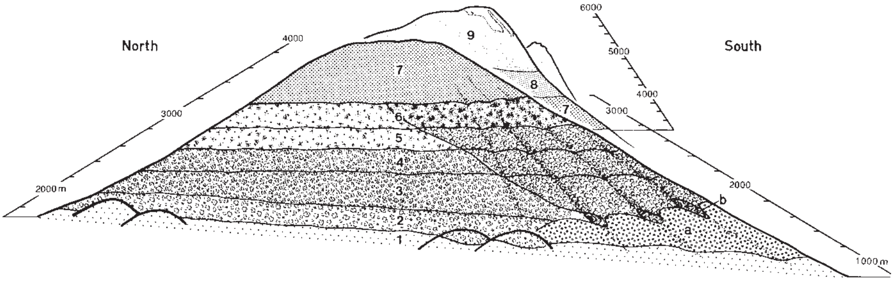

FIG. 7. Schematic north-south profile showing the western slope of Mt Kilimanjaro (Shira, Kibo, Mawenzi) with main altitudinal zones and vegetation types (from Hemp in press). 1: colline (savanna) zone; 2: submontane zone with *Croton-Calodendrum* forest; a: coffee-banana plantations in the sub and lower montane zone on the southern slope; b: lower montane gorge forests on the southern slope; 3: lower montane zone with *Cassipourea* forests on the northern slope and *Agauria–Syzygium–Ocotea* forests on the southern slope; 4: middle montane zone with *Cassipourea* forests on the northern slope and *Ocotea* forests on the southern slope; 5: upper montane zone with *Juniperus* forests on the northern slope and *Podocarpus-Ocotea* forests on the southern slope; 6: upper montane zone with *Juniperus* forests on the northern slope and *Podocarpus* forests on the southern slope; 7: subalpine zone with heathlands (*Erica* bush); 8: lower alpine zone with *Helichrysum* cushion vegetation; 9: upper alpine and nival zone, mainly bare of vegetation.

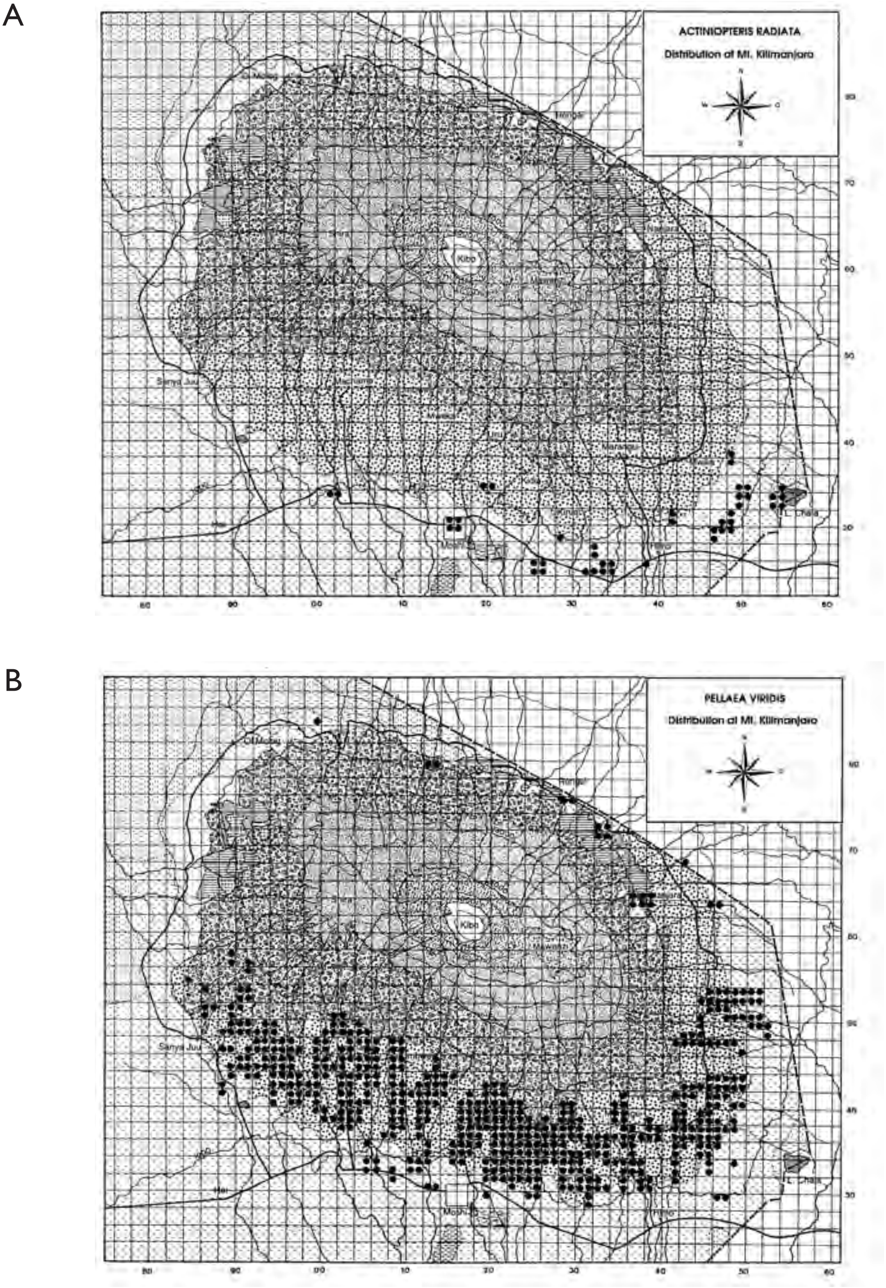

FIG. 8. Records of 4 ferns with different altitudinal and habitat preferences on Mt Kilimanjaro, at the base of the UTM grid. The scale of the squares is 4 km^2. Legend see in Fig. 1. The distribution of a) ***Actiniopteris radiata***, a lithophytic fern of the colline zone, concentrates on the south-eastern foothills, where secondary vents are common. b) ***Pellaea viridis*** is a typical fern of the submontane zone, which thrives naturally in *Croton-Cadodendrum* forests but has its main habitat as an apophyte in coffee-banana plantations on the southern and eastern slope.

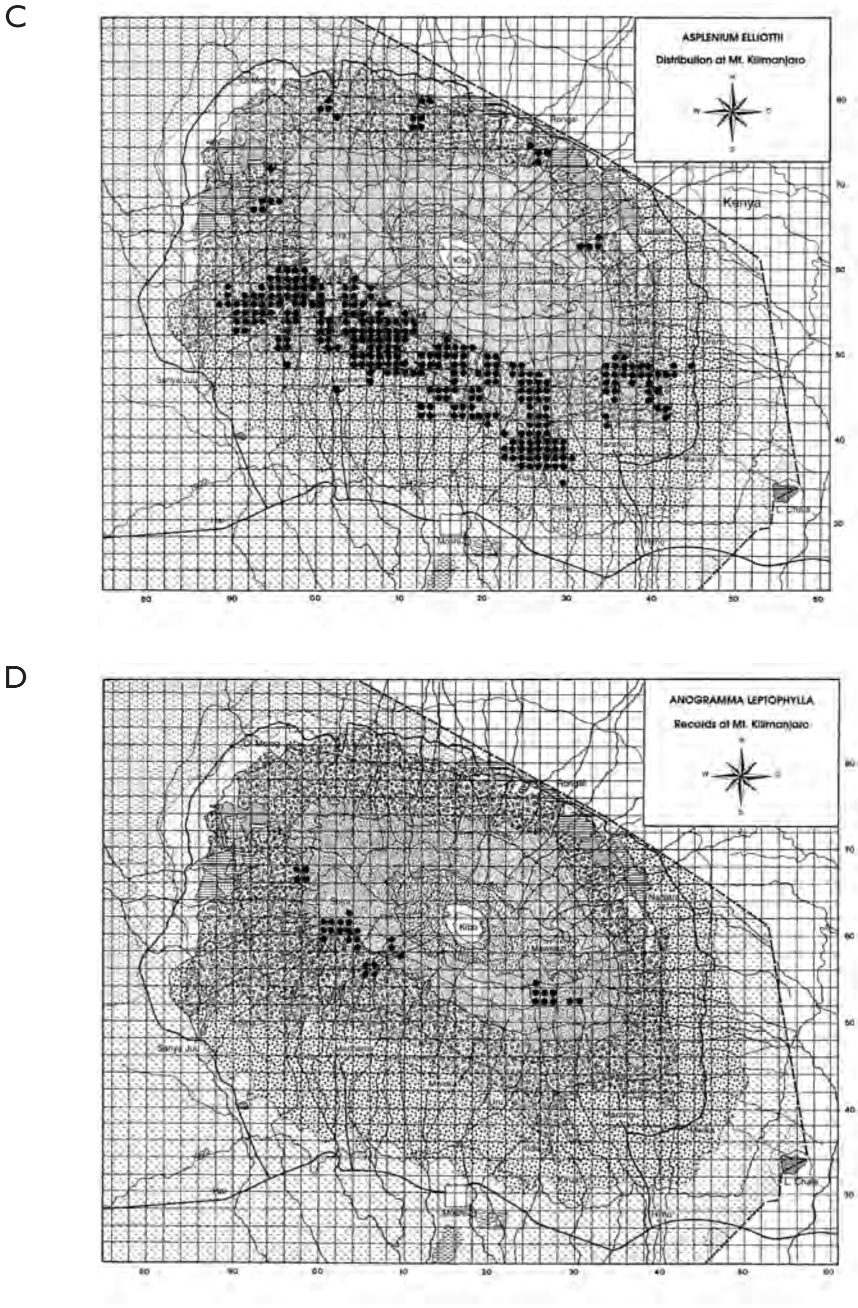

FIG. 8. cont. c) ***Asplenium elliottii*** grows as a common terrestrial in the montane forest belt of the whole mountain. d) ***Anogramma leptophylla*** is a fern of the (sub-)alpine zone. Gaps within the distribution area are mostly due to lack of data, for interpretation of the distribution pattern, therefore, compare the location of the transects shown in Fig. 1.

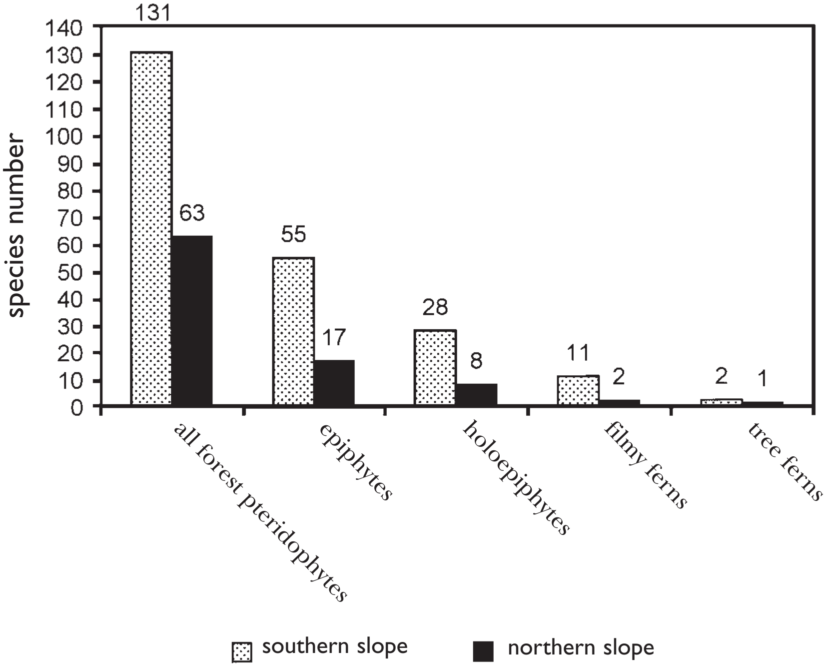

FIG. 9. Species numbers of forest ferns, epiphytic ferns (accidental, casual and holo-epiphytes), holo-epiphytic ferns, filmy ferns and tree ferns on the northern and southern slope of Mt Kilimanjaro.

The contrary results of many studies in respect of a continuous or discontinuous change of vegetation with altitude can be attributed – at least in the compared studies in East Africa – to a great part to different sampling methods and intensities (Hemp, in press a).

4.6 Ecological factors

4.6.i Northern versus southern slope

On the northern slope less than 50% of the pteridophyte taxa of the southern slope occur. This could be partly due to the smaller altitudinal range of the northern slope. However, this would explain only the lack of only 3 species that were found on the southern slope exclusively below 1000 m (see Table 1). Therefore the lack of nearly 70 taxa on the northern slope is mainly due to climatic differences: the forest belt of this part of the mountain receives only half of the precipitation of the southern slope. Further evidence for the key role of precipitation is attributed to the fact that only two filmy ferns (*Trichomanes melanotrichum* and *Hymenophyllum capillare*), one tree fern (comparatively drought-resistant) (*Cyathea dregei*) and only 17 epiphytic ferns (accidental, casual and holo-epiphytes, cf. Kress, 1986) and only 8 holo-epiphytes (Hemp, 2001b) were found on the northern slope (Fig. 9), three fern groups with high indicator value for humidity (Fig. 12). In contrast, epiphytes (54 and 27 species respectively) filmy ferns (11 species) and tree ferns (*Cyathea manniana* and *C.*

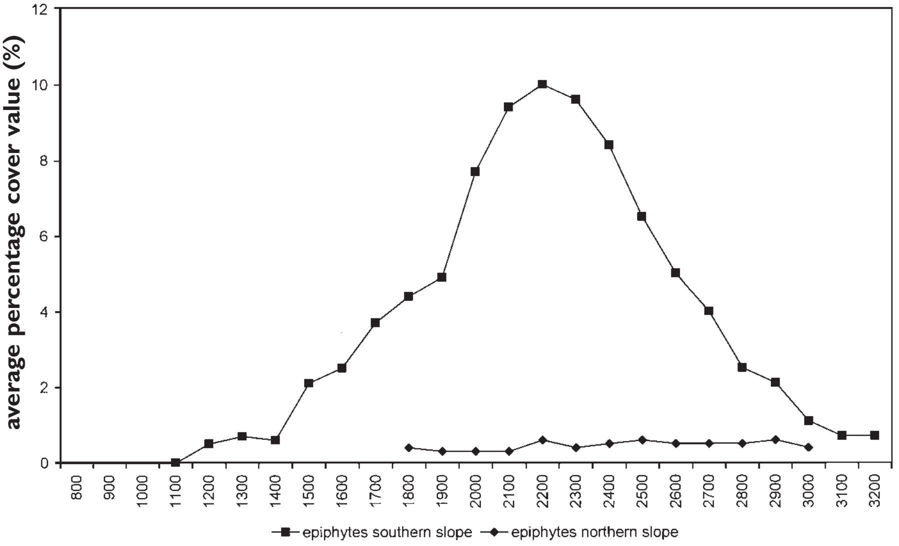

FIG. 10. Ecological importance as expressed by the average percentage cover value of epiphytic pteridophytes on the northern and southern slope of Mt Kilimanjaro.

humilis) are of high ecological importance on the moist southern slope (see distribution maps of *Cyathea manniana* in Hemp, 2001b, and distribution maps of filmy ferns in Hemp, 2001). This is shown for the epiphytic ferns in Fig. 10: whereas on the southern slope between 1800 and 3100 m epiphytes contribute in average about 5% of the leafy biomass on the northern slope the importance of this fern group remains small with 0.5%. Rainfall and moisture were shown by several authors (Dwzonko & Kornaś, 1978, 1994; Kornaś, 1993) to restrict occurrence of pteridophytes. Temperature (Jacobsen & Jacobsen, 1989) and soil fertility (Lwanga *et al.*, 1998; Tuomisto & Ruokolainen, 1993; Tuomisto & Poulsen, 1996) have also been reported as important factors.

Other reasons for differences in diversity, indirectly linked to precipitation, between both slopes of the mountain is the distribution of host trees for epiphytes. *Ocotea usambarensis*, the dominant tree of the moist forests of the southern slope carries a rich epiphytic flora and the epiphytic fern *Oleandra distenta* was exclusively found on this tree. Similar observations were made e.g. with *Asplenium hypomelas* and *Blechnum attenuatum*, which were restricted to the tree fern *Cyathea manniana* (Hemp, 2001b).

Moisture seems also to be the controlling climatic factor for differences in the altitudinal zonation as indicated by the different altitude of the transition between dry *Calodendrum* and wetter *Cassipourea* forests on the southern and northern slope. Precipitation on the lower slopes differs greatly, becoming equal with increasing altitude, where the same discontinuities were observed on both (north and south) slopes. Such a rising and condensation of altitudinal zones due to the "Massenerhebungseffekt" is a well known feature on dryer leeward slopes of tropical mountains (see e.g. Grubb & Whitmore, 1966; Grubb, 1971; Richards, 1996).

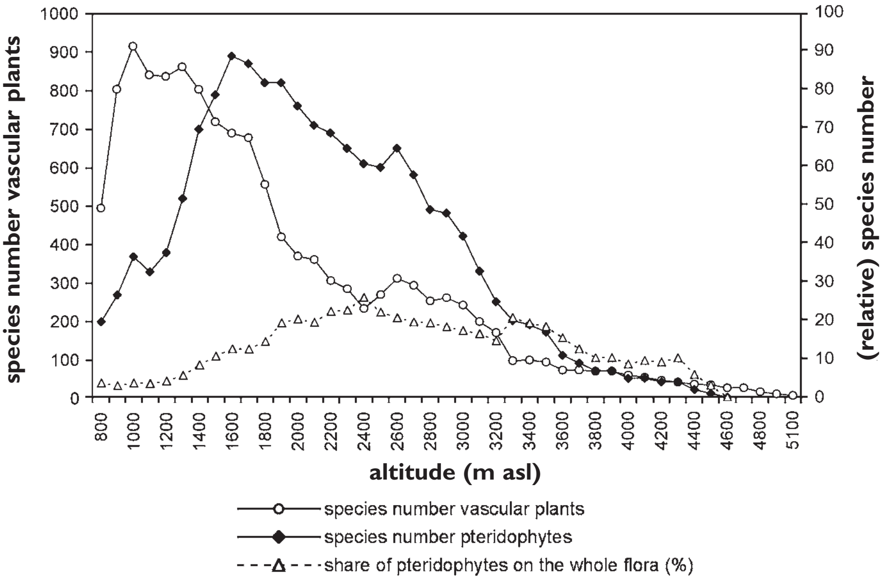

FIG. 11. Altitudinal changes of species numbers of pteridophytes and of all occurring vascular plants on the southern and south western slope of Mt Kilimanjaro as well as the share of pteridophytes on the whole vascular flora, based on the evaluation of 1,270 plots with about 2,000 species.

4.6.ii Altitudinal trends and patterns

Fig. 11 shows the species numbers of 2000 vascular plants at 100 m elevation intervals between 800 and 5100 m on the southern slope together with species numbers of pteridophytes. Vascular plants reach a maximum of over 900 species at 1000 m in the mosaic-type interface between the colline savanna and the banana-coffee plantations of the submontane zone, whereas the species number of the pteridophytes (nearly 90 species) culminated at 1600 m. This supports the well known phenomenon that plant species numbers are peaking in moderately cultivated or disturbed areas and not in natural, completely untouched areas. A reason is that anthropogenic influence does not only destroy natural habitats but sometimes enlarges the distribution of certain species by increasing habitat diversity. This can be shown by the distribution of *Pellaea viridis* (Fig. 8), which naturally thrives on Kilimanjaro in submontane *Croton-Calodendrum* forests. However, its main habitat and main distribution area are nowadays the coffee-banana plantations, the so-called Chagga home gardens, with their forest-like structure on the southern and eastern slopes. Other examples of such apophytes sensu Rikli (1903) (i.e. indigenous species, which could extend their natural distribution area due to human influence and occupy anthropogenic habitats), are *Adiantum poirettii* and *Christella dentata*, fern species of riverine forests in the colline and submontane zone of Kilimanjaro, which have nowadays the same distribution as *Pellaea viridis* in the coffee-banana plantations with their ramified irrigation system (Hemp, in 2005a). Neophytic fern species, i.e. introduced species, which became naturalized, also occur on Kilimanjaro. *Adiantum raddianum*, an introduced fern from America, inhabits shady embankments in the coffee-banana plantations; it is very widespread in such (anthropogenic) habitats and has the same distribution as the indigenous *Pellaea viridis*. In contrast, the introduced *Nephrolepis cordifolia* (L.) Presl did not naturalize, although it is cultivated everywhere in the coffee banana plantations as a hedge plant; it is therefore not included in Table 1.

Habitat diversity (beta diversity) is the main factor controlling both curves of species richness in Fig. 11 (Hemp in press b). Of interest in this context are the congruent peaks of the absolute species numbers of pteridophytes and all vascular plants at 2600 m at the lower border of the subalpine zone. It is at this altitude, that fires start to become important on Mt Kilimanjaro (Hemp & Beck, 2001), creating a mosaic of different fire induced successional stages of forest, shrub and tussock grassland stands. This high beta diversity – compared with the closed forest at lower altitudes and the monotonous heathlands at higher altitudes – leads to a high alpha diversity (Hemp, 2005b). The influence of fire is also indicated by the high share of geophytes and deciduous ferns in this altitude, which are fire-resistant in many cases (Kornaś, 1978, 1985). This is reflected by the bimodal discontinuous distribution pattern of deciduous, fire-tolerating fern species such as the geophyte *Pteridium aquilinum* and the hemicryptophyte *Dryopteris pentheri* which have a distribution gap in the central forest zone (Hemp, 2001a, b).

On the other hand the curve of the relative species numbers of ferns reflects clearly the moisture gradient on the mountain with their contribution to the whole flora culminating in the wettest altitudes. For forest ferns in general and particularly for epiphytes, filmy ferns and tree ferns living inside the forest, humidity is of highest importance. This can be shown by the relative cover values (Fig. 12). Between 2000 and 2400 m (within the altitude of highest precipitation) epiphytic ferns contributed nearly 9% of the leafy biomass in forests of Kilimanjaro. That epiphytic pteridophytes reach their greatest diversity in humid environments is also reported by Johansson (1989). Parallel peaks showed filmy ferns and tree ferns. On Mt Kinabalu (Borneo), tree ferns

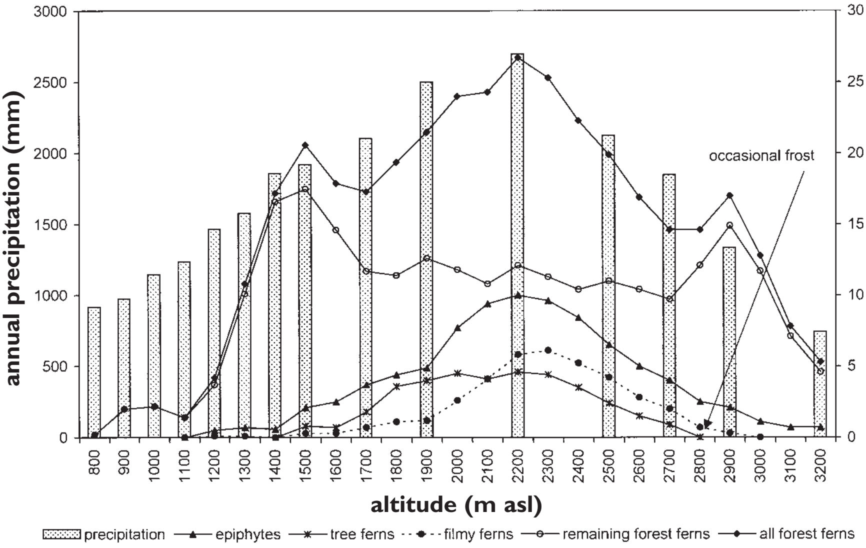

FIG. 12. Ecological importance as expressed by the average percentage cover value of forest pteridophytes in general (r = 0.9), epiphytic pteridophytes (r = 0.8), filmy ferns and tree ferns (r = 0.7) in the forests of the central southern slope of Mt Kilimanjaro in relation to mean annual precipitation (for all $p<0.05$). Rain data from Hemp (in press a).

of the genus *Cyathea* concentrated at similar altitudes from 2200 to 2500 m (Beaman & Beaman, 1997). The upper altitudinal distribution of the tree ferns however seems to be restricted by the occurrence of nocturnal frost during the cold period from July to August at 2700 m, causing also a distinct borderline of the altitudinal forest zonation (Hemp, in press a).

A non-environmental factor, which may contribute to a humped relationship between species richness and altitude is the geometric constraint on species ranges (Colwell & Hurtt, 1994; Colwell & Lees, 2000). The range of a set of species along an altitudinal gradient (or latitudinal or bathymetric) may be geometrically constrained e.g. by sea level as a lower boundary and the top of a mountain as an upper boundary. However, as both species curves (that of all vascular plants and of ferns) and altitudinal diversity trends within the different forest strata (trees, lianas, epiphytes etc.) (Hemp in press b) are not congruent, it is unlikely that this effect is of major importance for the observed altitudinal species distribution.

5 Conclusions

The high diversity of pteridophytes of Mt Kilimanjaro is due to the richness of various habitats resulting from an enormous altitudinal range and a luxuriant montane rainforest with high precipitation. Pteridophytes on Mt Kilimanjaro extend over nearly 4000 m altitude and show a detailed altitudinal zonation. The present study shows that pteridophytes are major components of various plant communities of Mt Kilimanjaro with distinct altitudinal and habitat preferences. With respect to species diversity and fern biomass, the montane forest is the most important habitat of pteridophytes on this mountain.

While geometric constraints may contribute to the general hump of species numbers at mid-altitudes, precipitation, minimum temperature and the number of habitats are mainly responsible for the observed diversity pattern; an additional factor is fire. In particular epiphytes, tree ferns and filmy ferns predominate in the zone of maximum rainfall on Mt Kilimanjaro and are therefore indicators of the wettest areas on this mountain.

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TREE SPECIES DIVERSITY IN RELATION TO TOPOGRAPHY AND HUMAN ACTIVITIES IN THE ATAKORA MOUNTAINS IN BENIN

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Abstract

Diversity, density and structure of plant communities were investigated in the Atakora Mountains, Benin. A survey of the tree species was carried out in 102 plots along transects from the top to bottom of hills on the western and eastern sides of the mountain chain. 112 woody species were recorded belonging to 37 families and 87 genera. The woody flora of the Atakora Mountains is dominated by Sudano-Zambezian species (44.6%) followed by tropical African (17.8%), Sudanian (11.9%) and Sudano-Guinean (11.9%) species. This spectrum indicates the role of the Atakora Mountains for the conservation of the original African flora. Also, the number of Guineo-Congolian species (5%) located along rivers and gullies show the refuge function of the mountains. Detrended correspondence analysis of the data resulted in the identification of seven plant communities. The landscape diversity explains the variability of the plant communities, each of them linked to particular substrate, topography and/or human activities. Diversity index and density varies between the plant communities with greatest values for the *Afzelia africana* and *Pterocarpus erinaceus* woodlands, and lowest values for farm parklands. The latter are relatively poor in tree species due to selective land clearing for shifting cultivation practice.

Résumé

Diversité des espèces d'arbre en relation avec la topographie et les activités humaines dans les montagnes de l'Atakora: Bénin. La diversité, densité et structure des communautés végétales furent étudiées dans les montagnes de l'Atakora au Bénin. Un inventaire des espèces d'arbre fut réalisé le long d' un tracé partant depuis le sommet d'une colline et aboutissant aux flancs Ouest et Est de la chaîne de montagnes. 112 espèces ligneuses furent reportées, appartenant á 37 familles et 87 genres. La flore ligneuse des montagnes de l'Atakora est dominée par les espèces soudano-zambéziennes (44.6%), suivies par les espèces d'Afrique tropicale (17.8%), Soudaniennes (11.9%) et Soudano-guinéennes (11.9%). Cette diversité indique le rôle des montagnes de l'Atakora dans la conservation de la flore originelle Africaine. Aussi, le nombre d'espèces Guineo-congoliennes (5%) situées le long des rivières et ravins démontre l'effet refuge de ces montagnes. Une analyse des correspondances redressée des résultats, conduit á l'identification de sept communautés végétales. La diversité du paysage explique cette diversité des communautés végétales, chacune liée á un sol particulier, á la topographie et/ou aux activités humaines. Le taux de diversité et densité varie entre les plus grandes valeurs pour les forets d'*Afzelia africana* et *Pterocarpus erinaceus* aux valeurs les plus basses pour les exploitations agricoles. Ces dernières étant relativement pauvres en espèces d' arbres due á une coupe sélective en vue du changement des pratiques agricoles.

Key words: Atakora Mountains, Benin, human activities, phytochoria, woodland

1 Introduction

The conservation of biological diversity should be one of the main objectives of studies on natural resources and ecosystems. One of the basic factors for conservation of biological diversity in forest and savanna landscapes is the understanding of disturbance regimes under past natural and semi-natural conditions. Numerous ecosystems are fragile due to their intrinsic factors or to the disturbances caused by human activities. Mountain ecosystems, for example, are very diverse ecosystems due to their high geodiversity, which favours the establishment of various plant communities (Nasi *et al.*, 2002). Despite their high plant diversity they are fragile systems as the topography with steep slopes is sensitive to erosion. Furthermore they are coveted by the population of the surrounding areas searching for cultivable land. The Atakora Mountains in the north of Benin consist of a chain of mountains covered mainly by savanna, woodlands, farm parklands and at some sites by islets of dry forest. Valleys, hill bottoms and moderate slopes on the hillsides are exploited by agriculture and cattle grazing. The chain of mountains shows several micro-ecosystems which can be explained with variations in landscape (Tente & Sinsin, 2002). Furthermore human impact also influences the structure and the dynamics of vegetation (Neeraj *et al.*, 2001). The Atakora Mountains potentially possess a high plant diversity, however, so far they are poorly investigated (Adjanohoun *et al.*, 1989; Hahn-Hadjali *et al.*, 2000).

The tree layer constitutes a permanent component of the vegetation that gives the main physiognomy to the land cover and permits the classification of vegetation types. This is of particular importance in areas where annual bushfires destroy the herbaceous layer. Therefore the objective of this study is to focus on the woody layer and to analyse the diversity of tree species with relation to landscape and human activities.

2 Material and Methods

2.1 Study area

The Atakora chain of mountains extends across three countries: the Atakora Mountains in Benin, Mount Togo in Togo, and the Akwapin Range in Ghana (Affaton, 1987). Located in the north-west of Benin (Fig. 1) between latitudes 10°40' and 11°28' N and longitudes 1°00' and 2°00' E, the Atakora Mountains form a southwest-northeast oriented chain with an altitude between 300 m and 600 m. They are essentially composed of quartzite and schist, and the soil is rocky but more gravely on hillsides and hilltops, and sandy, clayey or sandy-silt in the valleys. Climate is characteristic for tropical African regions with two seasons: a rainy season from May to October and a dry

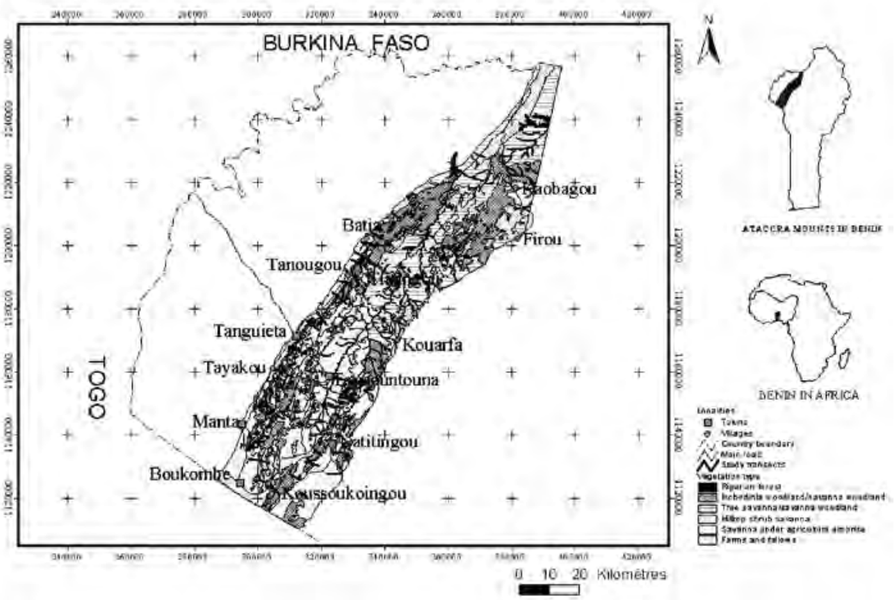

FIG. 1. The study area.

season from November to April. Because of the influence of the mountains, this region is among the higher rainfall regions in Benin with annual precipitation between 1200 mm and 1350 mm. Air temperatures are variable throughout the year with an annual average of about 28°C. The study area is located in the Sudanian zone (White, 1986), and corresponds to the phytogeographical district of the "massif de l'Atakora" in Benin (Adjanohoun *et al.*, 1989; Houinato *et al.*, 2000). Bushfires occur every dry season burning all species of the herb layer, so that bare soil is exposed under the tree stratum. Agriculture and pastoralism are the main economic activities. Valleys and plateaus are more often cultivated than hillsides due to their favourable soil conditions with more fertile sandy or sandy-siltic soils. This explains the degradation of the original valley vegetation in the Atakora Mountains.

2.2 Data collection

Surveys were carried out at several sites representative for the variation in vegetation and topography. Thus, plots were installed along transects from the bottom of the hill to the top on the eastern and western side of the mountain chain (Fig. 1). Thirty transects, each ± 5 km long were made and a minimum of three plots per transects were studied. The number of plots was increased in transects on complex topographical zones. Additionally, gully vegetation on hill sides and gallery forests along rivers and streams in valleys and on the plateaus were also sampled. In total 102 plots were investigated. Plot size varied following the vegetation type. In savanna, square plots of 900 m^2 (30 m × 30 m) were made, whist along rivers and streams rectangular plots of 500 m^2 (10 m × 50 m) were chosen as they fit better to the shape of waterways and the width of riparian forests. Because of the low tree density in parklands, plots of 2500 m^2 (50 m × 50 m) were made. In each plot, the tree species composition, and several ecological variables were recorded and coded afterwards for the analysis:

Topography: (slope, landscape position) 1. valley; 2. plain; 3. hill bottom; 4. hill side; 5. hill top
Vegetation cover using the Braun-Blanquet method: 1. 1%–4.9%; 2. 5%–24.9%; 3. 25%–49.9%; 4. 50%–74.9%; 5. 75%–100%
Human impact: 1. natural vegetation; 2. fallows; 3. farms
Soil texture: 1. sandy-silt; 2. sandy-clayey; 3. gravely soil; 4. rocky soil
Soil moisture: 1. dry station; 2. temporary presence of water (rainy season only); 3. permanent presence of water

For tree individuals, with stem diameter at breast height ≥ 10 cm, the dbh at 1.30 m above ground was measured.

2.3 Data analysis

Tree species diversity was calculated as: species richness (R), species diversity index (Shannon index H), evenness of Pielou (E), and a species abundance model (Maguran, 1988). Species abundance and stands were described by density and basal area. Species chorology following White (1986) was also analysed.

The relationship between landscape position and vegetation communities was investigated by using indirect gradient analysis techniques. They include ordination of plant communities by multivariate analysis: detrended correspondence analysis (DCA) and correlation analysis of community ordination axes on dominant environmental factors. The DCA ordination is chosen because it matches perfectly the following four criteria: (1) ecological interpretability, (2) effective spreading out of the points, in contrast to all points in a clump except for a few outliers, (3) avoidance of the arch distortion and (4) effectively revealing minor community gradient (Hill, 1979; Hill & Gauch, 1980). DCA analysis was performed using CANOCO software, version 4 (ter Braak & Smilauer, 1998).

To determine beta diversity many authors have used a similarity index along altitudinal transects. However, the distance between stands in ordination space is also a satisfactory measure of beta diversity if most variation in the data set is accounted for by the first component. In this case the estimation of beta diversity and ecological distances along unidimensional gradients by non-linear rescaling (as in DCA) is recommended (Økland, 1986a, 1986b; Eilertsen *et al.*, 1990).

3 Results and discussion

3.1 Species and family richness

112 tree species with dbh ≥10 cm, belonging to 37 families and 87 genera were recorded in the surveyed area. Species richness value of the Atakora Mountains woody flora is therefore comparable to the value obtained in a neotropical cloud forest of Monteverde, Costa Rica where Nalini *et al.* (1995) recorded 114 species belonging to 85 genera and 47 families. The most common families with at least 10 species are *Caesalpiniaceae, Combretaceae, Rubiaceae* and *Anacardiaceae* (Table 1). These families are also the most represented in the Sudanian woodland flora (Grondard, 1964). The most frequent species with relative frequency ≥20% are *Pterocarpus erinaceus*, *Lannea acida*, *Burkea africana*, *Crossopteryx febrifuga*, *Terminalia laxiflora*, *Detarium microcarpum*, *Vitellaria paradoxa*, *Combretum glutinosum*, *Afzelia africana*, *Daniellia oliveri*, *Khaya senegalensis*, *Hexalobus monopetalus*, *Strychnos spinosa*, *Parinari curatellifolia*, *Isoberlinia doka* and *Xeroderris stuhlmannii.*

TABLE 1. Family, genus and species richness of the Atakora Mountains woody flora.

Families	No. of genera	No. of species	Families	Number of genera	Number of species
Caesalpiniaceae	10	11	*Apocynaceae*	1	1
Combretaceae	4	11	*Araliaceae*	1	1
Rubiaceae	9	11	*Asteraceae*	1	1
Anacardiaceae	7	10	*Bignoniaceae*	1	1
Mimosaceae	5	8	*Capparaceae*	1	1
Moraceae	3	8	*Celastraceae*	1	1
Euphorbiaceae	4	5	*Chrysobalanaceae*	1	1
Fabaceae	5	5	*Dipterocarpaceae*	1	1
Sapotaceae	3	4	*Ebenaceae*	1	1
Loganiaceae	2	3	*Flacourtiaceae*	1	1
Meliaceae	3	3	*Myrtaceae*	1	1
Annonaceae	2	2	*Opiliaceae*	1	1
Arecaceae	2	2	*Polygalaceae*	1	1
Bombacaceae	2	2	*Rhamnaceae*	1	1
Clusiaceae	2	2	*Sapindaceae*	1	1
Ochnaceae	2	2	*Simaroubaceae*	1	1
Oleaceae	2	2	*Sterculiaceae*	1	1
Tiliaceae	1	2	*Verbenaceae*	1	1
Apiaceae	1	1	**Total**	**87**	**112**

3.2 Phytogeography

Species chorology is an indicator of ecological site conditions, as each species reaches its maximum abundance at its favourable site (Guinochet, 1973). The woody flora of the Atakora Mountains is dominated by Sudano-Zambezian species (44.6%) followed by tropical African (17.8%), Sudanian (11.9%) and Sudano-Guinean (11.9%) species (Fig. 2). This indicates that the original African flora is well conserved in this ecosystem. The Atakora Mountains constitute also a refuge for Guineo-Congolian species (5%) such as *Milicia excelsa*, *Antiaris africana*, *Zanha golungensis*, etc. which are found along rivers and gullies. In accordance with Masens (1997) the proportion of

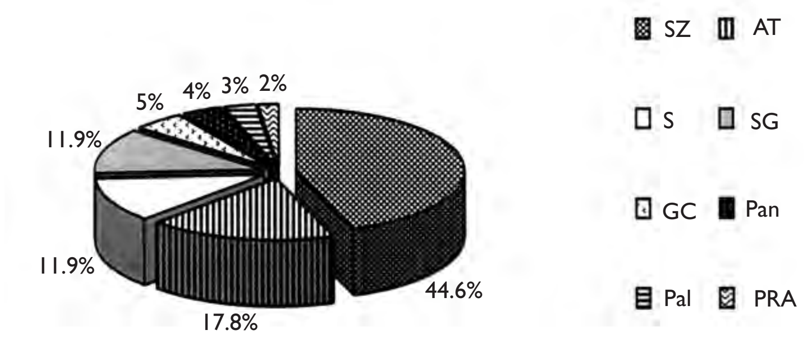

FIG. 2. Phytogeographical spectrum (SZ: Sudano-Zambezian, AT: tropical Africa, S: Sudanian base-element, SG: Sudano-Guinean, GC: Guineo-Congolian, Pan: pantropical, Pal: paleotropical, PRA: African pluri-regional).

TABLE 2. Correlation between ecological variables and ordination axes.

	Ordination axis	
	Axis 1	**Axis 2**
Landscape position	0. 6091	-0. 3846
Soil texture	0. 6042	-0. 4280
Soil moisture	-0. 7278	0. 2056
Slope	-0. 1941	-0. 2323
Altitude	-0. 0397	-0. 1553
Tree cover	-0. 5674	0. 1432
Human activities	0. 1138	0. 5204

large distribution area species decreases in less disturbed ecosystems. Sinsin (2001), studying *Isoberlinia* woodlands in northern Benin, also realised that the less disturbed plant communities present the highest abundance of endemic species in the concerned phytochoria, the so called base-element species.

3.3 Vegetation communities discriminated

The great variability of ecological factors in mountains and hilly regions explains the existence of various vegetation communities. The eigenvalues of the first axes were high and declined for the subsequent axes (see Fig. 3). The first two axes explained 12.6% of variance. Beta-diversity, a measure for the rate of species turnover, was estimated as the distance between stands on the two first axes. Plots of gallery forest (gf) and those of shrub savanna, the furthest plant communities on axis 1 in DCA ordination (Fig. 3), show a distance of 5.5 sd between each other. Also, on axis 2, parklands and shrub savanna are the most distant plant communities. Their furthest plots are extended about a distance >5.0 s.d. These results indicate a complete change in species composition between the sampled communities (Druit *et al.*, 1990; Hill & Gauch, 1980) which corresponds to a high value of beta-diversity. The first two axes of DCA ordination (Fig. 3) have significant ecological meaning (Table 2). The first axis presents high correlation with soil moisture, landscape position and soil texture. Soil moisture shows the highest but negative correlation with the axis indicating the importance of the soil moisture gradient. The axis presents an ecological series from riparian forests along rivers where moisture is high, to woodlands on the hill bottom and hill sides with medium soil moisture, to shrub savanna on the hilltop with dry soil conditions (Fig. 3). Similar results were found in the Aljibe Mountains, where Ojeda *et al.* (2000) realised that woody species distribution and abundance were associated with topographic and soil properties.

The second ordination axis of DCA reflects human disturbance as it presents the highest correlation (Table 2) with human activities (agriculture). This axis separates plots realised in farm parklands and those carried out in natural vegetation types.

Analysing the correlation between ecological variables (Table 3), it appears clearly that topography is a complex factor which influences other parameters. Landscape position is significantly correlated with altitude, soil texture and soil moisture. The latter is negatively correlated to the other factors (Table 3), which can be explained by the higher water availability in sites at lower altitude (e.g. valleys, foothills and plains). Human impact is also negatively correlated with the parameter of tree cover. This is related to the selective clearing of land for the implementation of fields which strongly reduces the tree cover.

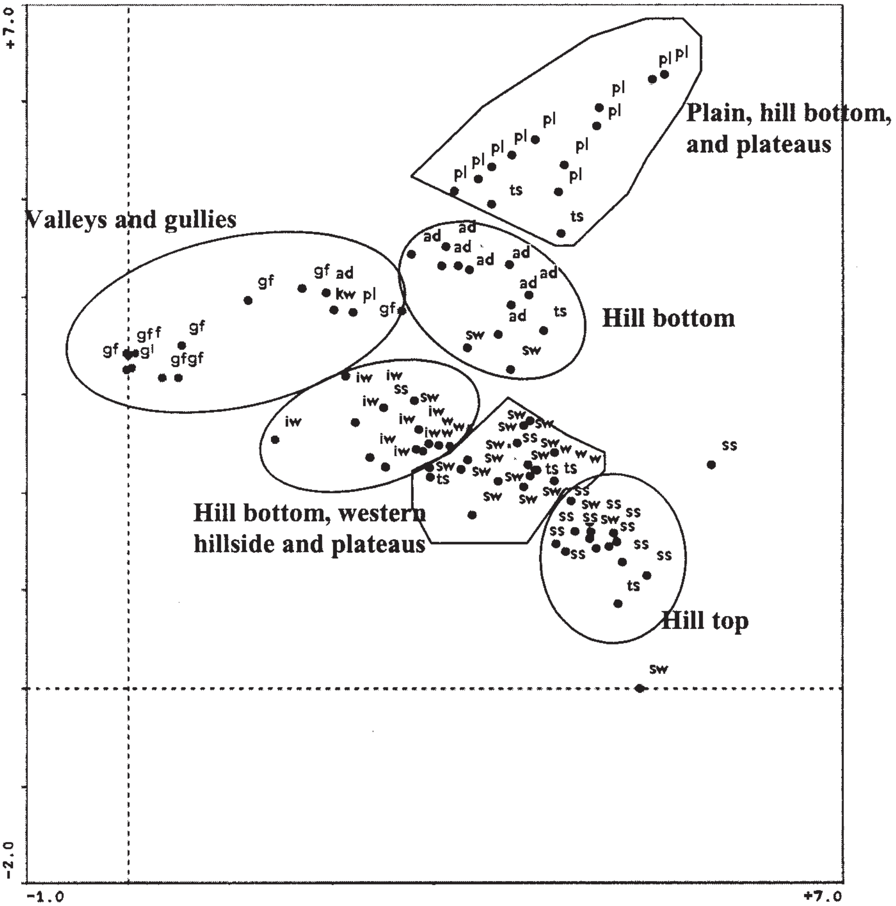

FIG. 3. Detrended correspondence analysis ordination of plots (axes: 1 horizontal and 2 vertical) (gf: gallery forest, iw: *Isoberlinia* woodlands, ad: *Anogeissus* woodlands, sw: savanna woodlands, ts: tree savanna, pl: parklands). Eigenvalues of the 4 axes: 1. 0.818, 2. 0.635, 3. 0.453, 4. 0.276; Total inertia 11.557. Cumulative percentage variance: 1. 7.1%; 2. 12.6%, 3. 16.5%, 4. 18.9%.

TABLE 3. Correlation (r^2) between ecological variables. *** p<0.001, ** p<0.01, * p<0.05.

Variables	Landscape position	Soil texture	Soil moisture	Slope	Altitude	Tree cover	Human impact
Landscape position	1.00						
Soil texture	0.43***	1.00					
Soil moisture	-0.48***	-0.51***	1.00				
Slope	0.15	0.30**	0.02	1.00			
Altitude	0.53***	0.24*	-0.23*	0.02	1.00		
Tree cover	-0.19	-0.14	0.21*	0.13	0.06	1.00	
Human impact	-0.09	-0.18	-0.07	-0.19	-0.12	-0.54**	1.00

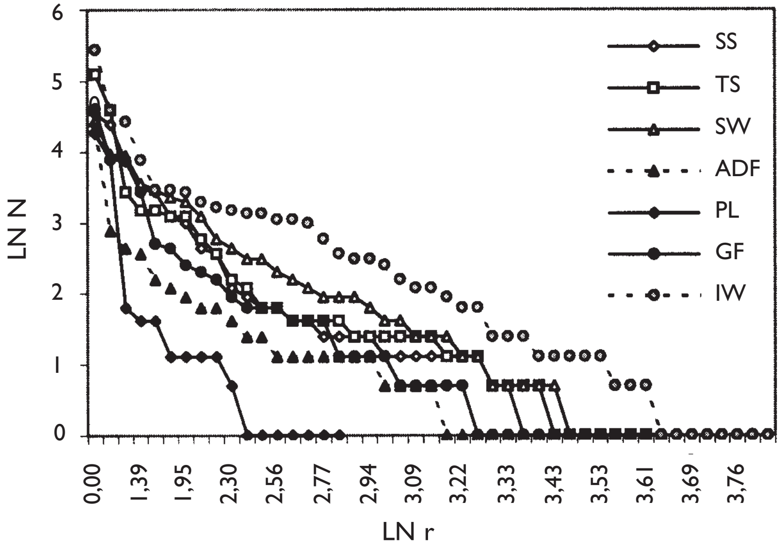

FIG. 4. Species abundance curve for all trees and lianas with dbh ≥10 cm (r: species rank, N: species abundance, GF: gallery forest, IW: *Isoberlinia* woodlands, ADF: *Anogeissus* woodlands, SW: savanna woodlands, TS: tree savanna, PL: parklands).

To summarise, the distribution pattern of the plant communities and species is governed by the topographic factor which is a complex factor influencing other factors as well (moisture, soil). The 102 samples in the ordination distinctly aggregate into six groups, each of those related to a particular landscape position and to human impact. These groups correspond with seven vegetation communities, as tree savanna and woodland savanna are not sufficiently discriminated by this analysis.

3.4 Description of vegetation communities

The distribution curve of species abundance recorded for all plant communities is shown in Fig. 4. The main two components of diversity (species richness and evenness) are expressed by the graphic: the extension of the curve to the right indicates species richness, the convexity or concavity of the curve indicates evenness (Frontier & Pichod-Viale, 1991). Parklands are the least diversified plant communities as the species abundance curve is concave and the least extended to the right. *Isoberlinia* woodlands and savanna woodlands are the most diversified plant communities as their curves are convex and the most extended at the right (LN r=5.25 for savanna woodland and LN r=5.49). The curves of the other plant communities are also quite extended to the right side, but their concavity indicates the dominance of only a few species.

3.5 Stand characteristics

Stand characteristics of the seven plant communities are summarised in Table 4. The *Berlinia grandiflora* and *Breonadia salicina* plant community of riparian forests is the most dense community (893.5 ± 229.3 trees.ha^{-1})with the highest value of basal area (49.5 ± 17 m^2.ha^{-1}) as well as the highest soil moisture, which offers adequate conditions for plant growth. It constitutes also a refuge for certain forest species such as *Milicia excelsa*, *Antiaris africana*, *Zanha golungensis*, *Pouteria alnifolia*, *Margaritaria discoidea*, *Albizia zygia*,

TABLE 4. Stand characteristics of vegetation communities.

	R	H (bits)	E	Density* (trees.ha^{-1})	BA* (m^2.ha^{-1})	Abundant species
Riparian forest	38	3.69	0.74	893.5 ± 229.3	49.5 ± 17	*Berlinia grandiflora, Syzygium guineense, Breonadia salicina, Garcinia ovalifolia, Uapaca togoensis, Vitex doniana, Polysphaeria arbuscula, Pentadesma butyracea, Diospyros mespiliformis*
Isoberlinia woodland	45	4.19	0.76	582.5 ± 154.4	14.8 ± 7.6	*Isoberlinia doka, Pterocarpus erinaceus, Monotes kerstingii, Lannea acida, Burkea africana, Khaya senegalensis, Daniellia oliveri*
Savanna woodland	38	4.25	0.81	602.5 ± 131.6	16.9 ± 6.8	*Afzelia africana, Pterocarpus erinaceus, Lannea acida, Strychnos spinosa, Daniellia oliveri, Detarium microcarpum, Hexalobus monopetalus, Burkea africana, Khaya senegalensis, Xeroderris stuhlmannii*
Tree savannas	37	3.5	0.70	515.2 ± 178.7	9,9 ± 5.5	*Burkea africana, Terminalia laxiflora, Detarium microcarpum, Crossopteryx febrifuga, Pterocarpus erinaceus, Lannea acida, Parinari curatellifolia*
Anogeissus leiocarpus dry forest	37	3.87	0.74	473.3 ± 289.5	20.1 ± 8.8	*Anogeissus leiocarpus, Acacia dudgeonii, Combretum glutinosum, Pterocarpus erinaceus, Nauclea latifolia*
Shrub savannas	38	3.60	0.74	352.4 ± 94.9	8 ± 4	*Detarium microcarpum, Burkea africana, Terminalia laxiflora, Strychnos spinosa, Crossopteryx febrifuga, Pterocarpus erinaceus, Lannea acida, Parinari curatellifolia*
Farm parkland	17	2.38	0.58	57.1 ± 20.1	5.7 ± 3.3	*Parkia biglobosa, Vitellaria paradoxa, Mangifera indica, Khaya senegalensis, Ficus exasperata*

which are less hygrophilous species in moist forest. The presence of these species, especially *Milicia excelsa* which is regularly distributed along the chain, indicates that this region was more moist before and probably covered by forests similar to those occurring at southern latitudes of the chain in Togo (Tchamié & Bouraima, 1997).

Anogeissus leiocarpus woodlands, which occur on plains at the bottom of the hill are remarkable through their emergent trees of *A. leiocarpus*, *Combretum glutinosum*, *Acacia dudgeonii*, etc. Stand characteristics are medium. This vegetation type constitutes at certain sites the boundary between riparian forests and savanna.

Isoberlinia woodlands occur at the foot of the hill on plateaus, western hill sides and on the mountain shoulders. With 45 species they possess the highest species richness (Fig. 4). Characteristic are emergent trees of *Isoberlinia doka*, *I. tomentosa*, *Pterocarpus erinaceus*, *Khaya senegalensis*, etc. as well as small trees of *Monotes kerstingii* and *Hexalobus monopetalus*.

Savanna woodland with *Afzelia africana* and *Pterocarpus erinaceus* occur at hill sides and on plateaus. They present the highest value of Shannon index (4.3 bits) and evenness of Pielou (0.8) which indicates a more regular distribution of individuals of the different species. The most emergent trees are *Afzelia africana*, *Khaya senegalensis*, *Pterocarpus erinaceus*, *Daniellia oliveri*, *Burkea africana*.

Tree and shrub savanna occur mainly at hill tops, the eastern hill sides and on certain plateaus. Shrub savanna are the least dense and the least diversified vegetation types among natural ones (Table 4). This can be explained by relatively dry soil conditions at the hill tops.

Another vegetation type is the farm parkland, which has the lowest value of stand characteristics (Table 4). This reflects the selective impact of human activities on plant diversity as well as on the modification of the physiognomy of the natural vegetation. Not only is tree density reduced, species richness is also low as only a few selected species are conserved. Parklands occur at all topographic positions where soil conditions are favourable and it is relatively easy to cultivate. The most frequent species are *Parkia biglobosa* and *Vitellaria paradoxa* which are the most abundant species of west African parklands (Boffa, 1995; Wala, 2001).

Woodland communities of the Atakora Mountains invariably differ in their physiognomy and their stand characteristics. These differences are related to the species composition as well as to the topographic factors. However, differences of stand characteristics between savanna of similar species composition indicate that factors other than the species composition influence the vegetation structure. The vegetation variation is related basically to topographic variability, which influences also soil moisture and texture as was shown by the indirect gradient analysis. Tchamié & Bouraima (1997) have also found that for similar climatic conditions landscape position and soil constitute the main factors for explaining the difference between vegetation communities. Likewise, Witkowski & O'Connor (1996) have pointed out that topo-edaphic gradients significantly influence floristic and stand characteristic variation in African savanna woodlands. With regard to the altitudinal gradient, no floristic or vegetation zonation occurred probably due to the low range of altitude, but decreasing of species diversity and stand characteristics at hill tops covered mainly by shrub savanna was observed. The decline of tree species diversity with increasing elevation and human disturbances has also been described in other studies on mountain regions such as in Central Himalaya (Neeraj *et al.*, 2001) and in the Querada de Oro forest of Belize, where the tree species richness was the highest at the bottom (Brokaw *et al.*, 1997).

4 Conclusions

This study has determined the current diversity of the woody vegetation of the Atakora Mountains and the correlation between vegetation communities and environmental factors. The Atakora Mountains show high values of alpha and beta-diversity. The woody flora of these mountains reflects a relatively good conservation status of the original flora of this region as it is dominated by Sudano-Zambezian, tropical African, Sudanian and Sudano-Guinean species. This mountain area also constitutes in some particular sites a refuge for certain endangered forest species such as *Milicia excelsa*, *Antiaris africana*, *Afzelia africana*, *Khaya senegalensis*. None of the recorded species can be considered orophytic as they appear also in the surrounding plains, and there was no distinct zonation of the vegetation according to the altitude due to weakness of the relief. However, soil moisture and texture correlated to topography; slope and human activities influence the distribution and the structure of the vegetation communities in the Atakora Mountains. Soil moisture and human activities are the most important factors explaining the differentiation of the Atakora mountain vegetation. This study provides environmental interpretations for the occurrence of various vegetation communities based on the correlation between vegetation ordination scores (DCA) and environmental factors.

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PHYTODIVERSITY DYNAMICS IN PASTURED AND PROTECTED WEST AFRICAN SAVANNAS

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Abstract

In the last decades vegetation changes in West African savannas due to changing climatic conditions and human impact have become more and more obvious. Whereas the dynamics of vegetation cover were intensively observed, the knowledge about changing species composition and phytodiversity dynamics remains scarce. For a better understanding of current dynamics, especially with regard to the impact of grazing, permanent plots were installed in protected and pastured areas in the Sudanian zone of Burkina Faso. By standardized floristic inventories and phytosociological relevés phytodiversity and species composition were analyzed. The investigations are part of a continent wide monitoring of the BMBF-funded BIOTA Africa project (http://www.biota-africa.de/). Results from the first inventories reveal a significantly higher species richness on the pastured plots, and also big differences in species composition. The pastured plots show a higher proportion of forbs and annual grasses the majority being typical elements of the segetal and ruderal flora brought by cattle into the savanna. The species richness of the woody layer is so far not affected by grazing. However, regarding the species composition of the different woody strata, for several woody species the regeneration seems to be disturbed in the pastured plots, which at long term might lead to their decline. Further monitoring is needed to understand these population dynamics in the long run.

Résumé

Phytodiversity dynamics in pastured and protected West African savannas. Pendant les dernières décennies les variations de végétation des savanes Ouest Africaines, dues au changement des conditions climatiques et á l'impact de l'homme sont devenues de plus en plus visibles. La dynamique du couvert végétal a été intensivement étudiée mais les observations sur le changement de composition des espèces et la dynamique de la phytodiversité demeurent plus rares. Pour une meilleure compréhension des dynamiques actuelles, principalement par rapport a l'impact du pâturage, des sites permanents furent installés dans des zones protégées et d'autres dans des zones consacrées au bétail dans la zone soudanienne au Burkina-Faso. La phytodiversité et la composition en espèces furent analysées par des inventaires standardisés de la flore et des relevés phytosociologiques. Ces investigations font part d'un projet de suivis á l'échelle du continent du BMBF financée par BIOTA projet Afrique (http://www.biota-africa.de). Les résultats des premiers inventaires révèlent une significative plus grande richesse en espèces dans les sites avec pâturage ainsi qu'une plus grande différence dans la composition des espèces. Les sites pâturés montrent une plus grande proportion en herbes messicoles et annuelles transportées par le bétail dans la savane. Jusqu'ici la richesse végétale en espèces de la strate arborée n'est pas affectée par le pâturage. Cependant concernant la composition en espèces des différentes strates arborées pour plusieurs espèces arbustives, la régénération semble modifiée dans les sites pâturés, ce qui a long terme pourrai conduire a leur déclin. Plus de suivis seront nécessaires pour comprendre la dynamique de ces populations á long terme.

Key words: Burkino Faso, pasture pressure, phytodiversity dynamics, savannas, West Africa

1 Introduction

Changes in vegetation cover and habitat degradation are increasing and accelerating in many West African savanna regions due to changing climatic conditions and human impact. This general development is still contrasted by a lack of detailed knowledge concerning the current state of plant diversity, species composition and their dynamics. In this context the impact of land use practices on vegetation development is of particular interest, to distinguish the effects of human activities and climate. This is stressed by the currently revived discussion on degradation and recovery of the Sahelian vegetation, based on results of satellite time series indicating an increase in seasonal greenness for large areas of the Sahel (UNEP/FAO/UNCCD, 2003). It is pointed out, that a current "greenness" value similar to a former state might result from a different species composition.

Livestock grazing is one of the important forms of land use, being a major influence on the composition and diversity of species not only in the Sahel (Le Houérou, 1998, 1996; Hiernaux, 1998; Toutain, 1999) but also in the Sudanian zone. Generally light grazing is considered as resulting in an increase in species richness (Naveh & Whittaker, 1979; Noy-Meir *et al.*, 1989) whereas heavy grazing leads to a decrease in species diversity (Olsvig-Whittaker *et al.*, 1993). Frequently observed changes associated with increasing grazing pressure are shifts from perennial to annual vegetation (Taddese *et al.*, 2002; Milton *et al.*, 1994), and heavy grazing can result in the loss of palatable plants and select for weedy, generalist species (Milton *et al.*, 1994; Huenneke & Noble, 1996; McIntyre & Lavorel, 2001). However, most of the studies were carried out in semi-arid areas and the consequences of livestock grazing can be diverse, and differ depending on the region. Species fostered by grazing in the Sahel of Niger (Hiernaux, 1998) include, for example, some of the best forage species. For the Sudanian zone detailed knowledge about the species composition and distribution in response to grazing pressure is still lacking. Partly this may be due to the fact that pastures are often at the same time fallows as part of shifting cultivation cycles, which complicates the interpretation of different species composition in response to pasture or fallow succession.

For a better understanding how grazing affects plant species composition and species richness in the Sudanian zone permanent plots were installed in protected and pastured areas in Burkina Faso. The investigations are part of a continent wide long term monitoring of the BMBF-funded BIOTA Africa project (www.biota-africa.de) to investigate biodiversity dynamics throughout a continental climatic gradient. The present results refer to the first inventories carried out in 2001.

2 Materials and methods

The study area is located in the eastern part of Burkina Faso (Fig. 1) in the northern Sudanian zone. The vegetation cover is composed of a mosaic of various types of woodland, grass, shrub and tree savannas, fallows and gallery forests. Nearly the whole area is pastured mainly by cattle and to lesser degree by small ruminants, and annual bush fires pass through. The region receives 825 mm of rain per annum; the rainy season lasting from April to October.

A typical Sudanian woodland savanna with a tree cover of about 60% was selected for the analysis of the grazing impact on plant species richness and composition. Two sites, distinguished by their degree of grazing, were chosen to establish the permanent plots. One is situated in a protected area in which only sporadic influence of wildlife becomes effective the other one is located in an area with heavy cattle grazing pressure. Stocking rates are unknown, as sedentary as well as transhuman herders use the communal rangeland. The grazing regime can be characterized as being heavily and continuously grazed.

At both sites five permanent plots each of a size of 1 ha were made. In every hectare plot smaller plots were installed: a 20 × 50 m^2 plot for making an inventory of the woody layer, and a 20 × 20 m^2 and 10 × 10 m^2 for the investigations of the herb layer. The different plot sizes for the woody and herb layer correspond to results of minimum area analyses for the adequate assessment of the different strata. The inventories are carried out according to standardized methods in the frame of the BIOTA research network. The following parameters were recorded:

- 100 × 100 m^2: list of all plant species
- 20 × 50 m^2 relevés of the woody layer: estimation of the percentage cover contributed by each species (Londo-scale: 10% intervals), divided into different strata (0–0.5, 0.5–1, 1–2, 2–5, 5–10, >10 m)
- 10 × 10 m^2 relevés of the herb layer: estimation of the percentage cover contributed by each species (Londo-scale: 10% intervals)

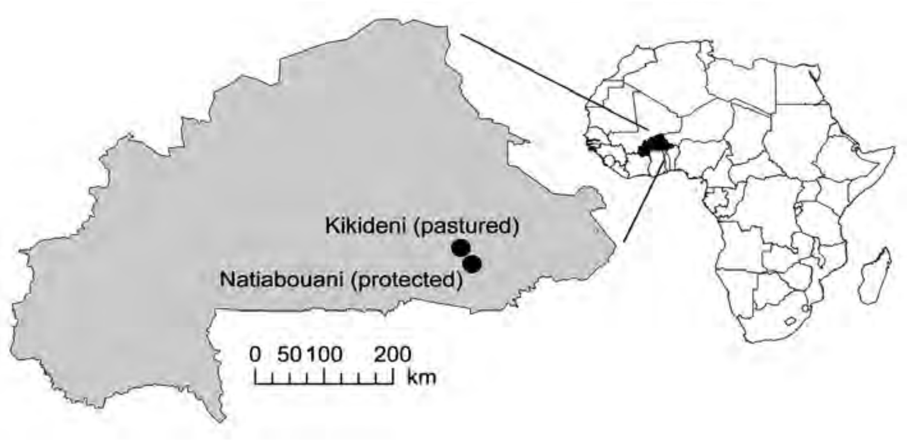

FIG. 1. The study area.

TABLE 1. Woody cover per strata for certain species in the 20 × 50 m^2 plots.

Species/strata	**0–0.5 m**	**0–5–1 m**	**1–2 m**	**2–5 m**	**5–10 m**	**0–0.5 m**	**0.5–1 m**	**1–2 m**	**2–5 m**	**5–10 m**
Vitellaria paradoxa	▓	░	░	█	█	░	░	░	░	░
Annona senegalensis	░	░	▓	░		░	░	▒		
Piliostigma reticulatum	░	░	█	█						
Pteleopsis suberosa	░	░	░	░						
Crossopteryx febrifuga	░	░	░	░		░	░	▒	▓	▓
Maytenus senegalensis	░	░	░	░		░	░	░	▓	░
Pterocarpus erinaceus	░					░	░	░		
Feretia apodanthera	░					░	░	░	░	
Dichrostachys cinerea	░					░	░		░	
Anogeissus leiocarpus					░		░	░	░	░
Lannea acida				░	░	░	░		░	
Acacia dudgeoni	░			░		░	░	░	▒	
Lonchocarpus laxiflorus						░	░	░		
Tamarindus indica						░	░			▓

░	▒	▓	█
0–1	2	5	10% (mean cover of 5 plots)

3 Results

3.1 Species richness

The first inventories in 2001 revealed for the hectare plot size a mean species richness of 81.4 in the protected site and 96.6 for the pastured site. Student's t-test showed that the species richness of all species is significantly higher in the pastured sites for both the 20 × 50 m^2 and 10 × 10 m^2 plots ($p = 0.066$) and the hectare plots ($p = 0.053$) (Fig. 2). Contrary to the differences in species richness of all species the plots of the woody layer (20 × 50 m^2 plots) contain in protected and pastured sites an equal number of species, which means that the woody layer's species richness is at the current state not affected by pasture. But the woody layer's evenness (Fig. 3) is significantly higher in the protected 20 × 50 m^2 plots ($p = 0.02$). This indicates that the woody species composition is more even in the protected area whereas some species dominate the woody stratum in the pastured plots (see also Table 1). For the herb layer, opposite tendencies can be detected. The pastured plots show a higher evenness while the dominance of some few tall grass species like *Andropogon gayanus* and *Hyparrhenia involucrata* leads to a lower value in the protected plots.

3.2 Life forms

The spectra of life forms for the plots clearly show a difference between the compared areas (Fig. 4). Not only the species richness is increased in pastured plots, but also the occurrence of therophytes and chamaephytes is significantly higher ($p < 0.001$) under grazing, whereas the number of hemicryptophytes is slightly increased ($p = 0.03$) in the protected plots.

Within the pastured plots the majority of the therophytes are typical elements of the segetal and ruderal flora of the Sudanian Zone, some of them also widely distributed in the Sahel (e.g. *Cassia tora*, *Zornia glochidiata*, *Microchloa indica*). These species are partly palatable species, some of them even good quality fodder (*Zornia glochidiata*), partly unpalatable herbs like *Cassia tora*. The higher share of chamaephytes in the

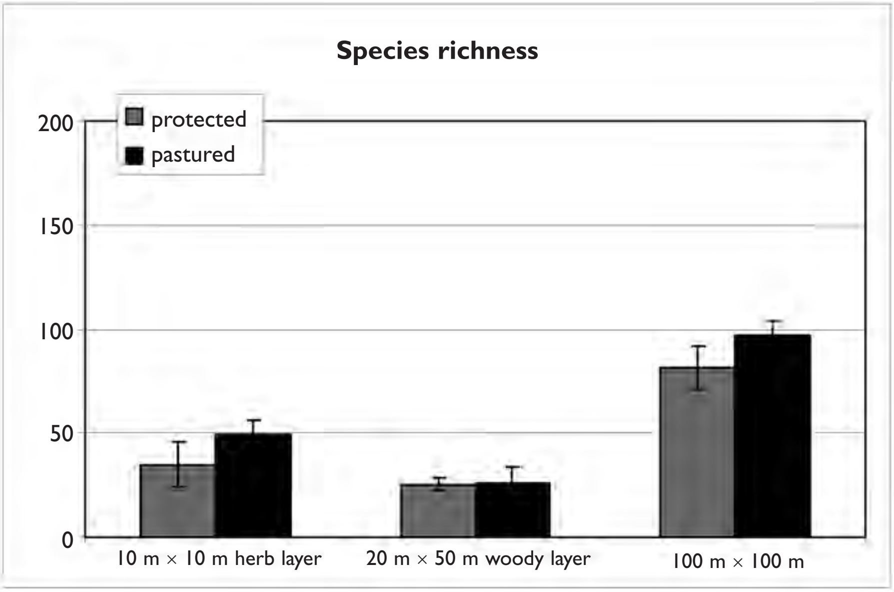

FIG. 2. Species richness in pastured and protected plots.
95% confidence intervals.

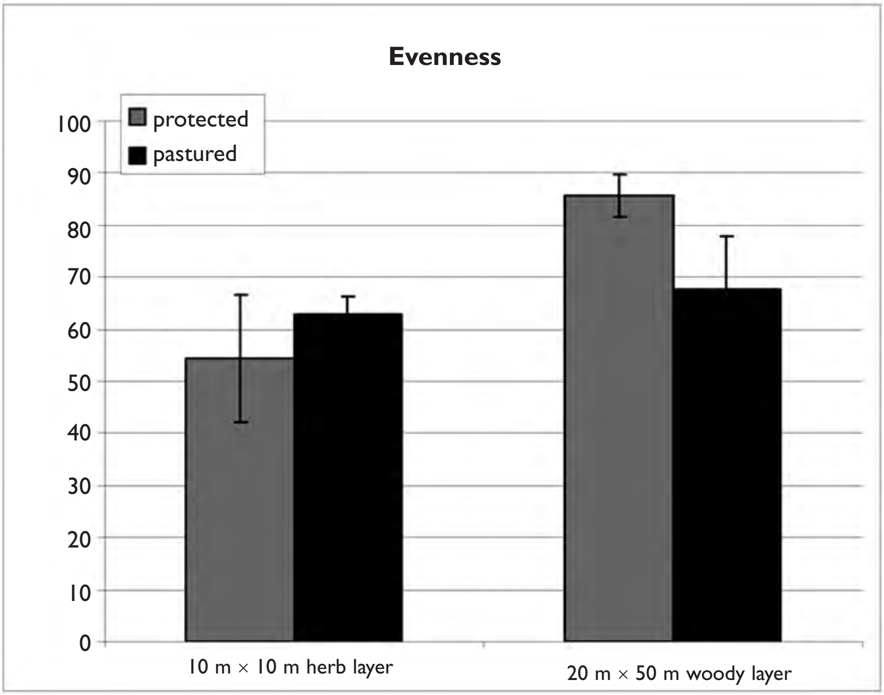

FIG. 3. Evenness in pastured and protected plots.
95% confidence intervals.

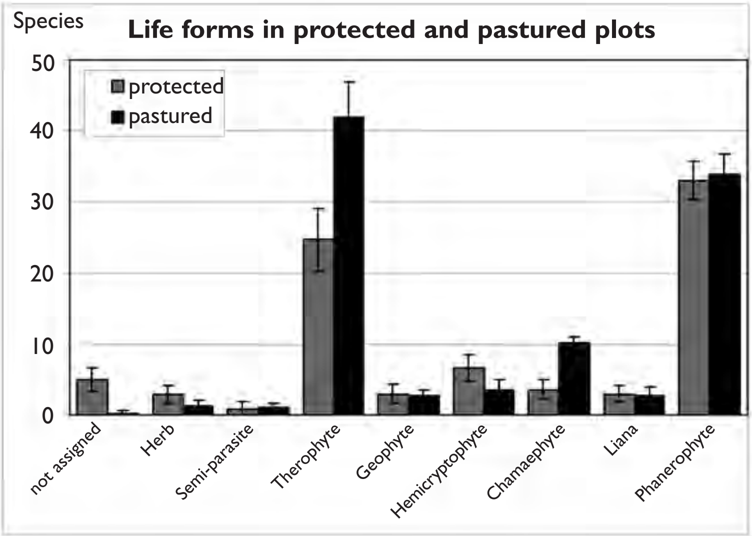

FIG. 4. Life forms in pastured and protected plots.

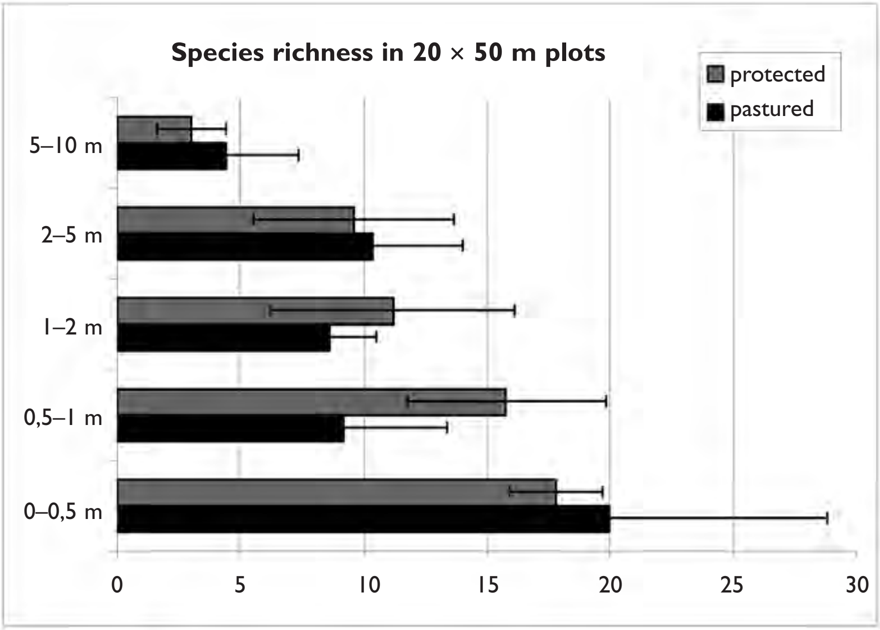

FIG. 5. Species richness in 20 × 50 m² plots.

pastured plots is due to the increase of unpalatable species (*Tephrosia pedicellata*, *Waltheria indica*), covering much of the herb layer. The protected plots however have a higher percentage of perennial grasses (hemicryptophytes) in terms of species richness and abundance.

3.3 Woody plants per stratum

Species richness as well as the mean cover of the woody layer was analyzed according to the different strata to detect differences in woody species regeneration in response to grazing. While the total species richness shows little difference, species richness is significantly higher for the 0.5–1 m stratum ($p = 0.05$) in the protected plots. All other strata have a similar species richness. The woody layer's mean cover is highly variable for both pastured and protected plots, being higher in the protected plots in the 0.5–1 m stratum and in the pastured plots in the strata 0–0.5 m and 2–5 m.

3.4 Woody species regeneration

With regard to the species composition of the woody layer the comparison of the pastured and protected sites reveals a different abundance per strata for several trees and shrubs (Table 1). Some of the woody species (*Crossopteryx febrifuga* to *Tamarindus indica*) are regularly distributed in all strata in the protected sites and can be found in the pastured plots only in the lowest stratum or in the highest without any juveniles. This indicates a disturbed regeneration for these species in response to heavy grazing.

Other species show a more regular occurrence and higher cover in all strata of the pastured plots (e.g. *Vitellaria paradoxa, Piliostigma reticulata*). This is partly due to the former exploitation of the site (fallow-field-cycles with protection of *Vitellaria paradoxa* more than 50 years ago) but in the case of *Piliostigma reticulata* and also *Annona senegalensis* it is an effect of the grazing influence.

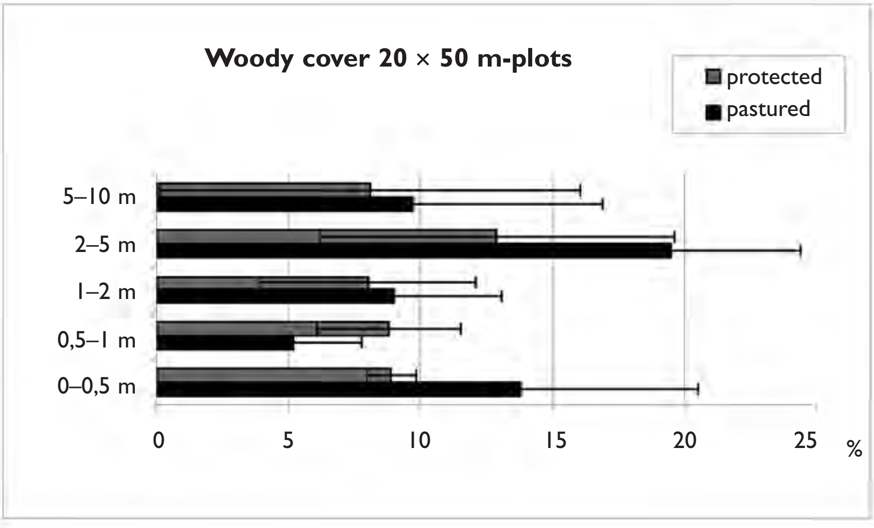

FIG. 6. Woody cover in 20 × 50 m² plots.

4 Discussion

The comparison of protected and heavily pastured sites clearly shows the effect of grazing by livestock on species richness, which is significantly increased under grazing. This result is in contrast with other studies, which have found either a decrease of species richness under grazing impact (Olsvig-Whittaker *et al.*, 1993) or no impact of heavy grazing at all on the number of species (Naveh & Whittaker, 1979; Todd & Hoffmann, 1999). This might be due to the fact that most of the studies were carried out in semi-arid regions, where savannas have a different vegetation structure. In the Sudanian Zone the vegetation of the protected sites is dominated by a two to three meters tall and very dense grass layer, composed mainly of perennial species, leaving little space for species underneath. When this dense grass layer is opened by grazing many annuals, pioneers and forbs can establish. The results of the evenness also indicate these differences between the pastured and protected sites. However, it is also possible that the increase of species richness under long-term impact of heavy pasture turns into a decrease. The grazing intensity on the investigated plots has increased only in the last few years according to the local population. Modeling experiments suggest, that vegetation changes due to overgrazing might take many years to become evident (Wiegand & Milton, 1996). Further monitoring will provide information on this.

With regard to the impact of grazing on the life forms and species composition the results show the typical shift from perennial herbaceous species to therophytes and chamaephytes. This compares favorably with several other studies that have found an alteration of the dominance of perennials in favor of annuals (Naveh & Whittaker, 1979; Todd & Hoffmann, 1999). The increase of geophytes observed by Todd & Hoffmann (1999) did not take place at our sites. This may be due to its former agricultural use.

The therophytes and chamaephytes which increase on the pastured sites are not just the unpalatable species. They consist of a number of unpalatable as well as some palatable species and even good fodder. These results confirm well with those of Hiernaux (1998) for Sahelian rangelands, were no relationship was found between species response to grazing and palatability. Others (Milchunas & Lauenroth, 1993; Todd & Hoffmann, 1999; McIntyre & Lavorel, 2001) have observed a selection for low growing prostrate growth forms in response to grazing.

While the herb layer shows distinct changes in response to grazing, the species richness of the woody layer is not affected. The comparison between pastured and protected sites broken down into strata, which might show changes in regeneration of the woody species, differs only in the species richness of the 0.5–1m stratum. The lower values in the pastured plots suggest the disturbance of woody regeneration by cattle at this height. Lower cover values in the same stratum stress this interpretation. This agrees partly with Higgins *et al.* (1999), who observed a lower level of regeneration of woody plants under higher pasture pressure in semi-arid savannas. However, in this regard the individual species response has to be considered. Regarding the cover distribution of the species per stratum, different species groups can be distinguished. Some of them (e.g. *Piliostigma reticulata*) are apparently increasing, whereas for others, like *Pterocarpus erinaceus* and *Anogeissus leiocarpus* the irregular occurrence in the different strata indicates a disturbed regeneration in the pastured plots, which in the long term is supposed to lead to their severe decline. These first results highlight the need for further studies on the impact of grazing pressure especially that on the woody vegetation.

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THE INFLUENCE OF GEOMETRIC CONSTRAINTS ON THE COLONISATION, SPECIATION AND RANGE EXPANSION OF ORCHIDS

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Abstract

Variation in species richness along a gradient is a well-known phenomenon and many attempts have been made to correlate this with various environmental factors. Recently, however, the potential influence of non-biological factors has also been highlighted. Species distributions might be constrained by hard geographical boundaries, such as the ocean surrounding an island, since ranges cannot extend either below the sea or above the highest point on the island. This means a greater probability of overlapping elevational ranges, and also therefore species richness, towards middle elevations. This has been termed the 'mid-domain effect' (MDE). The colonisation and speciation of island floras has fascinated biologists since the days of Wallace and Darwin, since their isolation restricts the number of possible hypotheses to explain evolutionary events. In this study, species richness of orchids (Orchidaceae) was studied along the elevational gradient both of the Mascarene Islands and of the islands of the Gulf of Guinea. Here we show how geometric constraints can effect speciation, future colonisation and range expansion of these insular orchids.

Résumé

Influence des contraintes géométriques sur la colonisation, la spéciation et l'expansion des orchidées. La variation de la richesse spécifique le long d'un gradient est un phénomène bien connu et qui a fait l'objet de beaucoup de tentatives de corrélation avec différents facteurs environnementaux. Néanmoins, récemment, la possible influence de facteurs non-biologiques a également été mise en évidence. La distribution des espèces pourrait être contrainte par des frontières géographiques, comme dans le cas de l'océan entourant une île où les aires de distribution ne peuvent s'étendre sous l'eau ou au-delà des sommets. La conséquence en est une plus grande probabilité de superposition d'aires de distribution en haute altitude et donc aussi une richesse spécifique supérieure aux zones de moyenne altitude. Ce phénomène a été appelé le 'mid-domain effect' (MDE). La colonisation et la spéciation des flores insulaires ont fasciné les biologistes depuis Wallace et Darwin car leur isolement réduit le nombre d'hypothèses pouvant expliquer les événements responsables de l'évolution. Dans cette étude, la richesse spécifique des orchidées (Orchidaceae) a été étudiée le long d'un gradient altitudinal dans les îles Mascareignes et les îles du Golfe de Guinée. Nous montrons comment des contraintes géométriques peuvent affecter la spéciation, la colonisation future et l'aire d'expansion de ces orchidées insulaires.

Key words: ecology, evolution, geometric constraints, mid-domain effect, Orchidaceae.

1. Introduction

The colonisation and speciation of island floras and faunas, in particular the study of isolated oceanic island archipelagos, has fascinated biologists since the days of Wallace and Darwin. As Stuessy & Ono (1998) recently stated,

> "*Oceanic island archipelagos are profoundly interesting ecosystems in which to ask questions about evolutionary patterns and processes. Their isolation from other land masses restricts numbers of plausible hypotheses that can be advanced to explain evolutionary events, often resulting in stronger scientific inferences. Island archipelagos may rightly be considered one of the best places on earth to understand origins and elaborations of biological diversity.*"

Variation in species richness along a gradient is a well-known phenomenon, and many attempts have been made to correlate this with environmental factors such as temperature, rainfall, productivity, etc, either singly or in concert (Rosenzweig, 1992, 1995; Rosenzweig & Abramsky, 1993; Rahbek, 1997, and references therein; Kaspari *et al.*, 2000). More recently, however, non-environmental factors have been highlighted (Colwell & Hurtt, 1994; Colwell & Lees, 2000).

One of the simplest, one-dimensional gradients is that of elevation. It is widely recognised that species richness patterns can be unimodal, peaking at mid-elevations (Rahbek, 1995, 1997; Heaney, 2001; Kessler, 2001; Md. Nor, 2001; Rickart, 2001; Sánchez-Cordero, 2001). If the mid-point of a species' range occurs at the mid-elevation level, then the species has a greater potential to occupy more of the domain, as it can extend to the very top and bottom of the island. If the mid-point of a species' range occurs near the top or the bottom of the elevational range, however, that species can extend only a little way either up or down in elevation. Widespread species are therefore constrained to having mid-points near the centre of the elevational gradient, whereas species with a small elevational range could be found anywhere over the elevational gradient. The greater the proportion of widespread species in a flora, the greater the likelihood that species richness will peak towards the middle of the domain, simply because the number of overlapping species ranges will be greatest at mid-elevations: localised species can be found anywhere over the domain, but widespread species are much more likely to be found at mid-elevations (Colwell & Lees, 2000). This phenomenon is termed the 'mid-domain effect' (MDE).

The concept was originally noted as a possible artefact in studies of species richness across environmental gradients (Colwell & Hurtt, 1994), and has yet to gain widespread acceptance as a possible explanation for species richness patterns. Although never proposed as being the sole or even the principal explanation for species richness patterns, the MDE has quickly generated a storm of protest (Bokma & Mönkkönen, 2000; Koleff & Gaston, 2001, Diniz-Filho *et al.*, 2002). The existence of the MDE can be assessed through randomisation simulations, placing empirical species ranges at random within a defined geographical domain and comparing the species richness patterns shown by this null model with those shown by the empirical data, which is the approach followed here. Few MDE studies to date have focused on flowering plants (but see Grytnes & Vetaas, 2002; Bachman *et al.*, 2004) and curiously only two MDE studies have been conducted into species richness patterns on tropical islands (Lees *et al.*, 1999; Bachman *et al.*, 2004). Following the pioneering work of MacArthur & Wilson (1967), much of the recent research into island biogeography has been centred on Hawaii (Myers, 1991; Cowie, 1995; Pax *et al.*, 1997), the Galapagos Islands (Wight & Simovich, 1985; Peck & Kukalovapeck, 1990; Yeakley & Weishampel, 2000) and the Canary Islands (Francisco-Ortega *et al.*, 1996; Kim *et al.*, 1996; Emerson *et al.*, 2000), with comparatively little interest being shown in the Mascarene and Gulf of Guinea Islands until quite recently.

In this paper, we investigate patterns of orchid species richness on two such archipelagos associated with the African continent, those of the Mascarene Islands and the Gulf of Guinea Islands, using the elevational gradient from sea level to the tops of these islands. We assess patterns of endemism across these archipelagos, investigate possible causes for the observed patterns of species richness with elevation, and suggest a possible scenario for the development of the Mascarene Islands orchid flora.

2 Methods

2.1 Study location

The Mascarene Islands, situated in the western Indian Ocean, are of volcanic origin and have never been connected to one another, or to any other landmass. The three main islands are Mauritius, La Réunion and Rodrigues, with La Réunion (55°30'E, 21°05'S) 150 km south-west of Mauritius (57°30'E, 20°20'S), Rodrigues (63°30'E, 19°40'S) 574 km east of Mauritius and Mauritius itself some 900 km east of its nearest landmass, Madagascar. La Réunion is the largest island in the region at 2,512 km^2, as well as the highest, rising to 3,069 m (Table 1) (Strahm, 1996a).

TABLE 1. Age and elevation of the Mascarene Islands.

Island	Elevation (m)	Age (myo)
La Réunion	3069	2.1
Mauritius	828	7.8
Rodrigues	393	?>7.8

2.2 Data

A preliminary enumeration of the Mascarene Islands' orchid flora, along with the collation of altitudinal data for 203 species from La Réunion, was compiled based on herbarium material (BM, CGE, E, G, K, MAU, P and REU), complemented with an extensive review of relevant literature and 16 months field study within the region from 1998 to 2000 (Roberts, 2001). This enumeration was then augmented with distributions outside of the Mascarene Islands for the non-endemic species, largely taken from Du Puy *et al.* (1999).

Following enumeration of the orchid flora, the percentage endemism at the species level was calculated for each of the three islands, and the Mascarene Islands as a whole, along with endemism for the broader regions of Madagascar and the Mascarene Islands together and the Mascarene Islands with the Indian Ocean as a whole. Then, for La Réunion, the number of species occurring at every 100 m altitude was determined for each of the following floristic components: (a) species endemic to La Réunion, (b) species shared only with Madagascar, (c) species shared with Mauritius and (d) total orchid flora (sum of a, b and c).

2.3 Analytical methods

An MDE null distribution was calculated for each floral component of La Réunion using the RangeModel software (Colwell, 2000). We used Model 4, which selects (with replacement) ranges from the empirical range-size frequency distribution (RSFD) and randomly places them in the domain (the elevation gradient). Model 5, which uses empirical midpoints and random range-sizes, was not used because the null model is too closely constrained by the empirical data (Koleff & Gaston, 2001). The purely theoretical Models 1–3 were also not used because of the implicit biological assumptions they make regarding RSFD's. The model was iterated 1000 times for each floristic component and the mean value for each altitudinal band taken as the null distribution; to account for possible artefacts in the null distribution from using too few or too many bins, bin sizes (≈ number of altitudinal bands) of 10, 15, 30 and 60 were used for each floristic component. The strength of the relationship between the observed species richness *versus* the richness values from the MDE null distribution was tested using a simple linear regression, on the assumption that the closer the slope (as shown by the r^2 value) is to the maximum value of 1, the more closely the MDE null model estimates the number of observed taxa along that elevational gradient (Bachman *et al.*, 2004).

2.4 Preliminary study into the Gulf of Guinea Islands

As a comparison, this same protocol for studying MDE patterns was then applied to similar data on the orchid floras of the Gulf of Guinea islands São Tomé and Príncipe (Table 2), from the enumeration of on Stévart and de Oliveira (2000), using the floral components (a) endemic, (b) non-endemic and (c) total.

TABLE 2. Age and elevation of the Gulf of Guinea islands.

Island	Elevation (m)	Age (myo)
Bioko	3308	Unknown (Dan Barfod, pers. com.)
Príncipe	935	31.0
São Tomé	2024	13.0
Annobon	654	4.8

3 Results

3.1 Levels of endemism

The Mascarene Islands orchid flora contains 219 species, with 68.0% endemic to the whole region (Table 3). Levels of endemism within the region vary, the lowest being found in Mauritius with 11.0%, followed by 14.3% for Rodrigues and up to 48.8% for La Réunion. 87.2% of species are endemic to the greater Madagascar – Mascarene region, and only 5.9% are also found outside the Western Indian Ocean as a whole.

TABLE 3. Distribution of endemism in the Mascarene Islands orchid flora.

Islands	No. Species	No. Endemics	Endemism (%)
Mauritius	100	11	11.0
La Réunion	203	99	48.8
Rodrigues	7	1	14.3
Mascarene Islands	219	149	68.0
Madagascar – Mascarene Is.	219	191	87.2
Indian Ocean – Mascarene Is.	219	206	94.1

The orchid flora of the Gulf of Guinea islands is almost as rich as that of the Mascarene Islands with 207 species; however only 26.1% are endemic to the archipelago (Table 4). Levels of endemism within the region are also lower than those seen in the Mascarene Islands, ranging from a low on Príncipe of only 10.9% to a high of 20.0% for São Tomé.

TABLE 4. Distribution of endemism in the Gulf of Guinea orchid flora.

Islands	Species	Endemics	%age Endemism
Annobon	22	3	13.6
São Tomé	100	20	20.0
Príncipe	64	7	10.9
Bioko	119	18	15.1
Annobon – Príncipe	133	35	26.3
Annobon – Bioko	207	54	26.1

3.2 Species richness gradients

Fig. 1 shows numbers of species of orchids across the elevational gradient of La Réunion, with the orchid flora divided into three floral components (endemics; those shared with Mauritius; those shared with Madagascar; and the total orchid flora). Although the greatest number of species are found at 1000 m, there is a clear variation in altitudinal distribution of the La Réunion orchid flora. The Mauritian component peaks in species richness at a lower altitudinal level (600 m) than the Malagasy component, and then tails off towards the maximum elevation; the Malagasy component peaks at 1000 m, in common with the total orchid flora; while the endemics peak much higher than the Mauritian component at 1200 m.

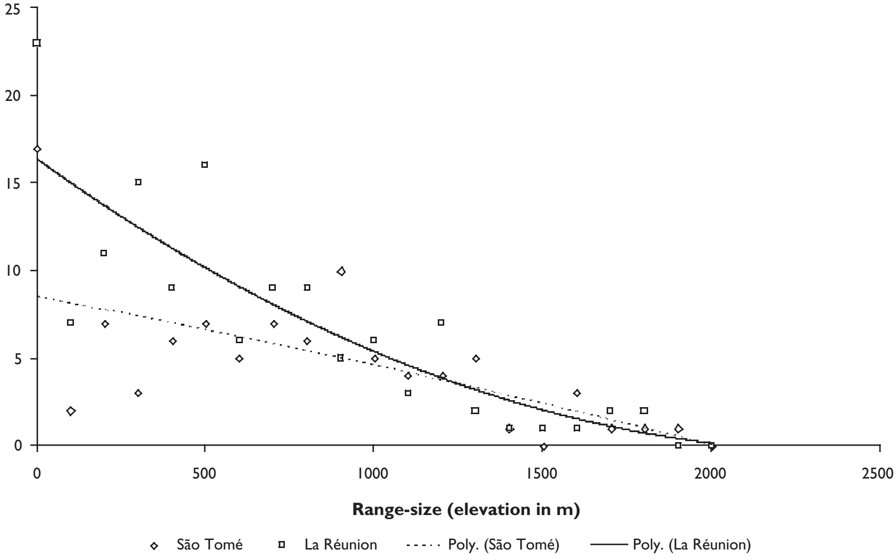

FIG. 1. Altitudinal distribution of the orchid flora of La Réunion.

3.3 MDE studies

The r^2 values given in Table 5 show the relationship between the observed orchid species richness along the altitudinal gradient of La Réunion and the MDE null model predictions. The MDE was found to explain only a quarter of the variance in the total observed richness patterns ($r^2 = 0.25 – 0.29$). The amount that the MDE explained in the various floral components varied from only one-twentieth of the variance in the Mauritian component ($r^2 = 0.05 – 0.06$) to around two-thirds for the endemic component ($r^2 = 0.61 – 0.64$).

r^2 values for the relationship between orchid species richness and the MDE null model along the altitudinal gradient of the Gulf of Guinea islands are shown in Table 6 and 7. MDE was found to explain around two-thirds of the variance in the total observed richness patterns for São Tomé ($r^2 = 0.60 – 0.65$) and Príncipe ($r^2 = 0.58 – 0.76$). The amount that the MDE explained in the various floral components varied little for both islands compared with that shown for La Réunion. No pattern consistent with varying bin size could be found for São Tomé, whereas the r^2 value of the total floral component of Príncipe was greatest, and that of the endemics the lowest.

4 Discussion

4.1 Data quality, area effects and interpolation

There are several potential drawbacks to this study:

Firstly, due to considerable habitat destruction and subsequent degradation of the Mascarene Islands (Strahm, 1989, 1996b), we will never know the total natural Holocene orchid flora of the archipelago. The vegetation of Rodrigues was totally destroyed before the first scientific survey was conducted in 1874 and much of the coastal and lowland vegetation of the other islands has been seriously degraded (Strahm, 1989). This may have had a marked impact on orchid diversity at lower altitudes where much habitat destruction occurs. A similar situation has occurred in the Gulf of Guinea islands; however, our poor understanding of the original floras of São Tomé and Príncipe is further exacerbated by our current lack of knowledge of the floras of the other islands, Annobon and Bioko.

Secondly, the use of herbarium specimen records may provide spurious results. For example, pre-twentieth century herbarium records, important for estimating species elevational ranges before extensive habitat clearance had taken place, are less likely to have accurate elevation records due to imprecision of maps and inadequate measuring equipment (Bachman *et al.*, 2004). This study, however, uses the best available data and is built directly on current taxonomic expertise, and much of the data for the La Réunion analysis are derived directly from individual herbarium records and for the Gulf of Guinea islands on the recent taxonomic account of Stévart and de Oliveira (2000).

Thirdly, this study has not accounted for the effects of different amounts of available land-area at different elevational bands. The relationship between area and number of species is well known with species richness increasing as the area increases, following the power-law model of Arrhenius (1921). Since in small oceanic islands the area of lowland greatly exceeds the area of highland, species richness might be expected to decline with elevation simply because the amount of available land-area does so, irrespective of any effects of altitude *per se*. Accounting for this variation in land-area with elevation can effect the patterns of observed richness along an elevational gradient (Rahbek, 1997; Sanders, 2002; Bachman *et al.*, 2004).

TABLE 5. Results of simple linear regression between observed species richness patterns and MDE null model predictions for La Réunion.

No. of bins	**Endemics**	**Malagasy**	**Mauritius**	**Total**
(Size of alt. band)	**r^2 values**			
60 (50 m)	0.61	0.32	0.05	0.25
30 (100 m)	0.63	0.32	0.06	0.28
15 (200 m)	0.63	0.35	0.05	0.27
10 (300 m)	0.64	0.38	0.06	0.29
Alt. max. of origin	3069 m	2876 m	828 m	3069 m

TABLE 6. Results of simple linear regression between observed species richness patterns and MDE null model predictions for São Tomé.

No. of bins	**Endemics**	**Non-endemics**	**Total**
(Size of alt. band)	**r^2 values**		
60 (33.7 m)	0.45	0.57	0.64
30 (67.5 m)	0.57	0.57	0.65
15 (135 m)	0.70	0.54	0.63
10 (202.4 m)	0.68	0.51	0.60

TABLE 7. Results of simple linear regression between observed species richness patterns and MDE null model predictions for Príncipe.

No. of bins	**Endemics**	**Non-endemics**	**Total**
(Size of alt. band)	**r^2 values**		
60 (15.6 m)	0.47	0.57	0.58
30 (31.2 m)	0.48	0.59	0.60
15 (62.3 m)	0.52	0.56	0.58
10 (93.5 m)	0.73	0.74	0.76

Fourthly, observations of the occurrence of a species are made in space and time. The problem is to use these observations to estimate the boundary of the range of the species. Of course, even when interest focuses on the one-dimensional range of a species, the observations themselves will be made in two dimensions. These two-dimensional locations are then converted into one-dimensional observations by retaining only their projections along the orientation of interest (e.g. elevation). The true boundary of a one-dimensional range is typically estimated by the pair of most extreme locations at which the species is observed. For example, when interest centres on altitudinal range, the upper boundary is estimated as the highest altitudinal location at which the species is observed and the lowest boundary is estimated as the lowest altitudinal location at which the species is observed. In reality these are rarely the extremes of the range, it is just where that taxon has been observed. As a result this can give rise to unimodal peaks in species richness along gradients since the range of a taxon may be poorly known at its geographical extremes. It has been suggested that this interpolation results in an overestimation of species richness towards the centre of the gradient (Grytnes & Vetaas, 2001). However, this interpolation is merely a pragmatic solution to an intractable analytical problem (Bachman *et al.*, 2004) typical of most studies of species richness along environmental gradients.

4.2 The mid-domain effect in the Mascarene and Gulf of Guinea island orchid floras

Currently, there is still great scepticism surrounding the importance of the mid-domain effect. So far only a handful of vascular plant studies have considered the MDE and even fewer have been based on taxa from tropical islands. However, results now suggest the existance of the MDE across a wide range of taxa and areas (Colwell & Hurtt, 1994; Lyons & Willig, 1997; Pineda & Caswell, 1998; Willig & Lyons, 1998; Colwell & Lees, 2000; Jetz & Rahbek, 2001; Grytnes & Vetaas, 2002; Sanders, 2002; Bachman *et al.*, 2004). The relationship between orchid richness and MDE along an altitudinal gradient for the various floral components of La Réunion shows an interesting pattern (Table 5). The MDE was found to explain the greatest variance in the endemics ($r^2 = 0.61 – 0.64$). This is not surprising since they have evolved within the geometric constraints imposed by the elevation of the island. The next highest was the Malagasy component ($r^2 = 0.32 – 0.38$); this may be because Madagascar rises to 2876 m, compared with La Réunion which rises to 3069 m. The Mauritian component on La Réunion had the weakest relationship with the MDE null model predictions ($r^2 = 0.05 – 0.06$) since Mauritius rises to only 828 m. This suggests that geometric constraints influence variation in species richness across the elevational gradient, and might effect speciation, future colonisation and range expansion as outlined in the scenario given below for the Mascarene Islands.

In contrast no such pattern could be seen in the results of the Gulf of Guinea Islands. This is likely to be due to their close proximity to the African mainland, leading to multiple colonisation events extending into recent times, and therefore a confused pattern with no clear picture emerging. The effect of proximity to major landmasses can be seen in the endemism data for the region; Annobon – Príncipe contains 26.3% endemism where as Annobon – Bioko has 26.1%. This lack of difference is even more pronounced if you consider that Bioko may have been connected to the mainland during to the last glacial period. In contrast, the levels of endemism found in the Mascarene Islands suggest that there is little movement outside the region but considerable movement within, since 68.0% of the region's, orchid flora is endemic.

The observed differences between the results for the Mascarene Islands and the Gulf of Guinea islands are not simply due to differences in the underlying range-size frequency distributions between the two archipelagos. If a flora was to be made up of numerous species with narrow ranges with few wide ranging species this should produce a smaller mid-domain effect, since these narrow-ranged species could be found anywhere within the domain, and species richness would thus be more even. Floras with a greater proportion of large-ranged species should show a greater mid-domain effect, since large-ranged species are more likely to be constrained to the middle of the domain. However, when comparing the range-size frequency distributions of La Réunion and São Tomé we find the opposite pattern (Fig. 2): La Réunion has a greater proportion of narrow-ranged species, yet still has a stronger mid-domain effect than does São Tomé.

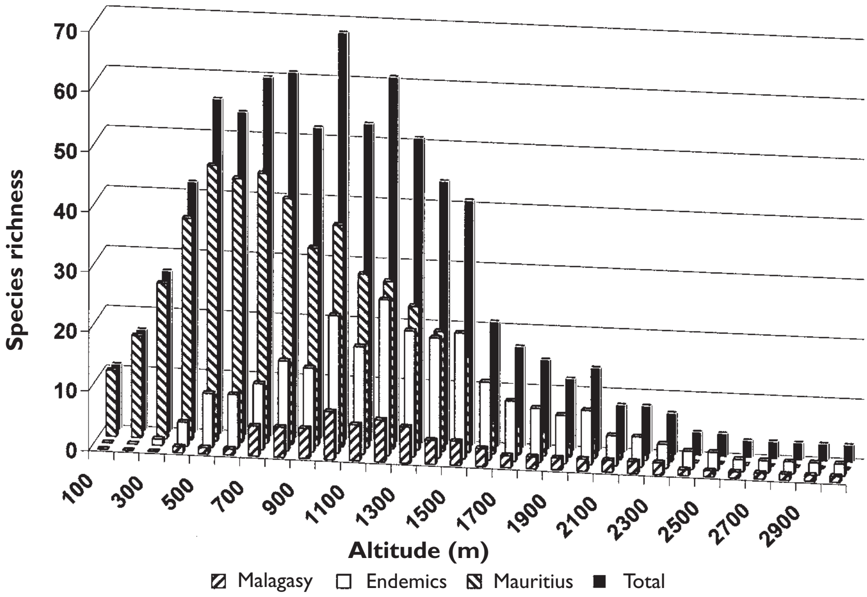

FIG. 2. Range size frequency distribution of the orchid floras of La Réunion and São Tomé.

4.3 Origin of the orchid flora of the Mascarene Islands

The following scenario, consistent with the differing ages and elevational profiles of the different islands, and thus the geometric constraints, of each island, is proposed for the genesis of the Mascarene archipelago's orchid flora:

1. After the formation of Mauritius approximately 7.8 my ago orchids of several different lineages from Madagascar colonised the island, followed by speciation.
2. Endemism would have been much higher on Mauritius at that time, as would be expected from such an isolated oceanic island orchid flora soon after successful colonisation and radiation.
3. La Réunion, formed 2.1 my ago, was rapidly colonised from Mauritius, thus reducing the level of endemism on Mauritius.
4. This rapid colonisation from Mauritius occurred mainly at low altitudinal levels on La Réunion, reflecting the geometric constraints imposed by the island on which the orchids had evolved.
5. Speciation on La Réunion of the acquired Mauritian orchids, along with colonisation of additional species from Madagascar, occurred. With the greater altitudinal range of La Réunion, newly-evolved species expanded their ranges into higher elevational bands than could the existing Mauritian component.
6. Few, if any, species could spread back to Mauritius from La Réunion due to the lack of high altitude sites and the presence of a well established orchid flora, and thus the Mauritian component in the orchid flora of La Réunion remains small.

The volcanic archipelagos of the African continent seem to have been largely forgotten but offer an excellent opportunity to study patterns of species richness. Although there is still great scepticism surrounding the existence of the mid-domain effect, it offers an exciting new area of research in the study of such patterns. Together with species-area relationships, the mid-domain effect can have a profound effect on species richness along a gradient, and should be considered in all studies of environmental determinants of species richness. Here we suggest, for the first time, that the study of the mid-domain effect can also help explain evolutionary patterns, through the effect of past geometric constraints on evolutionary processes.

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FLORE ET VÉGÉTATION DE L'INSELBERG MILOBO (MONTS DE CRISTAL, GABON)

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Abstract

This work analyzes the floristic composition of an inselberg surrounded by rainforest in the NW area of the Monts de Cristal in Gabon. This study lists the main plant formations and the characteristic species of the cline from the rock pavement to the distant rainforest. This work shows the importance of Caesalpiniaceae in the process of colonisation of this habitat.

Résumé

Le présent travail analyse la composition floristique d'un inselberg entouré par la forêt dense dans la région nord-ouest des Monts de Cristal au Gabon. Cette étude met en évidence les principales formations végétales et les espèces caractéristiques qui les composent, de l'ourlet arbustif, sur la dalle rocheuse, jusqu'à la forêt dense éloignée. Elle montre l'importance des Caesalpiniaceae dans le processus de colonisation de cet habitat.

Key words: Gabon, Monts de Cristal, Milobo, inselberg

1 Introduction

Les inselbergs sont des montagnes ou de groupes de montagnes isolées, souvent monolithiques, qui s'élèvent abruptement sur des plaines adjacentes dans les régions humides et semi-arides (Barthlott *et al.,* 1993). Pris au sens large, ils désignent des affleurements de roches d'origine granitique ou gneissique précambrienne, souvent en forme de dômes, s'élevant au-dessus des plaines. Certains ne sont pas boisés, d'autres portent à leur sommet une végétation arborescente basse ou arbustive. Les dômes rocheux posent, en effet, le problème de leur peuplement, que l'on peut imaginer soit dû à des transports, soit constituant des reliques d'une flore sèche ancienne continue. Il est, cependant, possible que les deux facteurs aient pu intervenir dans ce processus. L'originalité des inselbergs au Gabon tient au fait qu'ils sont éloignés de la savane et généralement entourés par la forêt dense. Ils présentent une flore et une végétation particulières, caractérisées par la présence de prairies naturelles et des lisières forestières à xérophiles et orophytes surtout dans la région de Minkébé au nord est du Gabon (Ngok Banak, 2003). L'existence de ces formations végétales et de cette flore particulière est interprétée par Reitsma *et al.* (1992), comme des vestiges de flores anciennes maintenues grâce aux conditions édaphiques.

Des études antérieures, sur la végétation des inselbergs et des dalles rocheuses, ont été menées dans plusieurs pays africains: Guinée (Schnell, 1952); Côte d'Ivoire (Adjanohoun, 1964; Bonardi, 1966; Guillaumet, 1967); Nigeria (Richards, 1957; Hambler, 1964); République centrafricaine (Sillans, 1951; 1952a); Cameroun (Mildbraed, 1922; Letouzey, 1968, 1985; Villiers, 1981); Guinée Équatoriale (Lejoly & Lisowski, 1999; Parmentier *et al.*, 2001); Gabon (Reitsma *et al.*, 1992). Cependant une majorité de ces travaux traitent principalement des pelouses et des prairies. Les études prenant en compte la végétation adjacente aux inselbergs sont très peu nombreuses. En Guyane française, de Granville (1979) a étudié un inselberg cerné par la forêt. Au Gabon, aucune étude intégrant la forêt environnante n'a été réalisée. L'objectif du présent travail est d'étudier la flore et la végétation de l'inselberg Milobo depuis la forêt dense jusqu'à la lisière.

2 Milieu d'étude

L'étude a été menée de juin à décembre 2001 au Gabon (Fig. 1), dans la région des Monts de Cristal qui appartient à la variante ouest du centre d'endémisme guinéo-congolais de White (1983). La flore gabonaise est estimée à plus de 7000 espèces avec plus de 22% d'endémiques (Brenan, 1978). Situé en pleine forêt dense, l'inselberg Milobo, cadre de notre étude, est localisé sur les coordonnées 00°55'N et 10°31'E, à proximité de la frontière avec la Guinée Équatoriale. Il est situé à 10 km au sud-ouest du village Mbé Akélayong et culmine à 850 m d'altitude. Il présente un dénivelé de 350 m environ caractérisé par la présence d'une plate-forme rocheuse longue de 300 m et d'une forêt au sommet. La zone présente des précipitations annuelles de plus de 3200 mm et une température moyenne annuelle de 26°C (Edicef, 1983).

3 Méthodes

Quatre transects de 1,5 km de long ont été réalisés en prenant pour point de départ la plate-forme rocheuse. Les parcelles ont été installées suivant les transects en tenant compte de l'homogénéité floristique et écologique. Les orientations des transects sont données par la boussole au départ des lisières respectives. Le long de ces transects, sur des zones homogènes, 5 parcelles ont été installées: 0,1 ha pour la lisière; 0,2 ha pour les parcelles situées entre la lisière et la forêt dense; 1 parcelle de 1 ha dans la forêt dense avec 4 sous-parcelles de 100 m^2 chacune; deux-sous parcelles de 25 m^2 sur la dalle rocheuse. Les inventaires ont été réalisés dans les parcelles A, B, C, D et E, de la lisière à la forêt dense. Les arbres de dbh ≥ 30 cm, pour la strate arborescente haute, et ceux compris entre 10 ≤ dbh < 30 cm pour la strate arborescente moyenne ont été recensé. La strate herbacée inventoriée désigne l'ensemble des végétaux herbacés, de jeunes plants et des recrûs ligneux. Les caractéristiques de chacune des parcelles sont reprises dans le tableau 1. Les déterminations ont été faites principalement sur base des flores existantes. Les espèces déterminées ont été vérifiées par comparaison avec les échantillons de l'herbier national du Gabon (LBV), de Belgique (BR) et de Wageningen (WAG). La nomenclature botanique adoptée est celle de Lebrun & Stork (1991, 1992, 1995, 1997).

Les matrices de relevés pour chaque strate ont été traitées séparément en fonction de la présence-absence des espèces, par le logiciel Canoco (ter Braak & Smilauer, 1998) pour obtenir des plans factoriels issus des *Detrended Correspondence Analysis* (DCA). Le tableau synthétique est obtenu à partir des groupes isolés de la DCA, en considérant les espèces dont la présence (fréquence d'une espèce exprimée en pourcentage par rapport au nombre total de relevés d'un groupe considéré) est inférieure à deux. Les classes de présence utilisées sont celles définies par Braun-Blanquet (1932).

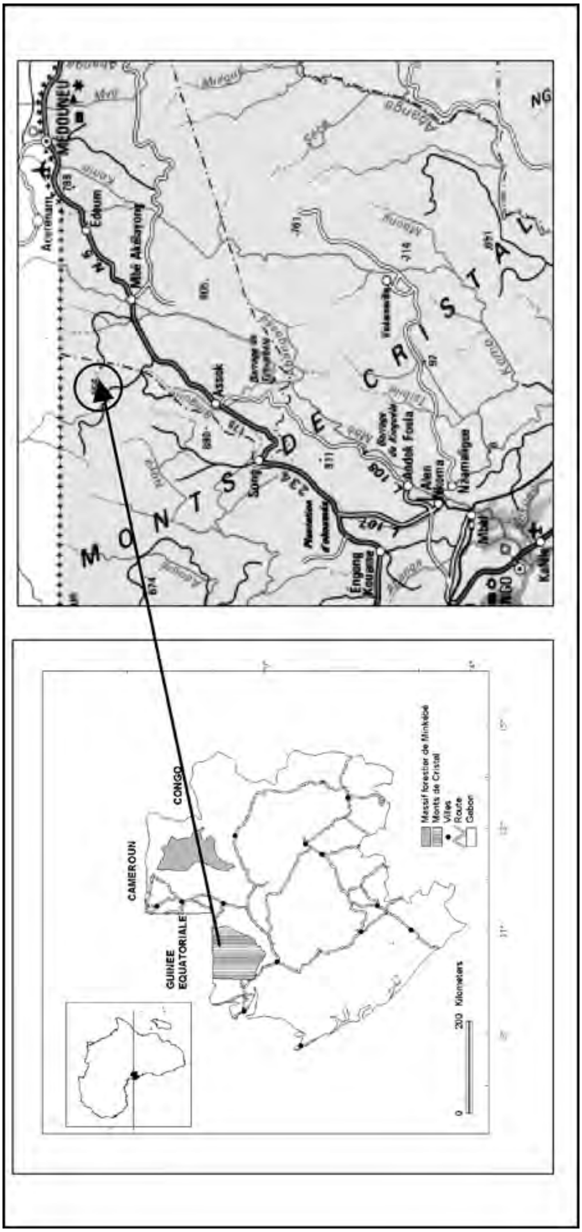

FIG. 1. Localisation du site d'étude

TABLEAU 1. Caractéristiques principales des parcelles étudiées.

Parcelles	**A_{NW}, A_{SE}, A_{SW}, A_{NE}**	**B_{NW}, B_{SE*}, B_{SW}, B_{NE},**	**C_{NW}, C_{SE}, C_{SW}, C_{NE},**	**D_{NW}, D_{ES}, D_{SW}, D_{NE},**	**E_{NW}, E_{SE}, E_{SW}, E_{NE},**
Surface (ha)	0,1	0,2	0,2	0,2	1
Longueur × largeur (m)	100 × 10	100 × 20	100 × 20	100 × 20	200 × 50
Limites de prélèvement	10cm ≤ dbh >30cm et dbh ≥ 30cm	10cm ≤ dbh >30cm et dbh ≥ 30cm	10cm ≥ dbh >30cm et dbh ≥ 30cm	10cm ≤ dbh >30cm et dbh ≥ 30cm	10cm ≤ dbh >30cm et dbh ≥ 30cm
Distance à la roche (m)	~1	~25	~100	~300	~1000
Profondeur du sol	< 5 cm	≤ 10 cm	< 20 cm	> 1m	> 1m
Type de formation végétale	Lisière	Forêt saxicole	Forêt intermédiaire	Forêt dense de bas de pente	Forêt dense

NW: nord ouest; NE: nord est; SE: sud est; SW: sud ouest; *: forêt sommitale

4 Résultats

4.1 Physionomie et structure

Le profil schématique des formations végétales étudiées est repris sur la Fig. 2:

- **La zone A:** elle correspond au manteau arbustif, localisée autour de la plate-forme rocheuse à une altitude moyenne de 750 m. Ses dimensions varient selon les versants, pouvant atteindre 125 m de long pour 5 à 10 m de large. Cette zone est caractérisée par son exposition aux fortes variations journalières de températures et par une faible profondeur du sol 1 cm en moyenne. Il s'agit du point, de vue structurale, d'une zone située en aval de l'ourlet arbustif et en amont de la forêt saxicole;
- **La zone B:** elle correspond à la forêt saxicole, il s'agit d'une formation sur colluvions, à sous-bois clair, localisée après la lisière. Elle se situe à une altitude moyenne de 710 m avec une pente de plus de 20% et une superficie variable selon les versants. La profondeur du sol varie entre 5 et 10 cm;
- **La zone C**: elle correspond à une formation intermédiaire entre la forêt saxicole et la forêt dense de bas d'inselberg. Elle se situe à une altitude moyenne de 675 m pour une pente très variable de 15 à 25% et une superficie pouvant atteindre 0,3 ha. L'enracinement y est beaucoup plus favorable et la profondeur du sol varie entre 10 et 20 cm;
- **La zone D**: elle correspond à la première formation forestière de bas d'inselberg. Elle se situe à une altitude moyenne de 600 m avec une profondeur du sol supérieure à 1 m. Cette formation est assez drainée car elle reçoit toutes les eaux ruisselantes issues des différents versants. Elle est aussi instable en raison des blocs de granites qui se détachent du sommet, ce qui explique la présence de trouées;
- **La zone E**: elle correspond à une formation témoin: la forêt dense la plus éloignée de la lisière. Elle est caractérisée par son éloignement de la lisière, entre 800 et 1100 m. L'altitude moyenne est de 630 m pour une pente moyenne de 15%;
- **La zone O:** elle correspond à un ourlet arbustif, il s'agit de la formation la plus exposée au climat externe (chaleur et lumières fortes) son altitude moyenne est de 760 m et sa pente atteint 50; aucune parcelle n'a été installée, par contre deux relevés ont été réalisés;

- **La zone B*:** elle correspond à la forêt sommitale localisée à 850 m d'altitude sur une pente moyenne inférieure à 3% pour une superficie de 0,2 ha. Le sol est constitué de débris végétaux (feuilles et bois morts) formant une couche meuble de 5 à 10 cm d'épaisseur, et où les racines se développent dans les anfractuosités de la roche.

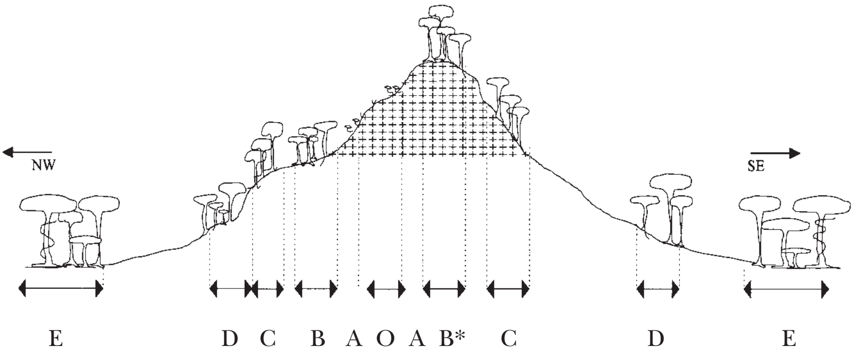

FIG. 2. Profil schématique des formations végétales étudiées.

Flore totale

Le nombre total d'espèces inventoriées est de 433, réparties entre 76 familles et 262 genres. La distribution taxonomique globale, indiquée sur le tableau 2 fait apparaître une proportion importante d'espèces ligneuses soit 367. Les herbacées et les ptéridophytes, avec respectivement 60 et 6 espèces, sont faiblement représentées. Les principales familles inventoriées sont reprises sur le tableau 3. Dans le groupe des ligneux, les Caesalpiniaceae avec 52 espèces et 29 genres sont les mieux représentées, suivies des Euphorbiaceae avec 41 espèces pour 25 genres. Pour les herbacées les Marantaceae constituent la famille la plus représentées avec 8 espèces et 8 genres, suivie des Cyperaceae avec 7 espèces pour 6 genres.

La répartition par strate fait apparaître pour la strate de dbh > 30 cm, 170 espèces reparties en 37 familles dont les plus importantes sont les Caesalpiniaceae (37), les Euphorbiaceae (15) et les Burseraceae (11). La strate d'arbres compris entre 10 et 30 cm de dbh est composée de 259 espèces et 41 familles dont les plus mieux représentées sont les Caesalpiniaceae (45), les Euphorbiaceae (29) et les Sterculiaceae (15). La strate sous- arbustive et herbacée est constituée de 272 espèces reparties en 70 familles parmis lesquelles Caesalpiniaceae (32), Euphorbiaceae (22) et Rubiaceae (15).

4.2 Végétation

Quatre-vingt relevés ont été réalisés, 40 pour les strates arborescentes et 40 pour la strate sous-arbustive et herbacée. Les matrices de relevés pour chacune des strates ont été soumises à la DCA pour obtenir des cartes factorielles, reprises sur les Figs. 3, 4 et 5.

La DCA (Fig. 3) appliquée aux 20 relevés de la strate des arbres de DBH ≥ 30 cm, a permis de dégager deux groupes (G1 et G2) dont la discrimination reflète les différentes formations végétales étudiées. La distribution sur l'axe 1 des deux groupes traduit un gradient roche-forêt qui est aussi un gradient de luminosité. Le premier groupe est constitué de 8 relevés, 48 espèces et 20 familles dont les plus

TABLEAU 2. Distribution taxonomique globale.

	Ligneux	**Herbacées**	**Total**
Dicotylédones			
Familles	51	13	64
Genres	210	18	228
Espèces	365	24	389
Monocotylédones			
Familles	2	10	12
Genres	2	30	32
Espèces	2	36	38
Ptéridophytes			
Familles		4	4
Genres		4	4
Espèces		6	6
Nombre total d'espèces	367	66	433

TABLEAU 3. Principales familles inventoriées.

Familles	**Nombre d'espèces**	**Nombre de genres**
Ligneux		
Caesalpiniaceae	52	29
Euphorbiaceae	41	25
Rubiaceae	23	18
Mimosaceae	17	11
Sterculiaceae	17	7
Anacardiaceae	15	4
Meliaceae	15	5
Annonaceae	14	10
Flacourtiaceae	14	4
Burseraceae	13	4
Olacaceae	13	13
Clusiaceae	12	5
Ebenaceae	11	1
Melastomataceae	10	4
Herbacées		
Marantaceae	8	8
Cyperaceae	7	6
Commelinaceae	5	4
Zingiberaceae	4	2

importantes sont les Caesalpiniaceae (9), les Burseraceae (8) et les Moraceae (5). L'espèce *Julbernardia letouzeyi* est la plus fréquente à la lisière où elle forme un cordon monotone expliquant de ce fait l'isolement sur la Fig. 3 des relevés 11 et 1 composés essentiellement de cette espèce. Les relevés restant sont en partie issus de la forêt saxicole dominée par *Gilbertiodendron mayombense*. Le deuxième groupe comprend 12 relevés réalisés dans la forêt dense de bas de pente. Il est composé de 165 espèces et 36 familles, dont les plus importantes sont les Caesalpiniaceae (35), les Euphorbiaceae (14) et les Burseraceae (11). Les espèces les plus fréquentes sont: *Aucoumea klaineana*, *Santiria trimera*, *Anthonotha pynaertii*, *Pentaclethra macrophylla*, *Dacryodes klaineana*.

La DCA (Fig. 4) appliquée aux 20 relevés issus de la strate des arbres de 10 dbh < 30 cm a permis d'isoler 2 groupes (G3 et G4) en individualisant le relevé 12 réalisé dans la forêt sommitale. L'isolement de ce relevé permet d'expliquer la discrimination observée sur l'axe 2 où sont repartis les deux groupes. Cet axe 2 traduit un gradient altitudinal et l'axe 1 le gradient lisière-forêt. Le groupe 3 est composé de 3 relevés issus de la lisière comprenant 20 espèces et 13 familles parmi lesquelles: Caesalpiniaceae (3), Annonaceae (2) et Euphorbiaceae (2). Les espèces les plus fréquentes sont : *Julbernardia letouzeyi*, *Cavacoa quintasii*, *Uvariopsis* sp., *Ficus camerounensis*, *Sterculia tragacantha*. Le groupe 4 est composé de 16 relevés issus de la forêt saxicole et de la forêt dense. Il est constitué de 244 espèces et 41 familles dont les plus représentées sont: Caesalpiniaceae (43), Euphorbiaceae (29) et Sterculiaceae (15). Les espèces les plus fréquentes sont: *Polyalthia suaveolens* var. *gabonica*, *Microdesmis afrodecandra*, *Scytopetalum klaineanum*, *Barteria fistulosa*, *Dialium bipindense* et *Diospyros crassiflora*.

La DCA (Fig. 5) appliquée aux 40 relevés de la strate sous-arbustive et herbacé a permis d'isoler cinq groupes (G5, G6, G7, G8, G9). L'axe 1 par rapport à l'axe 2 peut être interprété comme un gradient d'humidité et de luminosité, des formations forestières vers des formations ouvertes. Le groupe 5 est constitué de 28 relevés, réalisés dans la forêt dense, de 220 espèces et 56 familles parmi lesquelles: Caesalpiniaceae (30), Euphorbiaceae (20) et Mimosaceae (13). Les espèces les plus fréquentes sont: *Podococcus barteri*, *Afrocalathea rhizantha*, *Brazzeia soyauxii*, *Leptonychia echinocarpa*, *Hypselodelphis violacea*. Le groupe 6 est constitué de 6 relevés réalisés en lisière, de 73 espèces et 39 familles parmis lesquelles: Acanthaceae (5), Caesalpiniaceae (5) et Euphorbiaceae (4). Les espèces les plus fréquentes sont: *Dissotis barteri*, *Phyllanthus odontadenius*, *Impatiens mackeyana*, *Asparagus drepanophyllus*, *Memecylon collinum*, *Brillantaisia debilis*, *Solenostemon mannii*. Le groupe 7 comprend 2 relevés, issus de l'ourlet arbustif, 20 espèces et 12 familles parmi lesquelles Rubiaceae (4), Aspleniaceae (3) et Cyperaceae (3). Les espèces les plus fréquentes sont: *Virectaria belingana*, *Hymenodictyon biafranum*, *Clappertonia polyandra*, *Otomeria micrantha*. Le groupe 8 est constitué de 2 relevés réalisés en lisière relativement sèche, 31 espèces et 20 familles dont: Rubiaceae (5), Acanthaceae (3) et Clusiaceae (3). Les espèces les plus fréquentes sont: *Vepris trifoliolata*, *Chlorophytum alismaefolium*, *Dracaena camerooniana*. Le groupe 9 est composé de deux relevés réalisés dans la forêt sommitale, 39 espèces et 27 familles dont les plus importantes sont : Euphorbiaceae (4), Caesalpiniaceae (3), Clusiaceae (3). Les espèces les plus fréquentes sont: *Cyperus diffusus*, de loin la plus abondante, *Garcinia gnetoides*, *Thecacoris annobonae*.

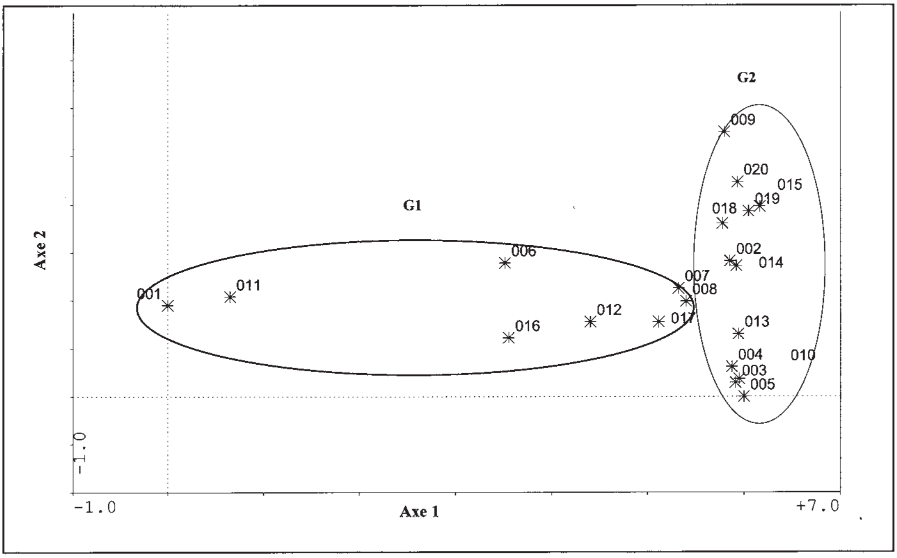

FIG. 3. Projection sur les axes 1 et 2 de la DCA appliquée aux 20 relevés de la strate (arbres de dbh > 30 cm).

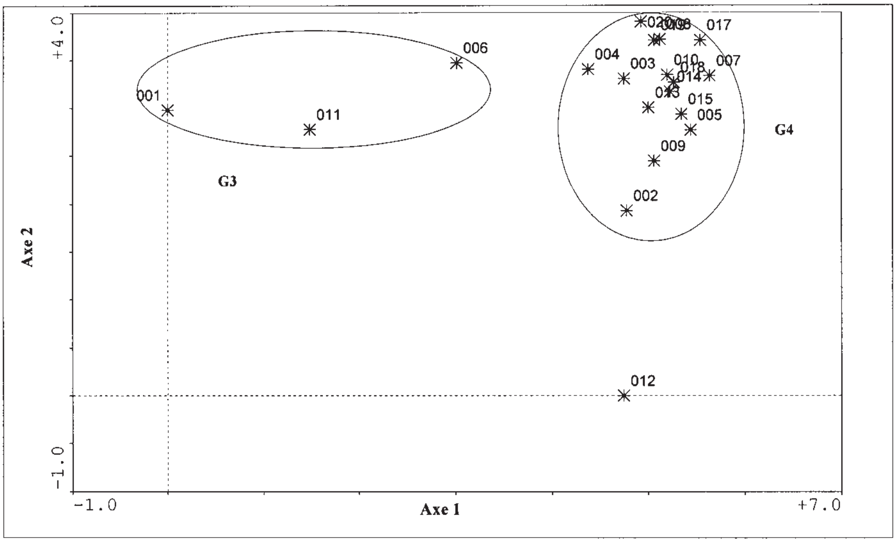

FIG. 4. Projection sur les axes 1et 2 de la DCA appliquée aux 20 relevés de la strate d'arbres de 10 ≥ dbh < 30 cm.

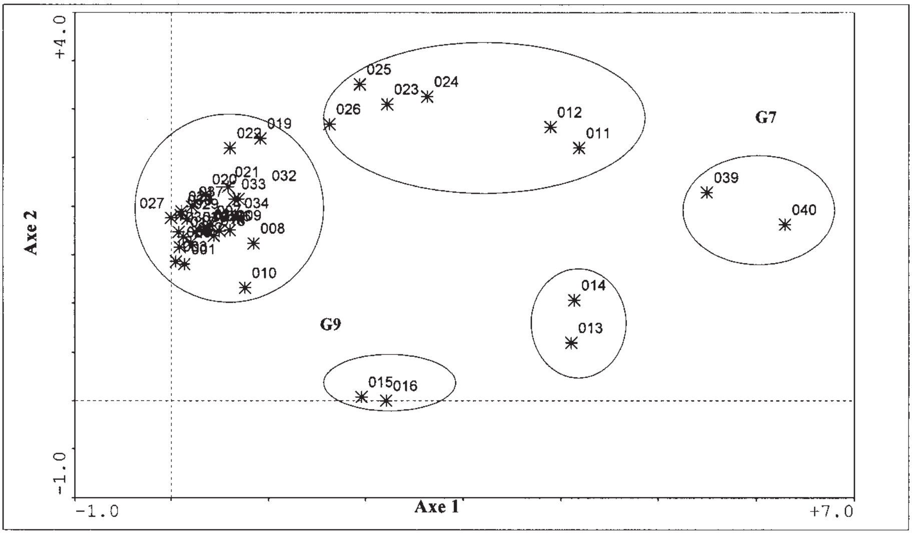

FIG. 5. Projection sur les axes 1 et 2 de la DCA appliquée aux 40 relevés de la strate sous-arbustive et herbacée.

5 Discussion

5.1 Flore

Les inventaires réalisés sur et autour de l'inselberg Milobo montrent clairement la prépondérance de la famille des Caesalpiniaceae. L'abondance de ce groupe taxonomique sur ce site est à mettre en relation avec la région dans laquelle se localise cet inselberg. En effet, la région des Monts de Cristal s'inscrit dans le domaine bas-guinéen atlantique comprenant le secteur nigéro-camerounais ou biafréen. Ce secteur, selon Letouzey (1968), est composé de forêts denses humides sempervirentes de basse et moyenne altitude, riches en Caesalpiniaceae. Wilks (1990) a confirmé l'importance de cette famille dans les Monts de Cristal. L'inselberg Milobo est une colline rocheuse qui, au regard de nos observations, nous semble en plein processus de récolonisation par la forêt dense environnante, expliquant de ce fait l'importante similitude floristique entre la forêt dense éloignée, la forêt de bas de pente et la forêt saxicole. Cependant la présence de ce groupe sur des zones dont la profondeur du sol est très faible pourrait être mise en relation avec la particularité de certaines tribus de Caesalpiniaceae, notamment les Macrolobieae (*Gilbertiodendron*, *Julbernardia*), qui seraient moins exigeantes (Wieringa, 1999). La faible représentation des monocotylédones particulièrement des Poaceae, des Cyperaceae et des Orchidaceae est très certainement liée à ce processus de reconquête de l'espace par la forêt dense mais aussi par l'isolement de cet inselberg dans la forêt.

5.2 Végétation

Selon Reitsma *et al.* (1992), la profondeur du sol offerte aux systèmes radiculaires des espèces joue le rôle de facteur limitant et détermine l'existence et la réparation des formations végétales. Les formations et les groupes isolés dans cette étude obéissent à cette exigence. Il ne s'agit pas de groupements au sens phytosociologique en raison de l'insuffisance de relevés effectués dans certaines formations. Cependant les groupes mis en évidence permettent de montrer la particularité d'un inselberg isolé dans la forêt dense.

Le tableau 4 présente les affinités entre les formations mises en évidence et les groupes isolés. La forêt dense regroupe la forêt éloignée de l'inselberg (zone E) et la forêt de bas de pente (zone D), localisée au pied de l'inselberg. Trois groupes isolés de la DCA appartiennent à cette formation, il s'agit des groupes G2, G4 et G5 clairement dominés par les Caesalpiniaceae. Ces groupes ont en commun une richesse spécifique élevée (plus de 150 espèces en moyenne) et une composition floristique voisine en raison des possibilités d'enracinement favorable. La forêt saxicole (zone B+C) est représentée par les groupes G1 et G6, caractérisés par une diminution de la richesse spécifique (moins de 80 espèces) liée à une diminution de la profondeur du sol. La compétition pour l'occupation de l'espace devenant importante, seules les espèces les mieux adaptées à ces types de conditions vont s'installer au détriment des espèces plus exigeantes. Selon Reitsma *et al.* (1992), la plupart des espèces qui dominent la forêt basse claire, qui correspond à la forêt saxicole, ne possèdent pas de dispositifs suffisamment efficaces pour permettre aux graines de parcourir de grandes distances. Ce qui concorde assez bien avec nos observations car les taxons les mieux représentés sont les Caesalpiniaceae et les Euphorbiaceae qui sont généralement (endo-) zoochores. La lisière (zone A) représentée par les groupes G1, G3 et G8, est caractérisée par une diminution significative de la richesse spécifique (moins de 50 espèces) fortement liée à l'épaisseur de la couche du sol. Elle met clairement en évidence la dominance dans les strates arborescentes de *Julbernardia letouzeyi*, Caesalpiniaceae signalée par Villiers (1981) sur la colline de Nkoltsia au Cameroun mais aussi par Reitsma *et al.* (1992) au Gabon. Cette espèce forme un peuplement le long de la lisière et se retrouve mono-dominante sur certains versants. La forêt sommitale (zone B*) est représentée par le groupe G9 dominé clairement par deux espèces *Cyperus diffusus* et *Pentadesma grandifolia*. Cette dernière est généralement signalée à des altitudes relativement élevées, ce qui explique probablement sa présence exclusivement au sommet de cet inselberg. L'ourlet arbustif (zone O) est représenté par le groupe G7 caractérisé par *Virectaria belingana*, *Hymenodictyon biafranum*, *Clappertonia polyandra*, espèces typiques de cette formation. Ces espèces ont été signalées dans cette formation dans la région de Piedra Nzas en Guinée Equatoriale par Parmentier *et al.* (2001).

La répartition des formations végétales sur l'inselberg Milobo isolé dans la forêt est liée à la profondeur du sol, à la topographie de l'inselberg mais aussi, probablement, aux types forestiers dominants de la région. La faible diversité observée dans les formations proches de la lisière est à mettre en relation avec d'une part, la richesse spécifique et, d'autre part, les conditions édaphiques particulières des inselbergs. En effet, dans les formations saxicoles proches de la lisière, l'épaisseur du sol réduit considérablement les potentialités d'enracinement, influençant de ce fait, la richesse spécifique. Par contre, la forte diversité observée dans les groupements forestiers n'est pas surprenante, surtout pour la région des Monts de Cristal dont l'importance en terme de biodiversité a été signalée par Wilks (1990).

TABLEAU 4. Affinités entre groupes isolés de la DCA.

Parcelles/ Zones	**Formations végétales et espèces caractéristiques**	**Arbres de dbh > 30 cm**	**Arbres de 10 < dbh > 30 cm**	**Strate sous arbustive et herbacée**
A	**Lisière**	**G1**	**G3**	**G8**
	Julbernardia letouzeyi	x	x	x
	Musanga cecropioides	x		
	Dissotis barteri		x	x
	Memecylon collinum			x
	Asparagus drepanophyllus			x
B+C	**Forêt saxicole**	**G1**		**G6**
	Gilbertiodendron mayombense	x	x	x
	Cavacoa quintasii		x	x
D+E	**Forêt dense**	**G2**	**G4**	**G5**
	Aucoumea klaineana	x		
	Barteria fistulosa		x	
	Brazzeia soyauxii			x
	Afrocalathea rhizantha			x
	Podococcus barteri			x
B*	**Forêt sommitale**		**R12**	**G9**
	Pentadesma grandifolia		x	x
	Cyperus diffusus			x
Rocher	**Ourlet arbustif**			**G7**
	Virectaria belingana			x
	Hymenodictyon biafranum			x
	Clappertonia polyandra			x
	Otomeria micrantha			x

6 Conclusion

L'étude de la diversité végétale de l'inselberg Milobo a permis de mettre en évidence 9 groupes végétaux dont la succession est fortement liée à la nature du substrat. Elle a, en outre, permis d'isoler cinq formations végétales à savoir: la forêt dense de bas d'inselberg, la forêt saxicole, la lisière, l'ourlet arbustif et la forêt sommitale. Par ailleurs, cette étude montre l'importance des Caesalpiniaceae aussi bien dans les formations forestières éloignées de la lisière que dans les formations saxicoles proches de celle-ci. La distribution taxonomique globale de l'inselberg Milobo rejoint celle observée dans la région des Monts de Cristal avec outre une forte présence des Caesalpiniaceae mais aussi une forte représentation des Rubiaceae et des Euphorbiaceae dans le sous-bois notamment. La profondeur du sol offerte aux systèmes radiculaires des espèces joue le rôle de facteur limitant et détermine donc l'existence et la réparation des formations végétales (Reitsma *et al.*, 1992). L'inexistence de pelouse sur l'inselberg Milobo pourrait justifier l'absence d'*Afrotrilepis pilosa*, Cyperaceae caractéristique des prairies sur inselberg et la faible représentation des taxons herbacés. Cependant, la poursuite des investigations sur les inselbergs forestiers de la région permettra de vérifier cette hypothèse.

7 Remerciements

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TABLEAU 5. Tableau synthétique.

Nombre de relevés	**8**	**12**	**3**	**16**	**28**	**6**	**2**	**2**	**2**
Nombre d'espèces	**48**	**165**	**20**	**244**	**220**	**73**	**20**	**31**	**39**
Groupes	**G1**	**G2**	**G3**	**G4**	**G5**	**G6**	**G7**	**G8**	**G9**
Julbernardia letouzeyi Villiers	III		V			III		V	
Musanga cecropioides R.Br. ex Tedlie	II	II							
Gilbertiodendron mayombense (Pellegr.) J.Léonard	V		III			IV			
Coelocaryon preussii Warb.	IV	IV		III	III	II			
Plagiostyles africana (Müll.Arg.) Prain	IV	V		V	IV				
Santiria trimera (Oliv.) Aubrév. & Pellegr.	III	V		V	IV				III
Staudtia gabonensis Warb.	III	IV		IV					
Dacryodes klaineana (Pierre) H.J.Lam	III	IV		V	IV				
Dacryodes buettneri (Engl.) Lam	III	IV		III	III				
Carapa procera DC.	III	III		V					
Desbordesia glaucescens (Engl.) Tiegh.	III	III		IV					
Prioria joveri (Normand ex Aubrév.) Breteler	III	III		III	IV				
Hymenostegia pellegrinii (A.Chev.) J.Léonard	III	III		III					
Chrysophyllum africanum A.DC.	III	II	III	II	III	II			
Homalium letestui Pellegr.	III	II			II				III
Distemonanthus benthamianus Baill.	III	II							
Vitex grandifolia Gürke	III	II							
Pterocarpus soyauxii Taub.	II	IV		III					
Pentaclethra macrophylla Benth.	II	IV		III					
Scytopetalum klaineanum Pierre ex Engl.	II	III		III	III				
Pycnanthus angolensis (Welw.) Warb.	II	III			IV				
Irvingia gabonensis (Aubry-Lecomte ex O'Rorke) Baill.	II	III							
Tetrapleura tetraptera (Schum. & Thonn.) Taub.	II	III							
Erismadelphus exsul Mildbr.	II	III							
Sterculia tragacantha Lindl.	II	II	III	II					
Ficus kamerunensis Mildbr. & Burret	II	II	III						
Strombosia pustulata Oliv.	II	II		IV	V				
Ficus exasperata Vahl	II	II							
Ganophyllum giganteum (A.Chev.) Hauman	II	II							
Vitex rivularis Gürke	II	II							
Trilepisium madagascariense Thouars ex DC.	II	II							
Treculia africana Decne.	II	II							
Parkia filicoidea Welw. ex Oliv.	II	II							
Cola lateritia K.Schum.	II	II							
Dacryodes edulis (G.Don) H.J.Lam	II	II							
Dacryodes igaganga Aubrév. & Pellegr.	II	III	III	III	III	III			
Dacryodes macrophylla (Oliv.) Laur.	II	III		IV					
Dialium pachyphyllum Harms	II	III		IV	IV				
Aphanocalyx cynometroides Oliv.	II	II							V
Aphanocalyx heitzii (Pellegr.) Wieringa	II	II			II				V
Anisophyllea polyneura Floret	II	II		IV	V				
Aubrevillea platycarpa Pellegr.	II	III		III					
Aucoumea klaineana Pierre	II	V							
Berlinia bracteosa Benth.	II	III							
Anthonotha pynaertii (De Wild.) Exell & Hillc.		IV		IV	III				
Tetraberlinia bifoliolata (Harms) Hauman		IV		III	IV				
Petersianthus macrocarpus (Beauv.) Liben		IV							
Xylopia aethiopica (Dunal) A.Rich.		III	III	II					
Polyalthia suaveolens Engl. & Diels		III		V	V	III			
Oubanguia africana Baill.		III		III	III				
Sindoropsis le-testui (Pellegr.) J.Léonard		III		III					
Drypetes gossweileri S.Moore		III		IV					
Klainedoxa gabonensis Pierre ex Engl.		III		III					
Beilschmiedia fulva Robyns & Wilczek		III		IV					
Coula edulis Baill.		III		III	III				

TABLEAU 5. continued.

Dacryodes normandii Aubrév. & Pellegr.	III		IV					
Diogoa zenkeri (Engl.) Exell & Mendonça	III		IV					
Symphonia globulifera L.f.	III			III				
Uapaca paludosa Aubrév. & Léandri	III			III				III
Chrysophyllum lacourtianum De Wild.	III			III	IV			
Prioria oxyphylla (Harms) Breteler	III							
Pseudospondias longifolia Engl.	III							
Bikinia le-testui (Pellegr.) Wieringa	III							
Canarium schweinfurthii Engl.	III							
Celtis tessmannii Rendle	III			III				
Cavacoa quintasii (Pax & K.Hoffm.) J.Léonard		IV	III		III			
Dichostemma glaucescens Pierre		III	III	III				
Anisophyllea purpurascens Hutch. & Dalziel.		III						
Baphia buettneri Harms		III	II					
Manilkara zenkeri Lecomte ex Aubrév. & Pellegr.		III	II	I			V	V
Scottellia klaineana Pierre		III	II					
Nesogordonia papaverifera (A.Chev.) Cap.		III	II					
Stachyothyrsus staudtii Harms		III						
Microdesmis afrodecandra Floret, Louis & Reitsma			V	IV	II			
Garcinia punctata Oliv.			IV	V	II			
Xylopia staudtii Engl. & Diels			IV	III				
Trichoscypha acuminata Engl.			IV					
Diospyros fragans Gurke			III	V	IV			
Ptychopetalum petiolatum Oliv.			III	IV				
Xylopia quintasii Engl. & Diels			III	III	IV			
Annickia chlorantha (Oliv.) Setten & Maas			III	III				
Dialium bipindense Harms			III	III				
Strombosia grandifolia Hook.f. ex Benth.			III	II				V
Garcinia kola Heckel			III					
Garcinia mannii Oliv.			III					
Gilbertiodendron ogoouense (Pellegr.) J.Léonard			III					
Heisteria parvifolia Sm.			III					
Heisteria trilesiana Hook.f.			III					
Myrianthus arboreus P.Beauv.			III					
Mareya micrantha (Benth.) Müll.Arg.			III					
Barteria fistulosa Mast.			III					
Drypetes angustifolia Pax & K.Hoffm.				V				
Ouratea arnoldiana De Wild. & T.Durand				IV	III		V	V
Rinorea caudata (Oliv.) Kuntze				IV	II			V
Myrianthus serratus (Tréc.) Benth. & Hook.				IV	II			
Podococcus barteri G.Mann & H.Wendl.				IV				
Haumania danckelmaniana (J.Braun & K.Schum.) Milne-Redh.				IV	III			
Hypselodelphis violacea (Ridl.) Milne-Redh.				IV	II			
Chytranthus angustifolius Exell				IV	II			
Dorstenia mannii Hook.f.				IV				
Garcinia smeathmannii (Planch. & Triana) Oliv.				IV				
Afrocalathea rhizantha (K.Schum.) K.Schum.				IV				
Ouratea elongata (Oliv.) Engl.				III	II			
Carpolobia gossweileri (Exell) Petit				III				
Begonia susaniae Sosef				III				
Blighia welwitschii (Hiern) Radlk.				III				III
Brazzeia soyauxii (Oliv.) Tiegh.				III				
Leptonychia echinocarpa K.Schum.				III	III			
Oncoba glauca (P.Beauv.) Planch.				III	III			
Grewia coriacea Mast.				III	II			
Laccodiscus ferrugineus (Baker) Radlk.				III	II			
Palysota bracteosa C.B.Clarke				III	II			V
Warneckea wildeana Jacq.-Fél.				III				III

TABLEAU 5. continued.

Pancovia pedicellaris Radlk. & Gilg	III				III
Dracaena goldieana Bullen ex Mast. & T.Moore	III				
Parkia bicolor A.Chev.	III				
Microdesmis puberula Hook.f. ex Planch.	III				
Rinorea cerasifolia M.Brandt	III				
Maesobotrya pauciflora Pax	III				
Mapania gabonica Cherm.	III				
Massularia acuminata (G.Don) Bullock ex Hoyle	III				
Memecylon afzelii G.Don	III				
Sorindeia juglandifolia (A.Rich.) Planch. ex Oliv.	III				
Trichilia tessmannii Harms	III				
Phyllanthus odontadenius Müll. Arg.	II	V			
Virectaria belingana N.Hallé	II	III	V	III	
Piptadeniastrum africanum (Hook.f.) Brenan	II	III			
Citropsis gabunensis (Engl.) Swingle & Kellerman	II	III			
Conceveiba africana D.W.Thomas	II	III			
Justicia insularis T.Anders.	II	III			
Costus engleranus K.Schum.	II	II	III		
Sorindeia winkleri Engl.	II	II			V
Pavetta hispida Hiern	II	II			V
Diospyros iturensis (Gürke) Letouzey & F.White	II	II			III
Culcasia striolata Engl.	III	II			
Rhynchospora corymbosa (L.) Britton	II		III	V	
Begonia clypeifolia Hook.f.	II			III	
Bertiera racemosa (G.Don) K.Schum.	II			III	
Costus letestui Pellegr	II			III	
Diospyros hoyleana F.White	II				V
Paurydiantha canthiiflora Hook.f.	II				V
Alchornea hirtella Benth.	II				III
Allophyllus welwitschii Gilg	II				III
Dicranolepis buchholzii Engl. & Gilg	II				III
Strephonema mannii Hook. f.	II				III
Newtonia leucocarpa (Harms) Gilbert & Boutique	II				III
Octolobus spectabilis Aubrév.	II				III
Marquesia excelsa R.E.Fr.	I	III		V	V
Garcinia gnetoides Hutch. & Dalziel	I	III		III	V
Dracaena camerooniana Baker	I	II		V	III
Thomandersia hensii De Wild. & T.Durand	I			V	
Olax gambecola Bail.	I				III
Asystasia gangetica (L.) T.Anders.		V			
Asystasia macrophylla (T.Anders.) Lindau		V			
Thecacoris lucida (Pax) Hutch.		V			III
Solenostemon mannii (Hook.f.) Baker		IV	III	V	
Brillantaisia lamium (Nees) Benth.		IV	III	V	
Dissotis barteri Hook.f.		IV	III	III	
Impatiens mackeyana Hook.f.		IV			
Clappertonia polyandra (K.Schum.) Bech.		III	V	III	
Asparagus drepanophyllus Welw.		III	V		
Schefflera barteri (Seem.) Harms		III		V	
Scleria bulbifera Hochst. ex A.Rich.		III			
Psychotria peduncularis (Salisb.) Steyerm.		III			
Commelina longicapsa C.B.Clarke		III			
Emillia lisowskiana Jeffrey		II	III		
Costus lateriflorus Baker		II		III	
Angraecum podochiloides Schltr.		II		III	
Brillantaisia debilis Burkill		II		V	
Calvoa monticola A.Chev. ex Hutch. & Dalziel		II		III	
Chlorophytum alismaefolium Baker		II		V	
Memecylon collinum Jacq.-Fél.		II		V	V

Tableau 5. continued.

Scleria boivini Steud.	II		III	
Asplenium africanum Desv.		V	V	
Hymenodictyon biafranum Hiern		V	III	
Microgramma owariensis (Desv.) Alston		V		
Otomeria micrantha K.Schum.		V		
Vernonia biafrae Oliv. & Hiern		V		
Diodia sarmentosa Sw.		V		
Kyllinga erecta Schumach.		V		
Ascolepis capensis (Kunth) Ridl.		V		
Asplenium jaundeense Hieron.		V		
Pellaea holstii Hieron.		III		
Asplenium vagans Baker		III		
Vepris trifoliolata (Engl.) W.Mziray			V	
Begonia mannii Hook.			V	
Bertiera batesii Wernham			III	
Buforrestia obovata Brenan			III	
Pentadesma grandifolia Baker f.				V
Cyperus diffusus Vahl				V
Thecacoris annobonae Pax & K.Hoffm.				V
Cryptosepalum klaineana				V
Epistemma rupestre H.Huber				V
Maranthes glabra (Oliv.) Prance				III

La classe de présence correspond à la présence ou fréquence d'une espèce. Elle est exprimée en pourcentage par rapport au nombre total de relevés d'un groupement considéré. Le tableau 6 indique les cinq classes de présence qui ont été définies par Braun-Blanquet (1932).

Classe de présence	Présence
V	Espèces présentes dans 80 à 100% des relevés
IV	Espèces présentes dans 60 à 80% des relevés
III	Espèces présentes dans 40 à 60% des relevés
II	Espèces présentes dans 20 à 40% des relevés
I	Espèces présentes dans 1 à 20% des relevés

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ECOLOGY OF RUBIACEAE ON CENTRAL AFRICAN INSELBERGS

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Abstract

Vegetation inventories were conducted on 16 groups of inselbergs in Cameroon, Equatorial Guinea and Gabon. Results on Rubiaceae are presented here; 126 species were identified in six plant formations. Some representatives have ecological preferences and are restricted to certain plant formations on the inselbergs. Statistical analyses (Twinspan, DCA) based on the relative abundance of Rubiaceae showed that the plant formations located side by side in the profile of inselbergs have most floristic similarities. Ecological factors (gradients of light, soil depth and moisture) could explain the preference of some taxa for specific plant formations. Tendencies in chorology are that the Guineo-Congolian element is by far the most important, with a few Sudano-Zambezian species. Results also show that ecological adaptations in Rubiaceae on inselbergs are correlated with their taxonomic position (at tribal level). Vegetation inventories made for ecological purposes usually limit themselves to woody plants or woody plants of a certain minimum size; however the results of this study show that inventorying all the representatives of a predominant family such as Rubiaceae is an interesting substitute.

Résumé

Ecologie des Rubiaceae sur les inselbergs d'Afrique centrale. Des inventaires de végétation ont été réalisés sur 16 groupes d'inselbergs au Cameroun, en Guinée Equatoriale et au Gabon. Les résultats relatifs à la famille des Rubiaceae sont présentés; 126 espèces ont été identifiées dans six formations végétales. Certains représentants ont des préférences écologiques et sont limités à des formations végétales spécifiques sur les inselbergs. Des analyses statistiques (Twinspan, DCA), basées sur l'abondance relative des Rubiaceae, ont montré que les formations végétales situées côte à côte dans le profil des inselbergs avaient beaucoup de similarités floristiques. Les facteurs écologiques (gradients de lumière, profondeur de sol et humidité) pourraient expliquer la préférence de certains taxons pour des formations végétales spécifiques. En matière de chorologie, la tendance est d'observer un élément guinéo-congolais très important et quelques espèces soudano-zambéziennes. Les résultats montrent aussi que les adaptations écologiques des Rubiaceae sur les inselbergs sont corrélées avec leur position taxonomique (au niveau de la tribu). Les inventaires de végétation réalisés dans un but écologique se limitent habituellement aux plantes ligneuses ou parfois même à celles dont la taille atteint une valeur minimale; néanmoins, les résultats de cette étude montrent qu'inventorier tous les représentants d'une famille prédominante, comme celle des Rubiaceae, constitue une alternative intéressante.

Key words: Central Africa, Rubiaceae, inselbergs, ecology, taxonomy, chorology

1 Introduction

1.1 Inselbergs

Inselbergs are isolated rocky outcrops mostly consisting of Precambrian granite or gneiss (estimated 10 to 50 million years old) (Barthlott & Porembski, 1998). They are scantily covered with soil and rise abruptly from surrounding plains. Their size varies from several square kilometres to only a few square metres. In some regions, large inselbergs may attain a height of more than 600 m above the surroundings with an altitude reaching 1000 m. In others, small outcrops rise only a few metres (Barthlott *et al.*, 1993; Barthlott & Porembski, 1998).

In the humid tropics, inselbergs provide an extremely harsh environment for plant life. Due to the thin soil cover, water storage capacity is low, and water run-off after rain is high. Exposed rock surfaces heat up considerably, resulting in surface temperatures regularly exceeding 50°C accompanied by a decrease in air humidity. Therefore, in humid regions inselbergs form xeric islands and may be considered microenvironmental deserts (Phillips, 1982). On the other hand, in arid regions inselbergs benefit from a higher moisture supply and are often considered favourable habitats for plants (Jürgens & Burke, 2000). In any case, because of the exceptional environmental conditions, the vegetation of inselbergs contrasts sharply with the surrounding vegetation and inselberg landscapes constitute a mosaic-like pattern of vegetation.

Biodiversity on inselbergs, both in temperate and tropical regions, was studied by Porembski & Barthlott (2000), who showed that on West African inselbergs, *Afrotrilepis pilosa* grassland was the most characteristic feature. As a result of a survey of about 100 inselbergs in all vegetation zones of Ivory Coast, 600 species were recorded, about 10% of which were characteristic elements, i.e. they occurred almost exclusively on inselbergs (Barthlott *et al.*, 1993). In the Namib Desert inselbergs provide refuge for species of higher rainfall areas and generally show higher plant richness than their arid surroundings (Burke, 2002). In central Africa, vegetation on inselbergs remains largely unknown. Vegetation data and species lists exist for Nkoltsia hill in Cameroon (Villiers, 1981) and for 13 Gabonese inselbergs (Reitsma *et al.*, 1992). In Equatorial Guinea, vegetation of four inselbergs was investigated by Lejoly & Lisowski (1999) and 14 sites were studied by one of us (Parmentier, 2002). In Gabon, Reitsma *et al.* (1992) described clearly distinguished and physiognomically defined plant communities on inselbergs. Parmentier *et al.* (2001) used a phytosociological approach to characterize the vegetation of the Piedra Nzas inselbergs in Equatorial Guinea. They distinguished ten vegetation units belonging to five plant formations: humid and dry grasslands, herbaceous fringes, shrubby fringes, forest fringes and saxicolous forests (see Fig. 2 in Parmentier, 2003). Natural grasslands of the inselbergs are composed of species well adapted to harsh environmental constraints. Species-poor dry grasslands dominated by *Afrotrilepis pilosa* are found on shallow soil or bare rock on the driest parts of the inselberg, strongly exposed to sun. Humid grasslands are located on the slopes of the inselbergs where there is a continuous water seeping from the upper saxicolous forest, or in depressions. Herbaceous, shrubby and forest fringes succeed between grassland and saxicolous forest. Forest fringes and saxicolous forests are characterized by their high species diversity and shelter many species absent from the surrounding rainforest.

Very few chorological data relative to species growing on African inselbergs exist (Seine *et al.*, 2000). Porembski (2000) and Seine & Becker (2000) showed that the relative number of widespread species is larger on inselbergs than in the regional flora. On West African inselbergs, the Guineo-Congolian element is commonly of little importance while widespread savanna elements (e.g. Sudano-Zambezian) are generally well represented. The prevalence of savanna elements was observed, particularly in the Taï rainforest of Ivory Coast (Porembski *et al.*, 1995). Endemic taxa were mentioned by most authors but their proportion in inselberg vegetation exhibits no common tendency, probably due to regional paleoclimate and vegetation history (Seine *et al.*, 2000). Some taxa with distribution disjunctions were also recorded (Barthlott *et al.*, 1993). Parmentier (2001) also underlined the presence of montane species at low altitude on an inselberg of Equatorial Guinea.

1.2 Rubiaceae family

The Rubiaceae family (more than 630 genera and approximately 11,000 species) is the fourth largest of the flowering plants (Robbrecht, 1988). In subsaharan Africa, Rubiaceae are represented by about 1900 species in 165 genera. In central Africa rainforests, it is the largest and most significant family in terms of numbers of species and individuals and forms a common component of the understorey (Hepper *et al.*, 1999).

1.3 Objectives

This study is part of an analysis of the results obtained from vegetation inventories conducted in central Africa. In a first stage, identification of specimens focused on several large plant families, inter alia Rubiaceae. The objectives of the present study were first to make a list of the rubiaceous taxa of central Africa inselbergs and to characterize their ecology. Many vegetation inventories made for ecological purposes limit themselves to woody plants or woody individuals of a certain minimum size but consider all families. We postulate here that inventorying all representatives of one predominant family could substitute for traditional relevés for characterizing vegetation. For these purposes, Rubiaceae represents a manageable subset of the flora as a whole as the family is diverse both in morphology and ecology. Floristic data on Rubiaceae were already used with success for testing hypotheses on the location of glacial rainforest refuges in Africa (Robbrecht, 1996) as well as to characterize the whole flora of Mount Cameroon region (Hepper *et al.*, 1999). Inselbergs are particularly interesting for the purpose of our study because they act as continental islands and offer a high potential for research in biogeography and biodiversity.

2 Material and methods

2.1 Study site

This study was conducted on 31 sites (inselbergs and rocky outcrops) in continental Equatorial Guinea, the Northern part of Gabon and South Cameroon (0°55'–3°10'N, 10°18'–12°48'E). Results of vegetation inventories were combined for sites close together and 16 groups of inselbergs were finally identified (Fig. 1).

Climate is equatorial with two dry and two humid seasons. Mean annual rainfall varies between 1600 mm in Bouamir (Cameroon) (Sonké, 1998) and 3500 mm in Monte Alèn and Engong (Equatorial Guinea). Temperature range is from 23°C to 26°C. Altitude is 500 to 850 m a.s.l. (except Monte Alèn and Engong sites where it is 1120 m a.s.l.) but the height of inselbergs never exceeds 150 m above the surrounding plain in this region.

2.2 List of species and chorology

Most material used for producing the list of species was collected by the authors (IP in Cameroon and Equatorial Guinea; JD, LN and IP in Gabon) and deposited at the Herbarium of the National Botanic Garden of Belgium (BR) and at the Université Libre de Bruxelles (BRLU). In total 448 specimens of Rubiaceae collected on central African inselbergs were identified. Most species of *Pavetta* and *Psychotria* need a revision to be identified and were not considered in our study.

Chorology of each species was established by reviewing and databasing a selection of specimens kept in BR and by mapping their geographical distribution. White's phytogeographical system for Africa (1993a) was chosen to interpret the distributional data with 'region' and 'domain' used instead of White's periphrases for the phytochoria.

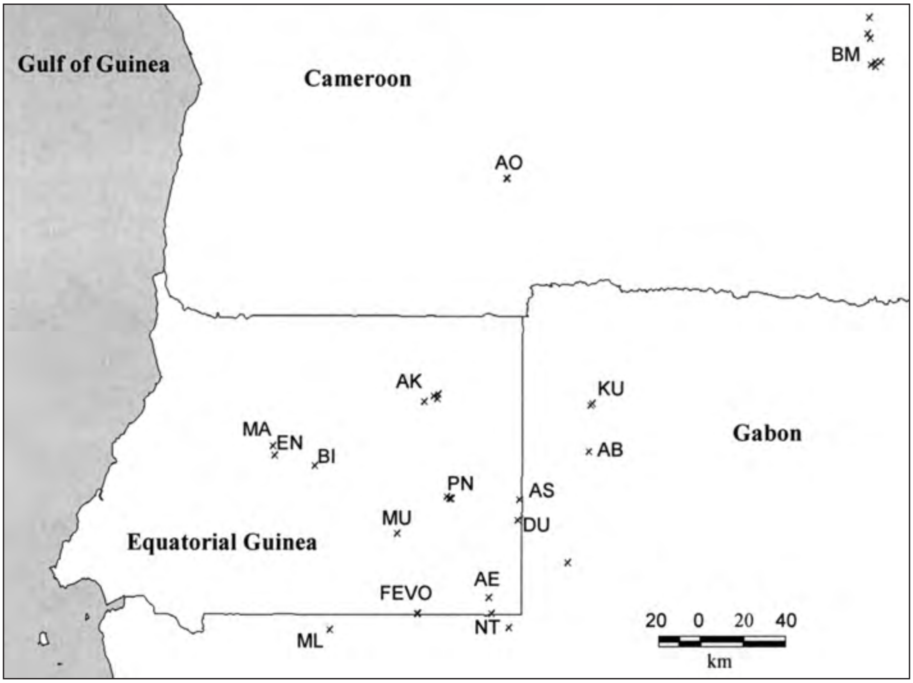

FIG. 1. Location of the 16 groups of inselbergs studied (AB: Assep-Bengong N01°38'E11°37'; AE: Akoak Ebanga N01°04'E11°12'; AK: Akuom N01°50'E10°55'; AO: Akookas N02°43'E11°16'; AS: Asoc N01°27'E11°19'; BI: Bicurga N01°35'E10°28'; BM: Boua Mir N03°10'E12°48'; DU: Dumu N01°22'E11°19'; EN: Engong N01°37'E10°18'; FEVO: Fene Voma N01°00'E10°54'; KU: Koum N01°49'E11°37'; MA: Monte Alèn N01°39'E10°17'; ML: Milobo N00°55'E10°31'; MU: Mungum N01°19'E10°48'; NT: Ntan N00°59'E11°12'; PN: Piedra Nzas N01°27'E11°02').

2.3 Distribution of species on the profile of inselbergs

For studying the distribution of species on the profile of inselbergs, information from 375 phytosociological relevés conducted in the region was added to ecological data given on the herbarium specimens. The plant formations used to analyse the distribution of species on the profile of inselbergs were those proposed by Parmentier *et al.* (2001) for the Piedra Nzas site: saxicolous forest, forest fringe, shrubby fringe, herbaceous fringe, dry grassland and humid grassland.

If information was available, the abundance of the species in each plant formation was calculated using the following coefficients (Braun Blanquet, 1932):

Percentage of abundance (% soil surface)	**Abundance coefficient**
1%, one individual	0.2%
≤ 5%, many individuals	2.5%
6–25%	15%
26–50%	37.5%
51–75%	62.5%
76–100%	87.5%

We then inferred the mean abundance value of each species in each plant formation. Therefore we calculated the relative percentage with regard to all plant formations in which the species was present. The transformed values of the data, ranging from 1 to 7 (1 = 0%< × <5%; 2 = 5%≤ × <10%; 3 = 10%≤ × <25%; 4 = 25%≤ × <50%; 5 = 50%≤ × <75% ; 6 = 75%£ × <100%; 7 = 100%), were used for the analyses.

The ordered two-way table from a plant formations-by-species matrix was obtained with Twinspan software (Hill, 1994). The detrended correspondence analysis (DCA) was processed by Canoco 4.5 (ter Braak & Smilauer, 2002). A dendrogram was produced from dissimilarity measuring by Euclidean distances and error sum of squares clustering (Ward's method).

3 Results

3.1 List of species

In total 126 species (sometimes further identified to infraspecific rank) in 52 genera of Rubiaceae collected on the inselbergs were identified. For 101 among the 126 identified species, data concerning the distribution on the profile of inselbergs was available. The relative percentage with regard to the plant formations was calculated for each species (log-scale from 1 to 7) and processed with Twinspan (Table 1).

3.2 Distribution on the profile of inselbergs

The DCA graph of plant formations based on the relative abundance of Rubiaceae (Fig. 2) and the dendrogram showing the dissimilarity of plant formations with regard to the relative abundance of Rubiaceae (Fig. 3) clearly indicate that the plant formations located side by side in the profile of inselbergs are also those having most floristic similarities. Such an ordering of plant formations on the DCA graph also demonstrates that distribution of Rubiaceae on the profile of inselbergs reflects the patterns of vegetation as a whole.

TABLE 1. Ordered two-way table from a plant formations-by-species matrix obtained by TWINSPAN analysis (Tribes: COF = Coffeeae; CRA = Craterispermeae; CRE = Cremasporeae; GAE = Gaertnereae; GAR = Gardenieae; HED = Hedyotideae; HYM = Hymenodictyoneae; IXO = Ixoreae; LAS = Lasiantheae; MUS = Mussaendeae; PAU = Pauridiantheae; PAV = Pavetteae; PSY = Psychotrieae; SAB = Sabiceeae; SPE = Spermacoceae; VAN = Vanguerieae; VIR = Virectarieae) (Chor: Chorological pattern. A = Afromontane; GCa = Guineo-Congolian with afromontane penetration; GCw = Guineo-Congolian wide (= Upper Guinea + Lower Guinea + Congolia); L = Lower Guinean endemics; LC = Lower Guinean & Congolian; LCm = Lower Guinean & Congolian with macrodisjunction; LCp = Lower Guinean & Congolian "pericongolian"; SZ = Sudano-Zambezian; UL = Upper & Lower Guinean; W = African wide) (Plant formations: SF = saxicolous forest; FFr = forest fringe; SFr = shrubby fringe; HFr = herbaceous fringe; HG = humid grassland; DG = dry grassland) (Relative percentage of abundance: empty = absent; 1 = 0%< × <5%; 2 = 5%≤ × <10%; 3 = 10%≤ × <25% ; 4 = 25%≤ × <50% ; 5 = 50%≤ × <75% ; 6 = 75%≤ × <100%; 7 = 100%).

Taxa	**Tribe**	**Chor.**	**SF**	**FFr**	**SFr**	**HFr**	**HG**	**DG**
Craterispermum caudatum Hutch.	CRA	UL	7					
Craterispermum ledermannii K.Krause	CRA	L	7					
Cuviera talbotii (Wernh.) B.Verdcourt	VAN	L	7					
Didymosalpinx lanciloba (S.Moore) Keay	GAR	LC	6	2				
Ecpoma hierniana (Wernh.) N. & F.Hallé	SAB	L	7					
Hymenocoleus nervopilosus Robbr. var. *orientalis* Robbr.	PSY	L	7					
Massularia acuminata (G.Don) Bullock ex Hoyle	GAR	GCw	7					
Oxyanthus gracilis Hiern	GAR	LC	7					
Oxyanthus laxiflorus K.Schum.	GAR	L	7					
Pauridiantha venusta N.Hallé	PAU	L	7					
Pavetta staudtii Hutch. & Dalz.	PAV	L	7					
Poecilocalyx crystallinus N.Hallé	PAU	L	7					
Psychotria minuta E.M.A.Petit	PSY	LCm	7					
Rothmannia hispida (K.Schum.) Fagerl.	GAR	GCw	6	1				
Rothmannia lateriflora (K.Schum.) Keay	GAR	LC	7					
Rothmannia urcelliformis (Schweinf. ex Hiern) Bullock ex Robyns	GAR	SZ	7					
Tarenna precidantenna N.Hallé	PAV	LC	7					
Tricalysia bequaertii De Wild.	COF	L	7					
Tricalysia gossweileri S.Moore	COF	L	7					
Tricalysia pedunculosa (N.Hallé) Robbr. var. *pedunculosa*	COF	L	7					
Bertiera batesii Wernh.	GAR	L	5		5			
Aulacocalyx jasminiflora Hook.f.	GAR	GCw	6	3				
Belonophora coriacea Hoyle	COF	LC	6	3				
Pavetta microthamnus K.Schum.	PAV	L	5	4				
Pavetta owariensis Beauv.	PAV	GCw	5	4				
Tricalysia pallens Hiern	COF	GCa	6	3	1			
Bertiera iturensis K.Krause	GAR	LCp	5	5				
Bertiera sphaerica N.Hallé	GAR	L	5	5				
Coffea mayombensis A.Cheval.	COF	L	5	5				
Hymenocoleus scaphus (K.Schum.) Robbr.	PSY	LC	5	5				

TABLE 1. continued

Taxa	**Tribe**	**Chor.**	**SF**	**FFr**	**SFr**	**HFr**	**HG**	**DG**
Pavetta hispida Hiern	PAV	L	5	5				
Camptopus letestui De Wild.	PSY	LC	4	4	4			
Hymenocoleus hirsutus (Benth.) Robbr.	PSY	GCw	4	4	4			
Oxyanthus speciosus DC. subsp. *speciosus*	GAR	GCw	5	4	3			
Rytigynia rubra Robyns	VAN	L	4	4	3			
Rytigynia umbellulata (Hiern) Robyns	VAN	SZ	4	4	4			
Chazaliella oddonii (De Wild.) E.M.A.Petit & B.Verdcourt var. *cameroonensis* B.Verdcourt	PSY	L	3	6				
Pauridiantha siderophila N.Hallé	PAU	L	1	6				
Pavetta cellulosa Bremek.	PAV	L	2	6				
Rothmania talbotii (Wernh.) Keay	GAR	LC	1	6				
Atractogyne gabonii Pierre	GAR	GCw		7				
Bertiera aequatorialis N.Hallé	GAR	L		7				
Bertiera lanx N.Hallé	GAR	L		7				
Bertiera subsessilis Hiern	GAR	L		7				
Chazaliella sciadephora (Hiern) E.M.A.Petit & B.Verdcourt	PSY	UL		7				
Lasianthus batangensis K.Schum.	LAS	GCw		7				
Leptactinia involucrata Hook.f.	PAV	LCm		7				
Mussaenda arcuata Poir.	MUS	W		7				
Pavetta camerounensis S.D.Manning	PAV	L		7				
Psilanthus mannii Hook.f.	COF	GCw						
Psydrax subcordata (DC.) D.M.Bridson	VAN	SZ		7				
Sabicea discolor Stapf	SAB	UL		7				
Sabicea goossensi De Wild.	SAB	L		7				
Sabicea laurentii De Wild.	SAB	LC		7				
Tarenna conferta Hiern	PAV	LC		7				
Aidia micrantha (K.Schum.) Bullock ex White	GAR	GCa	3	6	3			
Aidia ochroleuca (K.Schum.) E.M.A.Petit	GAR	LC		5	5			
Bertiera aethiopica Hiern	GAR	LC	1	6	3			
Bertiera racemosa (G.Don) K.Schum. var. *racemosa*	GAR	GCw		6	3			
Cremaspora triflora (Thonn.) K.Schum.	CRE	GCa		5	4			
Gardenia vogelii Hook.f.	GAR	LCm		5	5			
Lasianthus repens Hepper	LAS	LC		5	5			
Mussaenda erythrophylla Schum. & Thonn.	MUS	GCw		5	5			
Uncaria africana G.Don	HYM	GCw		5	5			
Vangueriella rufa (Robyns) B.Verdcourt	VAN	L		5	5			
Argocoffeopsis pulchella (K.Schum.) Robbr.	COF	L			7			
Bertiera bracteolata Hiern	GAR	UL			7			
Gardenia imperialis subsp. *physophylla* (K.Schum.) L.Pauwels	GAR	GCw			7			
Geophila renaris De Wild. & Th.Dur.	PSY	L			7			
Keetia hispida (Benth.) D.M.Bridson	VAN	GCw			7			
Keetia mannii (Hiern) D.M.Bridson	VAN	LCm			7			
Lasianthus mayumbensis Good	LAS	L			7			
Leptactinia mannii Hook.f.	PAV	L			7			

TABLE 1. continued

Taxa	**Tribe**	**Chor.**	**SF**	**FFr**	**SFr**	**HFr**	**HG**	**DG**
Poecilocalyx schumannii Bremek.	PAU	L			7			
Rytigynia verruculosa Robyns	VAN	LC			7			
Sacosperma paniculatum (Benth.) G.Taylor	HED	GCw			7			
Sherbournia bignoniiflora (Welw.) Hua	GAR	GCw			7			
Sherbournia streptocaulon (K.Schum.) Hepper	GAR	L			7			
Tarenna pallidula Hiern subsp. *pallidula*	PAV	LC			7			
Hymenocoleus rotundifolius (A.Chev. ex Hepper) Robbr.	PSY	LCm	2		6			
Pauridiantha canthiiflora Hook.f.	PAU	L	2		6			
Trichostachys aurea Hiern	PSY	UL		6				
Gaertnera paniculata Benth.	GAE	GCw		5	4	1		
Pseudosabicea mildbraedii (Wernh.) N.Hallé	SAB	LC		5	4	2		
Rytigynia neglecta Robyns	VAN	A		3	6	3		
Hymenodictyon biafranum Hiern	HYM	L		4	4	4		1
Psychotria peduncularis (Salisb.) Steyerm.	PSY	GCa	4	3	3	3	1	
Psydrax parviflora (Afz.) D.M.Bridson subsp. *parviflora*	VAN	GCa	4	3	3	3		
Hymenodictyon floribundum (Hochst. & Steud.) B.L.Robinson	HYM	SZ	4	4	3	2		3
Otomeria guineensis Benth.	HED	GCw			5	5		
Spermacoce intricans (Hepper) H.M.Burkill	SPE	L		1	3	6		
Leptactinia arnoldiana De Wild.	PAV	LCp		2	2	6		
Mussaenda tenuiflora Benth.	MUS	LC				7		
Sabicea longepetiolata De Wild.	SAB	LCp				7		
Spermacoce exilis (L.O.Williams) C.D.Adams	SPE	L				7		
Virectaria procumbens (Sm.) Bremek.	VIR	GCw				7		
Virectaria belingana N.Hallé	VIR	L		2	4	5	1	
Virectaria herbacoursi N.Hallé var. *petrophila* N.Hallé	VIR	L		1	3	4	3	2
Otomeria micrantha K.Schum.	HED	LC		2	3	4	3	3
Oldenlandia lancifolia (Schumach.) DC.	HED	W			1			6
Virectaria multiflora (Sm.) Bremek.	VIR	GCw						7

The taxa listed below were not processed with TWINSPAN because no information was available concerning their distribution on the profile of inselbergs.

Taxa	**Tribe**	**Chor.**
Bertiera globiceps K.Schum.	GAR	LCm
Bertiera racemosa (G.Don) K.Schum. var. *elephantina* N.Hallé	GAR	L
Chassalia corallifera (A.Cheval. ex De Wild.) Hepper	PSY	GCw
Chassalia cristata (Hiern) Bremek. subsp. *cristata*	PSY	LC
Geophila obvallata F.Didr.	PSY	L
Heinsia crinita (Afzel.) G.Taylor	MUS	GCw
Hymenocoleus globulifer Robbr.	PSY	L
Ixora minutiflora Hiern subsp. *minutiflora*	IXO	L
Keetia tenuiflora (Hiern) D.M.Bridson	VAN	GCw
Mussaenda polita Hiern	MUS	L
Parapentas setigera (Hiern) B.Verdcourt	HED	GCw

TABLE 1. continued

Taxa	Tribe	Chor.
Pauridiantha callicarpoides (Hiern) Brem	PAU	L
Pavetta gracilipes Hiern	PAV	L
Pseudosabicea batesii (Wernh.) N.Hallé	SAB	L
Psilanthus lebrunianus (Germain & Kesler) Leroy ex D.M.Bridson	COF	LC
Psydrax arnoldiana (De Wild. & Th.Dur.) D.M.Bridson	VAN	LC
Rutidea glabra Hiern	PAV	L
Rutidea membranacea Hiern	PAV	GCw
Sabicea capitellata Benth.	SAB	LC
Sabicea duparquetiana H.Baillon ex Wernh.	SAB	L
Sabicea pilosa Hiern	SAB	L
Sherbournia ailarama N.Hallé	GAR	L
Tricalysia oligoneura K.Schum.	COF	LCp
Uncaria donisii E.M.A.Petit	HYM	L
Vangueriella orthacantha (Mildbr.) D.M.Bridson & B.Verdcourt	VAN	GCw

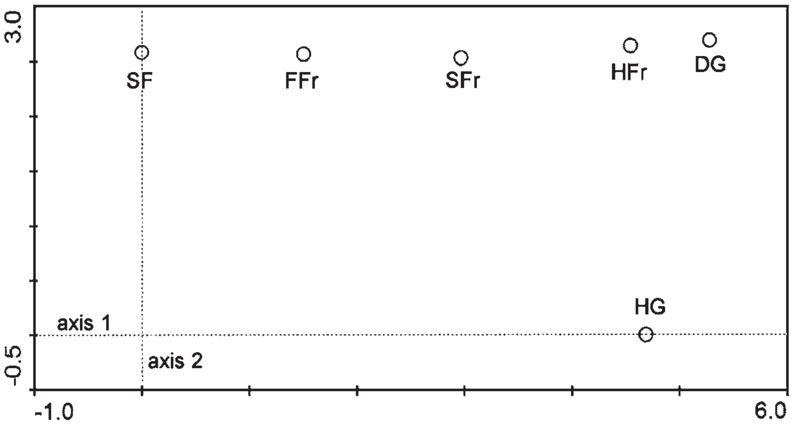

FIG. 2. DCA graph of plant formations based on the relative abundance of Rubiaceae (Plant formations: SF = saxicolous forest; FFr = forest fringe; SFr = shrubby fringe; HFr = herbaceous fringe; HG = humid grassland; DG = dry grassland).

Parmentier (2003) showed that microclimate and soil characteristics differ between plant formations of inselbergs in Equatorial Guinea. She underlined that the main ecological gradient among the formations corresponds to pH and soil depth variations. Soil is much reduced in grasslands and herbaceous fringes and is responsible for the limitation of water supply; soil depth increases when following the profile and reaches a maximum value under saxicolous forests. Soil pH was proved to be significantly lower in the forest fringe and the saxicolous forest than in the other plant formations. Light and temperature also greatly differ from the grasslands surrounded by rocky bare soil to the undergrowth of saxicolous forests.

According to these findings, we interpret axis 1 of DCA graph (Fig. 2) as a strong ecological gradient corresponding to variation in soil depth, pH, light and temperature. Axis 2 is probably linked to soil moisture as it separates the dry grasslands from humid grasslands.

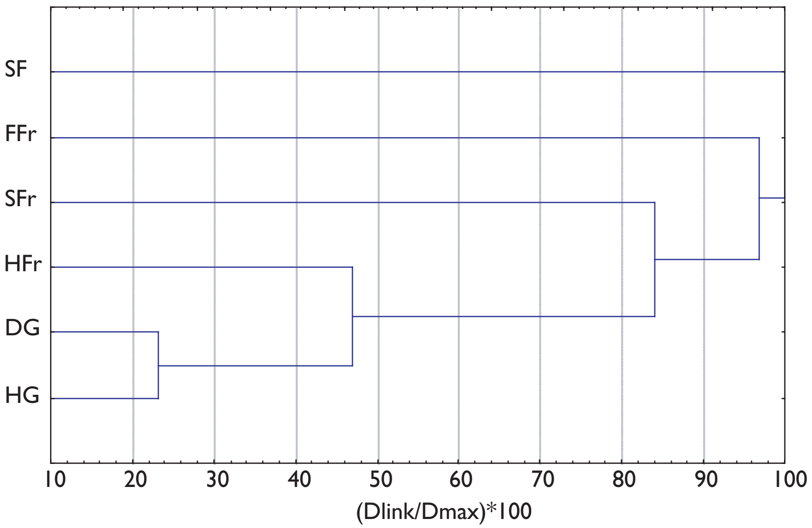

FIG. 3. Dendrogram of dissimilarity of plant formations to relative abundance of Rubiaceae (Plant formations: SF = saxicolous forest; FFr = forest fringe; SFr = shrubby fringe; HFr = herbaceous fringe; HG = humid grassland; DG = dry grassland).

A cluster analysis (Fig. 3) shows that a clear gap separates the woody formations (saxicolous forests, forest fringes and shrubby fringes) from the herbaceous formations (herbaceous fringes, humid grasslands and dry grasslands). Within these groups, dissimilarities are particularly low between saxicolous forests and forest fringes on one side and between forest fringes and shrubby fringes on the other side. The Rubiaceae composition varies gradually within the woody formations with a number of species common in formations located side by side in the profile.

Among the most remarkable Rubiaceae taxa of central African inselbergs are:

- *Hymenodictyon floribundum*, a shrubby species with a wide ecology that is found from 500 m to 1850 m a.s.l. in savanna, woodland, moist evergreen forest and montane forest in the whole Sudano-Zambezian area. In central Africa, *H. floribundum* characterizes rock outcrops and inselbergs. During this study, it was found abundantly in all plant formations except in humid grasslands. A second species of the genus, *H. biafranum* also characterizes inselbergs but its distribution is more restricted (Lower Guinean). This species is mainly observed in vegetation fringes, rarely in dry grasslands.
- *Otomeria guineensis* and *O. micrantha*, two closely related species and hard to distinguish (based on colour of corolla and shape of corolla tube). *O. guineensis* mainly grows in lowland forests but it was also collected by us in shrubby and herbaceous fringes of inselbergs. *O. micrantha* is generally found between 800 m and 1100 m a.s.l. and is an inselberg specialist where it is uniformly found in all formations except in saxicolous forests. Some rare individuals of *O. micrantha* were also observed in lowland forests between 350 and 550 m a.s.l.

- *Virectaria*, a genus well represented on central African inselbergs. The most characteristic species is the endemic *Virectaria herbacoursi* var. *petrophila* found in all formations excepted in saxicolous forests. *V. belingana* is absent from both saxicolous forests and dry grasslands, *V. procumbens* only occurs in shrubby fringes and *V. multiflora* is restricted to dry grasslands.

We compared the taxonomic (tribal) position of the species with their ecological preference on the inselbergs. Fig. 4 presents the proportion of species from each Rubiaceae tribe found in the different plant formations. Species belonging to the Gardenieae are only present in the woody plant formations of the inselbergs (saxicolous forest, forest fringes and shrubby fringes). Moreover 14 among the 44

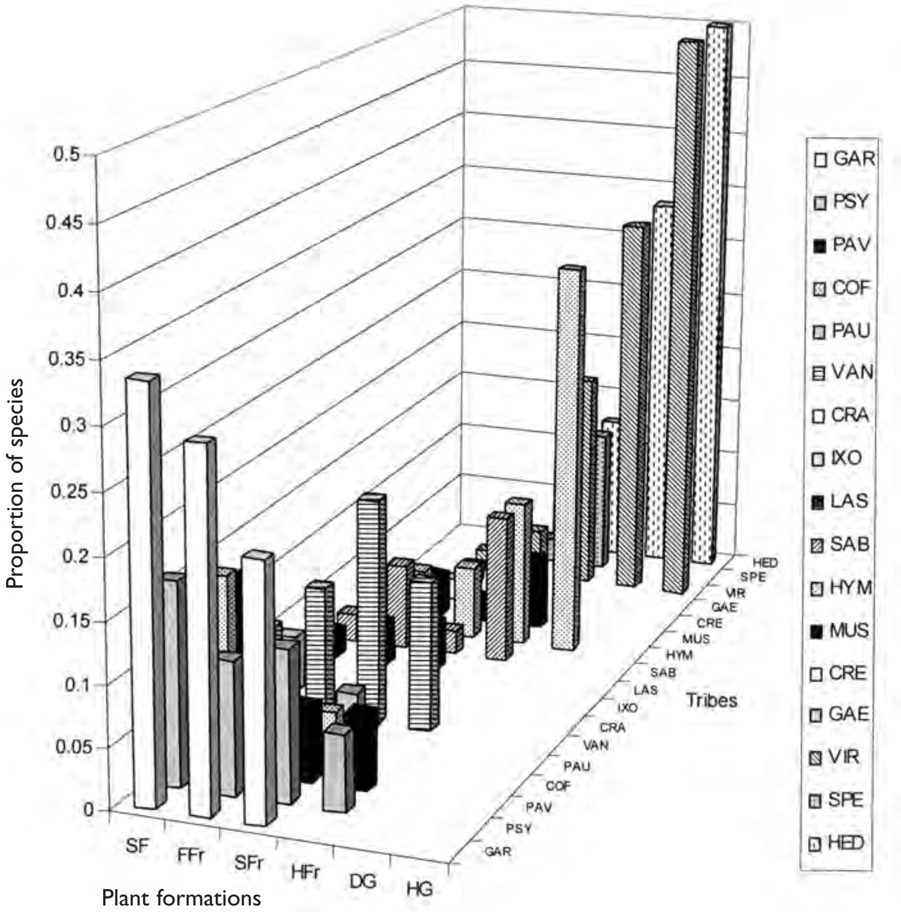

FIG. 4. Proportion of species from each Rubiaceae tribe in the different plant formations. (Tribes: COF = Coffeeae; CRA = Craterispermeae; CRE = Cremasporeae; GAE = Gaertnereae; GAR = Gardenieae; HED = Hedyotideae; HYM = Hymenodictyoneae; IXO = Ixoreae; LAS = Lasiantheae; MUS = Mussaendeae; PAU = Pauridiantheae; PAV = Pavetteae; PSY = Psychotrieae; SAB = Sabiceeae; SPE = Spermacoceae; VAN = Vanguerieae; VIR = Virectarieae) (Plant formations: SF = saxicolous forest; FFr = forest fringe; SFr = shrubby fringe; HFr = herbaceous fringe; HG = humid grassland; DG = dry grassland).

species found in saxicoulous forests (33%) and 16 among the 57 species found in forest fringes (29%) are Gardenieae. Comparatively, formations like humid and dry grasslands are species-poor and dominated by shrubby or herbaceous representatives of Hymenodictyoneae (2 among 6 species in dry grasslands), Hedyotideae (2 among 6 species in dry grasslands; 1 among 2 species in humid grasslands) and Virectarieae (2 among 6 species in dry grasslands; 1 among 2 species in humid grasslands).

Tribes show obvious 'ecological preferences' e.g. the predominantly woody Gardenieae, Psychotrieae and Pavetteae occur mainly in woody formations and the Hymenodictyoneae, Virectarieae, Spermacoceae and Hedyotideae dominate the open formations.

Hallé (1967) suggested a rainforest origin for the Rubiaceae, followed by a radiation in areas with a marked dry season. He hypothesized that the Gardenieae should have given rise to more competitive tribes such as Mussaendeae, 'Oldenlandieae' (now Hedyotideae) and Spermacoceae that are found where the ecology is more constraining and competition between species is rough.

Relation between ecological preferences and the evolution status of tribes would be an interesting study once the phylogeny of the family as a whole is better understood.

3.3 Chorology

Table 1 gives the distribution pattern of each species. For some poorly collected species, this information (mainly based on BR specimens) needs confirmation through additional collections. General tendencies in the chorology of Rubiaceae from central Africa inselbergs are:

- The Guineo-Congolian element is by far the most important of the family in number of representatives (in total 119 species or 94.4%). Nevertheless, different patterns can be differentiated within the Guineo-Congolian distribution type:
  - Guineo-Congolian wides (GCw) (26 species or 20.6%) are found in all three domains distinguished by White (Lower Guinea, Upper Guinea and Congolia); among them are *Otomeria guineensis*, *Virectaria multiflora* and *Virectaria procumbens.*
  - Five species (3.9%) (e.g. *Psychotria peduncularis*, *Tricalysia pallens*, ...) have a wide ecology and penetrate the afromontane region (GCa) where they occurred in montane forests up to 2000 m a.s.l.
  - Twenty-two species (17.5%) are linking elements of the Lower Guinean and Congolian domains (LC) (e.g. *Otomeria micrantha*).
  - Some species of the previous category are never found in the central part of the Congo Basin. Such a chorology was already underlined by Léonard (1965) who defined a "secteur périphérique Congo-Cameroun" to characterize a similar distribution for some Euphorbiaceae. Among these four species (3.2%) with a Lower Guinean and pericongolian distribution (LCp) are *Leptactinia arnoldiana, Sabicea longepetiolata*, ...
  - Among the linking elements of the Lower Guinean and Congolian domains (LC), six species (4.8%) show remarkable macrodisjunctions (LCm) i.e. they are found in Lower Guinea and in the Kivu region (e.g. *Gardenia vogelii, Hymenocoleus rotundifolius*, ...).
  - Lower Guinean endemics (L) constitute the most important group within the Guineo-Congolian element (51 species or 40.5% of the total number of Rubiaceae). Most of them are found on inselbergs but also grow in the surrounding rainforest. *Hymenodictyon biafranum*, *Virectaria belingana* and *Virectaria herbacoursi* var. *petrophila* are restricted to inselbergs and rocky outcrops.

  - Five species (3.9%) have a disjunct distribution and occur in Upper and Lower Guinea domains (UL). Possibly this is a relict distribution pattern caused by the Pleistocene climatic perturbations.

- The Sudano-Zambezian element (SZ) is very limited among Rubiaceae collected on central Africa inselbergs (4 species or 3.2%). Porembski *et al.* (1995) already mentioned that the percentage of Sudano-Zambezian elements is higher on inselbergs in the savanna zone of the Sudanian region of West Africa than in the Guineo-Congolian rain forests. Sudano-Zambezian species concerned here are absent from the surrounding rainforest and only known from inselbergs where they find similar ecological conditions. The most remarkable example of Sudano-Zambezian element found here is *Hymenodictyon floribundum,* the presence of which is strictly limited to inselbergs in central Africa.
- Only one species (0.8%), *Rytigynia neglecta,* with a strict Afromontane distribution (A) (altitude range 1750–2400m) was found on inselbergs from 580 m to 750 m a.s.l.
- Finally, two widely distributed species (1.6%) (*Mussaenda arcuata* and *Oldenlandia lancifolia*) can be considered African wides (W).

The analysis of the percentage of species per plant formation according to their phytogeographical distribution (Fig. 5) shows that Guineo-Congolian elements (GC) are generally dominant. In this figure, Guineo-Congolia region is considered in a wide sense and includes GCa, GCw, LC, LCm, LCp and UL chorological types as defined above. Lower Guinean endemics (L) constitute the second most important group in percentage. Sudano-Zambezian elements occur in all formations except in humid grasslands.

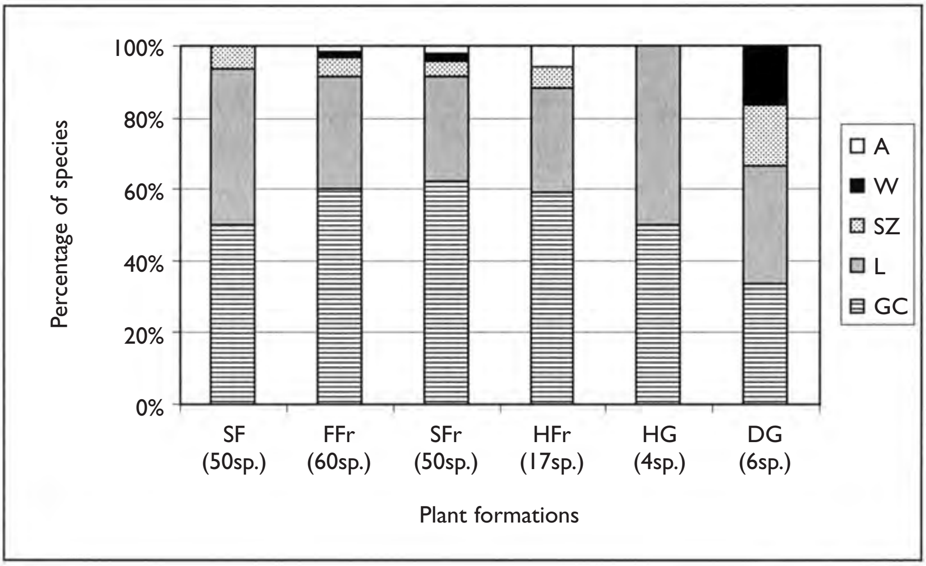

FIG. 5. Percentage of species per plant formation according to phytogeographical distribution (Chorological patterns. GC = Guineo-Congolian; L = Lower Guinean endemics; SZ = Sudano-Zambezian; W = African wide; A = Afromontane) (Plant formations: SF = saxicolous forest; FFr = forest fringe; SFr = shrubby fringe; HFr = herbaceous fringe; HG = humid grassland; DG = dry grassland; number of species in brackets).

4 Conclusion

The floristic richness of the central African inselbergs studied here can be first explained by their location in a region between the refugia of the South Cameroon Plateau and that of the Crystal Mountains (Sosef, 1994). So inselbergs probably acted as refugia in times of climatic change by supporting species that are now usually found in savannas (Porembski *et al.*, 1995). As discussed by several authors (White, 1993b; Robbrecht, 1996), distribution patterns in this region have been heavily influenced by Pleistocene events and many taxa are refuge endemics or show refuge disjunctions. Moreover, the biodiversity is strengthened by the contrasting ecological conditions encountered today on the inselbergs themselves. The list of species established by this study clearly shows that these explanations for the floristic richness on the inselbergs also hold for Rubiaceae.

The most abundant element in these inselberg Rubiaceae is the Guineo-Congolian one; in this category Lower Guinea endemics prevail, but linking species with the Congolian domain are also well represented. Several species showing this chorology and particularly the herbaceous representatives (*Otomeria*, *Spermacoce*, *Virectaria*) are characterized by a large degree of morphological variability that gives evidence of ongoing processes of speciation. This was only observed in the most derived tribes (Hedyotideae, Spermacoceae and Virectarieae) and is probably favoured by the harsh environmental conditions encountered in the open formations on inselbergs.

On East African and Madagascan inselbergs, the rubiaceous genus *Anthospermum* is a remarkable and characteristic element (Barthlott & Porembski, 1998); the genus is not reported from the study area (Puff, 1986), the only species (*A. asperuloides*) found in the region is restricted to Bioko, Mount Cameroon and Dschang district (Cameroon) at altitudes from 2300 to 3650 m. In the case of central African inselbergs, the most characteristic species are the Sudano-Zambezian element *Hymenodyction floribundum*, largely found in many plant formations on inselbergs and *Virectaria herbacoursi* var. *petrophila*, a common herb of the dry grasslands and the only endemic Rubiaceae known from central African inselbergs.

With the aim to characterize the vegetation of inselbergs as a whole, the representatives of the family Rubiaceae have been analysed by Twinspan and DCA methods. The results of this study are quite conclusive as they show similar floristic affinities among plant formations and reveal the same patterns of vegetation as those obtained from previous studies which considered the results of classical phytosociological relevés (Parmentier *et al.*, 2001). It appears that inventorying all representatives of a large and predominant family such as Rubiaceae is a valuable substitute to more complete and time-consuming vegetation inventories made for ecological purposes. On central African inselbergs, the same method could probably also be successful with families such as Euphorbiaceae, Caesalpiniaceae or Melastomataceae.

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VEGETATION DESCRIPTION AND CONDITION ASSESSMENT OF PROTECTED RANGELANDS OF ALAGAE AND NETELI, IN THE MAIN ETHIOPIAN RIFT VALLEY

Ali Seid Mohammed

Abstract

Rangeland management aimed at animal production can reduce, maintain or even increase range plants diversity. Although the maintenance of biodiversity has become one of the goals in ecosystem management, the relationship between diversity and ecosystem characteristics such as the level of herbivory, productivity, and vegetation structure are still poorly understood. The way that management actions constrain (or perhaps magnify) rangeland biodiversity must clearly be understood for sustaining both productivity and biodiversity in rangelands. The purpose of this study was to investigate the floristic diversity and productivity aspects of protected and/or managed rangelands in the Main Ethiopian Rift (MER), semi-arid agro-ecological zone. In this study, the major issues addressed include floristic diversity, vegetation description, herbaceous biomass estimation, and range condition assessment. For the study we used a combination of ecological survey (Zürich Montpellier) method and a standard range condition assessment technique (adopted for the South-Eastern Ethiopian Rangelands). TWINSPAN computer program was used to make vegetation classifications. We examined the relationships between herbaceous biomass production and plant diversity in four native range sites differing in range condition in the Open Grasslands (2), and Wooded Grasslands (2) in semi-arid AEZ of MER. The results of this study have revealed the unique vegetation and rich plant diversity of two protected rangelands in the MER. Range condition of the four range sites ranged from poor to good and was found to be supported by herbaceous biomass production and grazing indicator species. Herbaceous biomass production follows a quadratic relationship with range condition. There is some indication that the humpback model appears to be functional in the MER rangelands. Important information generated has pictured the need for optimizing productivity and biodiversity conservation and elicited information on how agricultural and biodiversity conservation interest should be integrated for the sustainable utilization of rangelands.

Résumé

Description de la végétation et évaluation de l'état des zones de pâturage protégées de Alagae et Neteli dans la vallée du 'Main Rift' Ethiopien. La gestion des grands pâturages destinés à la production animale peut réduire, maintenir ou même augmenter la diversité végétale. Bien que le maintien de la biodiversité soit devenu un des objectifs de sa gestion, la relation entre la diversité et les caractéristiques de cet écosystème, à savoir l'herbivorie, la productivité et la structure de la végétation, est encore très mal connue. La manière dont les activités liées à la gestion limitent (ou augmentent) la biodiversité des pâturages doit être clairement comprise pour maintenir tant la productivité que la biodiversité de ces écosystèmes. L'objectif de cette étude était d'étudier la diversité floristique et les aspects de la productivité de pâturages protégés et/ou gérés dans le 'Main Rift' Ethiopien (MER), une zone agro-écologique semi-aride. Dans cet étude, les thèmes principaux traitent de la diversité floristique, de la description de la végétation, de l'estimation de la biomasse herbacée et de l'évaluation de l'état des pâturages. Pour cette étude, nous avons utilisé en combinaison une méthode d'inventaire écologique (Zürich-Montpellier) et une technique d'évaluation standard de l'état des pâturages (adoptée pour les pâturages du sud-est éthiopien). Le logiciel TWINSPAN a été utilisé pour classifier la végétation. Nous avons examiné les relations entre la production de biomasse herbacée et la diversité des plantes dans quatre sites naturels et dans des conditions variées dans les savanes herbeuses (2) et dans les savanes boisées (2) de l'AEZ semi-aride du MER. Les résultats de cette étude ont révélé la végétation unique et l'importante diversité végétale de deux pâturages protégés dans le MER. Les quatre sites étaient caractérisés par des états divers (conditions mauvaises à bonnes) et étaient évalués sur base de la production de biomasse herbacée et par la présence d'espèces indicatrices du broutement. La production de biomasse herbacée suit une relation quadratique avec l'état de la zone. Il semble que le modèle humpback puisse être fonctionnel dans les pâturages du MER. Les informations importantes tirées de ce travail ont montré le besoin d'optimiser la productivité et la conservation de la biodiversité. Elles ont aussi permis d'imaginer la manière d'intégrer les intérêts agricoles et ceux liés à la conservation de la biodiversité pour une utilisation durable des pâturages.

Key words: Ethiopian Rift Valley, floristic diversity, grassland, rangeland management, sustainable utilization

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AFRICAN VASCULAR PLANT SPECIES RICHNESS: A COMPARISON OF MAPPING APPROACHES

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Abstract

For research and applied purposes, reliable data are needed. However, knowledge on how these data can be used and interpreted is equally important. We present three new maps of African vascular plant species richness which are inventory-based, i.e. the underlying data are richness figures of geographic units. They are compared with three other types of diversity maps, including taxon-based maps, i.e. maps based on distribution data for individual species. The first comparison is made with respect to the flow of data and information, thereby also demonstrating some of the main differences between taxon-based and inventory-based approaches. Second, we compared the maps with respect to criteria which guide the production and use of diversity maps. These criteria are: availability of data, labour-intensity, repeatability and subjectivity of methods, accuracy of results, compatibility with geographic standards and applicability for further research, conservation and didactic purposes. The results suggest that there is no single best method. Different types of maps have very different strengths and weaknesses, depending on which criterion is considered. We propose to further refine mapping methods by using richness figures from floras and other inventories to calibrate taxon-based data.

Résumé

Richesse spécifique des plantes vasculaires africaines: comparaison d'approches cartographiques. Des données fiables sont nécessaires tant pour la recherche qu'à des fins appliquées. Néanmoins, la connaissance de la manière dont ces données peuvent être utilisées et interprétées est également importante. Nous présentons trois nouvelles cartes de richesse spécifique des plantes vasculaires africaines basées sur un inventaire, autrement dit sur des valeurs de richesse d'unités géographiques. Elles sont comparées avec trois autres types de cartes de diversité, notamment des cartes de taxons, c'est-à-dire basées sur des données de distribution d'espèces individuelles. La première comparaison concerne le flux de données et d'information, démontrant de cette manière certaines des différences majeures entre les approches «taxon» et «inventaire». Ensuite, nous avons comparé les cartes sur base de critères guidant la production et l'utilisation des cartes de diversité. Ces critères sont: la disponibilité des données, l'intensité du travail nécessaire, la répétitivité et la subjectivité des méthodes, la fiabilité des résultats, la compatibilité avec des standards géographiques et l'applicabilité pour de futures recherches, pour la conservation et à des fins didactiques. Les résultats suggèrent qu'il n'existe pas une seule méthode qui soit meilleure que les autres. Les différents types de cartes ont des atouts et des faiblesses en fonction du critère que l'on considère. Nous proposons à l'avenir d'affiner les méthodes cartographiques en utilisant les valeurs de richesse fournies par les flores et autres inventaires pour calibrer les données basées sur les taxons.

Key words: distribution data, diversity, mapping methods, species richness

1 Introduction

Both for research and for applied purposes such as the conservation and sustainable use of biodiversity, reliable data in adequate form are an important prerequisite. Equally important, however, is the knowledge on these data. Hence, with respect to biodiversity mapping we need to know about the spatial distribution of data quality, about how to adequately interpret and use these maps, and about which method one should choose when mapping biodiversity.

The aim of the present paper is to provide both: First, we present three new maps of vascular plant species richness each of which represents the African part of a global analysis. And second, we compare six different types of diversity maps, including the three which are presented here, with regard to their structure, underlying methods and qualities for applications.

2 Three maps of African plant species richness

Various maps of African plant diversity using different methods have been published (see section "Comparison of maps" and Table 3 below). We present three new maps of vascular plant species richness which are here referred to as a) map of standardized raw data, b) isotaxa map and c) ecoregions map. The latter is the first of its kind for Africa whereas the former two are revised versions of maps by Mutke *et al.* (2001) and Barthlott *et al.* (1999).

All three maps are based on the same global data-set compiled from floras, checklists and other types of literature. It is composed of the numbers of vascular plant species in various types of geographic units (GUs). These GUs include natural units such as deserts and mountain ranges, and administrative/political units such as provinces, countries and national parks. The data base contains 587 GUs for Africa, of which only a subset was selected for each analysis (215 for the isotaxa map and 239 for the ecoregion map). The basic structure of the data set is shown in Table 1.

TABLE 1. Three records from the underlying data set serving as examples to illustrate its basic structure

Geographic Unit	**Number of species**	**Area [km²]**	**Biome**	**Source**
Taï National Park	1300	3 500	Tropical moist broadleaf forests	Davis *et al.* 1994
Ténéré	20	200 000	Desert	Le Houérou 1986
Louga District (Senegal)	592	29 674	Savanna	Ba & Noba 1998

2.1 Map of standardized raw data

The species numbers were standardized by area by applying the species-area model of Arrhenius (1921):

$$(S_1/S_2) = (A_1/A_2)^z \qquad \text{(equation 1)}$$

where S_1 is the species number of the study area (i.e. the GU), S_2 the species number of the standard area (in our calculations 10,000 km^2), A_1 the size of the study area, A_2 the standard area and z a parameter the value of which was empirically determined by regression analysis for each biome individually. The values were calculated for the global extent of each biome because the data set was too small to yield significant results when splitting it up into continents. The only exception is the "Tropical and subtropical moist broadleaf forests" biome, for which enough data were available to calculate z values for subregions (see Table 2).

TABLE 2. Values of z by biome (delineation of biomes after Olson *et al.* 2001). N: Number of suitable records in global data set.

Biome	**z**	**p**	**N**
Deserts and xeric shrublands	0.11	0.054	99
Flooded grasslands and savannas	0.12	0.007	66
Temperate coniferous forests	0.14	0.019	54
Montane grasslands and shrublands	0.17	0.007	43
Tropical and subtropical grasslands, savannas, and shrublands	0.18	0.001	78
Mediterranean forests, woodlands and scrub	0.20	0.000	52
Tropical and subtropical dry broadleaf forests	0.21	0.001	54
Tropical and subtropical moist broadleaf forests (Africa and Australia)	0.24	0.000	31

Not all richness data found in literature were suitable for our purposes. For example, when the difference in size between the GU and the standard area was too large, the error resulting from the standardization procedure was expected to be too large to yield reliable results. Furthermore, GUs were classified as unsuitable when the spatial distribution of species richness was rated to be very uneven, as in Algeria where most species are concentrated along the Mediterranean coastal region.

The resulting map is shown in Fig. 1a.

2.2 Isotaxa map

The method of producing isotaxa maps has been in use for a long time (e.g., Lebrun, 1960; Malyshev, 1975). However, the term "isotaxa" was introduced relatively recently (Barthlott *et al.*, 1996). Isotaxa are the boundaries between zones of equal taxon richness (species richness, genus richness, family richness etc.).

The isotaxa map of African vascular plant species richness presented here was made in a manual procedure with the intention to fill the data gaps in the map of standardized raw data and to account for another shortcoming: even if we excluded GUs which were rated too heterogeneous in floristic composition, species richness can still be expected to be unequally distributed within most of the remaining GUs. For example, the standardization procedure yields one figure of species richness per 10,000 km^2 for Burkina Faso, but richness in the drier Northern part of the country can be expected to be lower than in the wetter Southern part.

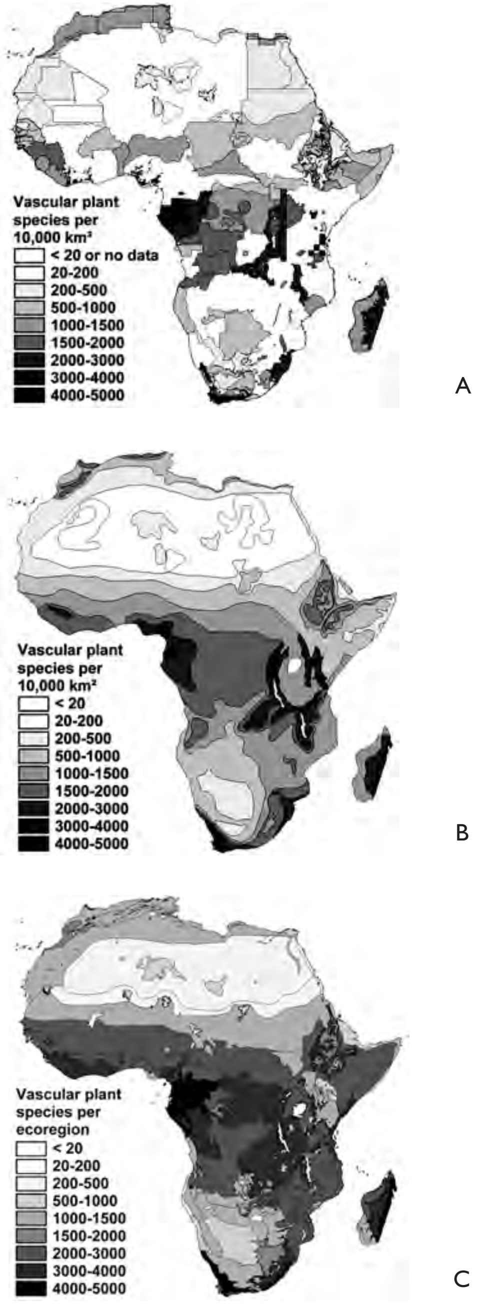

FIG. 1. Three maps of African vascular plant species richness. a: Standardized raw inventory data on species richness. b: Isotaxa map of species richness. c: Ecoregion species richness map. Since the values on the ecoregions map are not standardized by area, it should be noted that larger ecoregions tend to have higher species numbers and when ecoregions consist of several subunits the number of species is always given for the whole ecoregion.

In addition to the map of standardized raw data, a large set of quantitative and qualitative information was consulted in this process, including maps of vegetation types, precipitation, topography and temperature. Additionally, for regions with no adequate coverage of inventory data, taxon-based maps were consulted where deemed appropriate.

The resulting map is shown in Fig. 1b.

2.3 Ecoregions map

We estimated species richness for each of the African ecoregions as delineated by Olson *et al.* (2001). All ecoregions were subject to an individual assessment, deriving estimates of species numbers from the richness data mentioned above and from a variety of additional information. To this end, richness values of geographic units overlapping with an ecoregion were extrapolated up, or in some cases down, to the size of the ecoregion using equation 1. Hence, the resulting species numbers are still affected by the effect of area because ecoregions are different in size. Larger ecoregions thus tend to be higher in species richness than smaller ones. However, we chose to determine the total species number per ecoregion because conservation planning within an ecoregion should aim to protect all species, or at least as many as possible.

The resulting map of species richness is shown in Fig. 1c (see appendix for data table; the delineations of ecoregions can be downloaded as ArcView/ArcInfo compatible GIS data file from www.worldwildlife.org/ecoregions).

In order to get a measure for the reliability of results, the suitability and quality of data available for estimating species richness was rated for each ecoregion. This was made on a subjective basis applying both biological and geographical criteria. The geographical suitability depends on how well the boundaries of ecoregions and GUs match. The biological suitability was rated lower when species numbers included an unidentified number of aliens or subspecies, when we had reason to assume that the species numbers reflected an anthropogenically altered situation or when the reliability of the source was rated poor. The resulting scores are given in Appendix 1.

2.4 Comparison of maps

The three maps presented above and three other types of maps, namely modelled inventory-based grid maps, inventory-based endemism richness maps and taxon-based maps were compared in two different ways.

First, we compared them with respect to the flow of data and information (Fig. 2). Within this flow, five sequential steps can be distinguished. For each step, we compared inventory-based maps (lower part of Fig. 2) with taxon-based maps (upper part of Fig. 2).

Collection data form the most important basis for the majority of biodiversity studies. The collection localities are usually scattered over large areas. However, for certain areas, focused compilation of collection data has been done to yield checklists or floras, sometimes but not necessarily as a result of very intense collecting activities within that area. Monographical work, in contrast, brings together collection data for a certain taxonomic group no matter where collections have been made.

Map collections such as the Distributiones Plantarum Africanarum (Jardin Botanique National de Belgique, 1969–) build upon these compilations of collecting localities for single taxa. In contrast, richness statistics such as those included in Groombridge (1992) and flora guides such as Frodin (2001) compile data from floras and checklists. In principle, most of the data mentioned above can be used both for

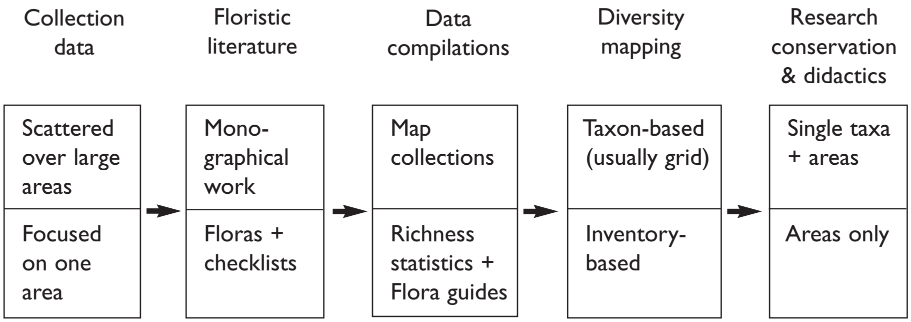

FIG. 2. Schematic overview on the flow of data in biodiversity mapping. The upper boxes are relevant mainly for taxon-based mapping, the lower boxes mainly for inventory-based mapping.

inventory-based and taxon-based mapping, but in practice the two approaches usually differ in how intensely they use these types of data. For taxon-based maps, mainly the data shown in the upper part of Fig. 2 are used whereas the data shown in the lower part are more relevant for inventory-based maps. As far as the further use for research, conservation and didactic purposes is concerned, inventory-based maps can only be used for questions related to areas. Information on single taxa is only available when a taxon-based mapping approach is followed. The results of the comparison are schematically summarised in Fig. 3.

Second, we compared the maps with respect to criteria which guide the production and use of diversity maps on continental or global scale. These criteria are:

1. Are data readily available in published or unpublished form?
2. How labour-intensive is the method?
3. How repeatable is the method and does it include subjective decisions?
4. How is the estimated accuracy of results, taking into account both errors in the underlying data and errors resulting from the processing of data?
5. To which degree is the resulting map compatible with widespread geographic standards?
6. To which degree can the map be used for further research such as testing biogeographic hypotheses or performing ecological analyses, including calculations of the correlation between richness and abiotic factors?
7. To which degree can the map be used for conservation planning?
8. To which degree can the map be used for didactic purposes, especially for a wider audience?

Many of these aspects build upon the understanding of data flow as discussed above. The results of the comparison including references to some examples of published maps are shown in Table 3.

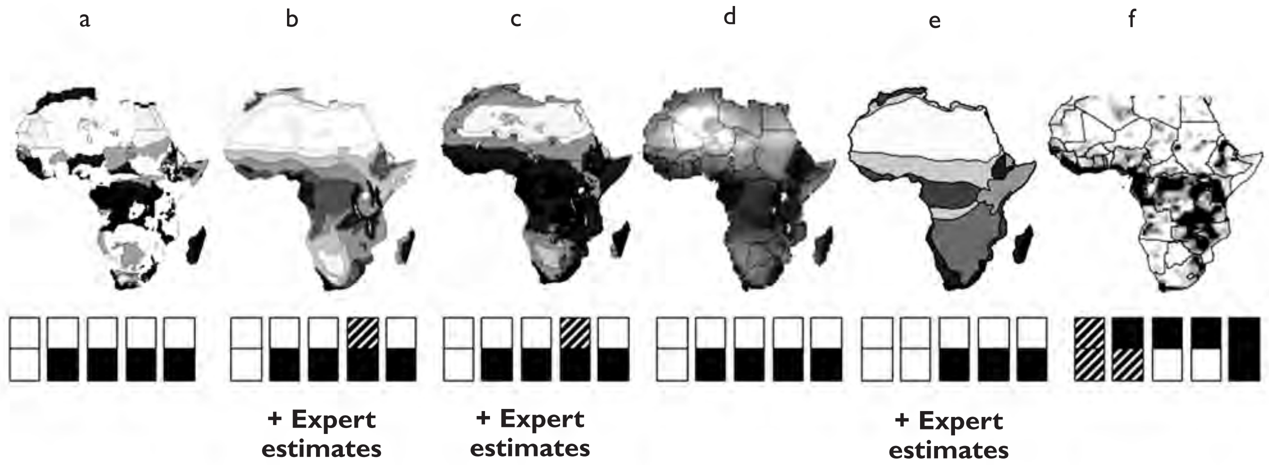

FIG. 3. Comparison of diversity maps with respect to the flow of data. The ten boxes below each map correspond to the respective boxes in Fig. 2. Steps which are directly related to each map are shown in black, those which are only partly involved are hatched. a) Standardized raw inventory data on species richness, b) Isotaxa map of species richness, c) Ecoregion species richness map, d) Modelled inventory-based grid map (Mutke *et al.*, 2001), e) Endemism richness map (Kier & Barthlott, 2001), f) Taxon-based grid map (Wolfgang Küper, unpublished data); note that the Mediterranean area is not included due to the lack of distribution data suitable for the GIS based mapping on a 1° scale.

TABLE 3. Criteria which guide the production and use of diversity maps on continental or global scale. Columns a to e refer to various types of inventory-based maps, column f refers to the category of taxon-based maps. A summarizing evaluation of each type of map with regard to each criterion is given with the symbols + (positive), o (neutral) and – (negative). For example, labor-intensity for inventory-based maps was rated comparatively low, yielding a positive evaluation (+).

	a. Standardized raw inventory data on species richness	**b. Isotaxa map of species richness based on inventory data**	**c. Ecoregion species richness map based on inventory data**	**d. Modelled inventory-based grid map**	**e. Inventory-based endemism richness map**	**f. Taxon-based grid maps**
1) Availability of data	**+** Better than for all other types of maps mentioned here but for many areas no appropriate data are available at all.	**+** Better than for e and f, comparable with c. In addition to a, non-quantitative data are included.	**+** See b.	**+** See a, but abiotic data are also needed.	**o/–** Usually worse than for all other types of maps mentioned here, but this depends on available chorological work. E.g., to make a rough survey resulting in mean values for the African phytochoria (Kier & Barthlott 2001) data availability was rather good.	**–** Large amounts of data are available, but usually in a form which is labour-intensive to process (digital data sets usually don't cover a large proportion of a continent's flora, millions of herbarium specimens still need to be revised and digitized)
2) Labour intensity	**+** Lower than for all other types of maps mentioned here.	**+** Much lower than for f, comparable with c and e. Higher than for a which forms the basis for this type of maps.	**+** Comparable with b.	**+** Higher than a, lower than f. Once the method is established, lower than b+c.	**+** Depends on available chorological work (see above), but in general rather low.	**–** Usually much higher than for inventory-based maps (see above).
3) Repeatability + subjectivity of methods	**+** High repeatability, almost no subjective decisions involved.	**–/o** High repeatability/few subjective decisions in areas where good data exist, opposite in data gaps.	**–/o** See b.	**o** High repeatability but subjectivity involved in choosing value of parameters for modelling and weighting	**–/o** See b, very much depending on available chorological work.	**+/o** High repeatability. Reducing sampling artefacts by modelling ranges includes subjective decisions.
4) Accuracy of results	**+/o** Underlying data (before standardized by area) are usually comparatively precise, sampling artefacts affect them much less than taxon-based maps. Standardizing by area results in errors depending, among others, on the difference between standard area and area of the geographic unit.	**o** For underlying data see a. The manual process of drawing isotaxa yields results which are partly hypothetical and the precision of which is difficult to quantify because subjective decisions have to be taken and no predefined mapping units are used.	**o** For underlying data see a. When data for an ecoregion are scarce or of bad quality, subjective decisions affect the precision of data. However, the use of predefined mapping units (ecoregions) creates a good framework for the quantification of data quality (see Table 4).	**–/o** For underlying data see a. Errors in the map result from, inter alia, the simplifying nature of models and biodiversity being not only a result of abiotic factors. The modelling can partly account for sampling biases but results of this procedure are partly hypothetical.	**o** Depends on underlying chorological work. When data for a mapping unit are scarce or of bad quality, subjective decisions affect the precision of data. However, the use of predefined mapping units creates a good framework for the quantification of data quality.	**o** Depends on underlying data which are often heavily affected by sampling artefacts (Nelson *et al.* 1990). Modelling can account for this but the results are partly hypothetical. When range maps are only available for parts of the flora, the degree of representativity is unclear.

TABLE 3. continued

	a. Standardized raw inventory data on species richness	**b. Isotaxa map of species richness based on inventory data**	**c. Ecoregion species richness map based on inventory data**	**d. Modelled inventory-based grid map**	**e. Inventory-based endemism richness map**	**f. Taxon-based grid maps**
5) Compatibility with geographic standards	**o** Data can be converted to fit other geographical standards (e.g., grid or ecoregions). Resulting inaccuracies depend on differences in geometry.	– See a. However, the spatial distribution of the precision is difficult to quantify and limits to the applicability in quantitative analyses exist (see below).	+ Directly compatible with all other data based on the ecoregions map of Olson *et al.* (2001).	+ Directly compatible with all other data based on the same grid. Conversion to other grids and non-grid geographic standards possible within certain limits.	**o** Directly compatible with all other data based on the same chorological system. However, these systems are rarely a standard for a wide array of data.	+ See d. (for an example of an analysis which makes ample use of this compatibility, see Brooks *et al.*, 2001)
6) Applicability for further research	+ High because data are relatively precise. However, the spatial extent of each data point varies and for many areas no appropriate data are available. Some applications require unstandardized values.	– Due to subjective decisions incorporated in the map, the value for quantitative analyses is low. Danger of circular reasoning when investigating the correlation with factors which guided the production of the map.	– See b.	**–/o** See b, but degree of subjectivity is lower.	– Most analyses will rather be based either on richness or on endemism than on a factor combining both.	+ High due to 1) the data being available for individual taxa, 2) good compatibility with standards, 3) broad spatial extent, 4) (almost) standard size of data points, 5) repeatability. Strongest limit is the inclusion of sampling artefacts (Taplin *et al.*, 2003). With modelled maps, danger of circular reasoning can exist (see b).
7) Applicability for conservation	**o** The map can guide conservation decisions within the limits species richness has as a criterion of conservation value. Richness values have to be interpreted as approximate mean values for a geographic unit. Map provides no answers for data gaps.	**o** The possible sources of errors mentioned above should be taken into account. For the use of species richness, see a.	+ Comparable with b. However, a major advantage for conservation purposes is the compatibility with the ecoregion map by Olson *et al.* (2001) which is used by WWF and other conservation organizations (see above).	**o** See c, but accuracy of results is often limited (see above)	**+/o** Combining richness and endemism creates a better index for conservation value than richness alone. However, the use is limited by the low spatial resolution.	+ A taxon-based data set which is either complete or representative provides the best available data basis for conservation decisions because it enables various analyses including, e.g., complementarity (Williams *et al.*, 1996).

TABLE 3. continued

	a. Standardized raw inventory data on species richness	**b. Isotaxa map of species richness based on inventory data**	**c. Ecoregion species richness map based on inventory data**	**d. Modelled inventory-based grid map**	**e. Inventory-based endemism richness map**	**f. Taxon-based grid maps**
8) Applicability for didactic purposes	– When the aim is to demonstrate data gaps, this map is appropriate for didactic purposes. However, it is of limited value to give an impression of general diversity patterns.	+ Broadscale patterns of diversity can be recognized very easily at a glance.	+/o Entities (ecoregions) can directly be addressed and described which is an advantage for didactics. Recognizing diversity patterns on the map is more difficult than on b. Some ecoregions consist of several separate areas which can be misleading. Since ecoregions are different in size, the effect of area should be addressed appropriately.	o Absence of clearly visible natural entities is usually a disadvantage when communicating diversity patterns, especially to a wider audience.	– Broadscale patterns of an indicator for conservation value can be recognized easily. However, the idea of combining richness and endemism is difficult to communicate to a wider audience. Furthermore, a very rough spatial resolution with mean values for large phytochoria such as in Kier & Barthlott (2001) can be misleading.	+/o There is a huge range of possibilities of visualizing taxon-based data for didactic purposes. However, the absence of clearly visible natural entities on most taxon-based maps is usually a disadvantage when communicating diversity patterns, especially to a wider audience.
9) Examples	Fig. 1a; Mutke *et al.* (2001)	Fig. 1b; Lebrun 1960, Malyshev (1975, 1999), Barthlott *et al.* (1996, 1999); Currie (1991), various maps in Groombridge & Jenkins (2000)	Fig. 1c; previous maps of ecoregion species richness (e.g., Krupnick & Kress, 2003, Ricketts *et al.* 1999) have been made with a taxon-based approach	Mutke *et al.* (2001)	Kier & Barthlott (2001)	Linder (2001), Lovett *et al.* (2000), Francis & Currie (2003), Küper *et al.* (2004)

3 Discussion

As the results of the comparison presented in Table 3 suggest, different types of maps have different strengths and weaknesses depending on which specific requirements one has with regard to diversity maps.

A map showing the standardized (or unstandardized) raw inventory data on species richness such as Fig. 1a can often be produced rather quickly, yielding a comparatively reliable data basis. However, it provides no answers for the many data gaps on it which is a disadvantage for many applications. Based on such maps, isotaxa maps can be produced with relatively low effort as already pointed out by Gaston (1998).

One of the main strengths of isotaxa maps is the application for didactic purposes, because for the human eye, a map with clear classification and isolines is easier to interpret at a glance than a grid map showing continuous gradients and a certain amount of "noise" (i.e., fluctuations of species richness or any other index which are presumably not the result of a distinct and real natural phenomenon). Of course, taxon-based maps can also be further processed to be better suitable for didactic purposes and in principle, they can also form the basis for isotaxa maps. However, this will often be at the expense of the repeatability of methods, e.g. when trying to differentiate between "noise" and real phenomena.

When based on inventory data, maps displaying species richness per ecoregion have similar characteristics as the other inventory-based maps mentioned above with regard to most of the criteria investigated here. One important difference is the compatibility with a geographic standard, namely the ecoregions as delineated by Olson *et al.* (2001). This is especially an advantage with regard to conservation, the purpose for which they were principally designed. Of course, species richness alone is only of limited value for conservation. More important for choosing priority areas is complementarity, i.e. choosing protected areas in a way that overlap between species inventories is reduced, a target which can usually only be reached with taxon-based data. However, choosing ecoregions from different biogeographic realms and biomes as in the Global 200 approach (Olson & Dinerstein, 1998) can partly overcome this problem on the global scale even when no taxon-based data are available. Another important difference between ecoregion maps and other maps is the applicability for didactic purposes which, depending on what aspect of diversity is to be conveyed, can be either worse or better than for the maps described above. The idea of dividing the earth's surface into distinct natural units which can thus be directly addressed and characterized is certainly a major advantage for educational purposes.

Modelled inventory-based grid maps share many advantages but also disadvantages of the aforementioned maps and taxon-based maps. The main disadvantages are presumably the limited applicability for didactic purposes and the uncertain accuracy of results. The latter is mainly due to the simplicity of models and the fact that biodiversity is not only a result of abiotic factors but also of a variety of other factors including history and biotic interaction.

Endemism richness maps differ from the aforementioned maps in that they do not only display species richness but an index combining richness with endemism. This makes them a better tool for conservation purposes, provided it fits the required spatial scale. The best starting point for the production of endemism richness maps are taxon-based data. When the latter are not available, approximate values can be calculated with an inventory-based approach. However, with this method the spatial resolution will usually be very limited because reliable index values can only be produced in three cases: first, when the percentage of endemics in a mapping unit is high, or second, when the species number in a mapping unit compared with its size is so low that endemism richness will fall in the lowest of the classes distinguished on the map, and third, when reliable chorological data on the flora of the mapping unit are available (for a detailed discussion see Kier & Barthlott, 2001). As far as didactic purposes are concerned, the higher complexity of the endemism richness index can be a disadvantage. The assessment with regard to most of the other criteria investigated here depends very much on the underlying chorological data.

Inventory-based maps have, in general, limited possibilities for application because they only display one indicator of biodiversity such as species richness. A further limit, as mentioned above, is that they only display data for areas and cannot answer questions related to individual taxa. In contrast, the main advantage of taxon-based mapping projects is that they yield a data base which can be used for a wide array of indicators and analyses. This is an important asset with regard to broadscale conservation decisions which should be based on a wider array of data than just species richness. Further advantages of taxon-based approaches are, in most cases, the higher repeatability of methods and a higher spatial resolution. However, compared with inventory-based approaches, compiling a taxon-based data base is usually much more labour-intensive. In some cases, e.g. when mapping vascular plant species richness at the global scale, it will take many more years or even decades until the database for taxon-based mapping with an appropriate accuracy will be available. Furthermore, the results of taxon-based mapping are more influenced by sampling artefacts than those of inventory-based mapping because it is much easier to find accurate data on the number of species in a region than to find accurate range maps for each species. This problem can be addressed by modelling which, however, produces results that remain hypothetical until data from collections or observations become available. Further problems with modelling are that the available abiotic data (precipitation, temperature etc.) are often of limited quality and that models reduce the complex causes for the distribution of ranges and diversity to a very limited and simplified set of factors and algorithms.

Most examples of diversity maps within all of the six categories mentioned here do not display the current state of biodiversity. There are mainly two reasons for this. First, most of the underlying data have been produced years or even decades ago, and for practically no group of organisms, continental-scale data are available which show the current state. Second, when methods to fill data gaps are applied, they usually result in patterns which reflect the natural state and do not include anthropogenic changes. This can be misleading for all sorts of applications, especially for conservation. However, with more intense methodological efforts, integrating satellite data of current land use and other factors, these shortcomings can be partly overcome.

On the long chain of data flow (Fig. 2) problems of subjectivity, arbitrariness and low repeatability can be involved in various ways. Inventory data can, e.g., include arbitrariness when richness estimates are used. But also range maps used for taxon-based mapping, even if they are in grid format and thus look rather precise, are not necessarily a product of repeatable processing of collection data but can be the result of subjective expert estimates. When using predefined units such as ecoregions (Fig. 3c and Table 3, column c), grid cells (Fig. 3d+f and Table 3, columns d and f) and phytochoria (Fig. 3e and Table 3, column e), the question of subjectivity and arbitrariness regarding their delineation can be raised.

The delineation of grid cells is usually rather random than subjective. However, it can be viewed as arbitrary because shifting the location of a grid can lead to fundamental changes in results. For example, a grid cell can be ranked highly important in one analysis because by chance, it is located on the intersection of two or more different vegetation types. Shifting the same grid cell in a way that it only includes one vegetation type would considerably lower most diversity indices applied to it.

Ecoregions and phytochoria are delineated with the intention of avoiding the problem of mixing, at their respective scale, different communities in one mapping unit. However, it remains difficult to do so in an objective manner which leads to these sorts of geographic standards being subjective to a certain degree.

For the inventory-based maps shown in Fig. 1b and c, some taxon-based maps and a wide range of other quantitative and qualitative information have helped to fill gaps in the inventory data. Such an approach, in which the authors use all available information they deem relevant, is thus very comprehensive and integrating, but it can be faced with the criticism of high subjectivity and low repeatability.

4 Conclusion

Which map one will choose to produce or use depends on various criteria as shown above. Altogether, due to different advantages and disadvantages, there is not one single best method and hence not one single best type of diversity map. We rather suggest to view them as complementing and validating each other. Hence, one option towards the production of more precise mapping results with a highly repeatable method would be to develop methods of numerically calibrating taxon-based data with inventory data.

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APPENDIX 1. Numerical results of the plant species richness assessment of the ecoregions of Africa. Species: number of vascular plant species estimated for the ecoregion. Range: lowest and highest estimate (no range is given when a very precise species number for the ecoregion was found in literature). Underlying data: Suitability and quality of underlying data (1 = good, 2 = moderate, 3 = poor, 4 = very poor).

ID	**Ecoregion Name**	**Species (range)**	**Species (working figure)**	**Under-lying data**
30101	Albertine Rift montane forests	3000–4000	3500	2
30102	Atlantic Equatorial coastal forests	5500–6800	6000	2
30103	Cameroonian Highlands forests	3000–4000	3300	4
30104	Central Congolian lowland forests	3200–4300	3600	2
30105	Comoros forests	1300–1700	1500	2
30106	Cross-Niger transition forests	1800–2600	2100	3
30107	Cross-Sanaga-Bioko coastal forests	3700–4400	4000	2
30108	East African montane forests	3500–5000	4000	3
30109	Eastern Arc forests	2900–3600	3200	2
30110	Eastern Congolian swamp forests	1600–2400	2000	3
30111	Eastern Guinean forests	3000–3500	3200	2
30112	Ethiopian montane forests	3000–5000	4000	3
30113	Granitic Seychelles forests	260–300	280	2
30114	Guinean montane forests	2400–3000	2700	2
30115	Knysna-Amatole montane forests	600–1800	1000	3
30116	KwaZulu-Cape coastal forest mosaic	1500–2800	2000	3
30117	Madagascar lowland forests	5000–7000	6000	2
30118	Madagascar subhumid forests	2500–4000	3200	3
30119	Maputaland coastal forest mosaic	2500–3000	2700	2
30120	Mascarene forests	900–1200	950	2
30121	Mount Cameroon and Bioko montane forests	3000–3800	3300	3
30122	Niger Delta swamp forests	1200–1800	1500	3
30123	Nigerian lowland forests	2800–3200	3000	2
30124	Northeastern Congolian lowland forests	3200–4300	3600	2
30125	Northern Zanzibar-Inhambane coastal forest mosaic	2700–4500	3300	3
30126	Northwestern Congolian lowland forests	3500–5000	4100	3
30127	Sao Tome and Principe moist lowland forests	900–1100	950	2
30128	Southern Zanzibar-Inhambane coastal forest mosaic	2400–3500	2800	3
30129	Western Congolian swamp forests	1700–2500	2100	3
30130	Western Guinean lowland forests	3100–3600	3300	3
30201	Cape Verde Islands dry forests	–	257	1
30202	Madagascar dry deciduous forests	1800–2400	2100	2
30203	Zambezian *Cryptosepalum* dry forests	800–1700	1300	4
30701	Angolan Miombo woodlands	1800–3200	2400	3
30702	Angolan Mopane woodlands	900–1400	1100	3
30703	Ascension scrub and grasslands	–	25	1
30704	Central Zambezian Miombo woodlands	3300–4300	3800	3
30705	East Sudanian savanna	2000–2700	2300	3
30706	Eastern Miombo woodlands	2500–3300	2800	3
30707	Guinean forest-savanna mosaic	2200–3000	2500	3
30708	Itigi-Sumbu thicket	500–1500	1000	4
30709	Kalahari *Acacia-Baikiaea* woodlands	1300–1900	1400	3
30710	Mandara Plateau mosaic	400–800	600	4
30711	Northern *Acacia-Commiphora* bushlands and thickets	1100–1500	1300	2
30712	Northern Congolian forest-savanna mosaic	2100–2900	2500	3
30713	Sahelian *Acacia* savanna	1200–1400	1300	2
30714	Serengeti volcanic grasslands	500–1500	1000	4

APPENDIX 1. continued

ID	Ecoregion Name	Species (range)	Species (working figure)	Underlying data
30715	Somali *Acacia-Commiphora* bushlands and thickets	2300–3000	2600	2
30716	Southern *Acacia-Commiphora* bushlands and thickets	1800–2800	2300	3
30717	Southern Africa bushveld	1000–2000	1500	3
30718	Southern Congolian forest-savanna mosaic	2700–3500	3000	3
30719	Southern Miombo woodlands	1800–3000	2200	3
30720	St. Helena scrub and woodlands	–	60	1
30721	Victoria Basin forest-savanna mosaic	2300–3000	2500	2
30722	West Sudanian savanna	1700–2500	2100	2
30723	Western Congolian forest-savanna mosaic	3000–3700	3300	2
30724	Western Zambezian grasslands	600–1200	800	4
30725	Zambezian and Mopane woodlands	2200–3200	2500	3
30726	Zambezian *Baikiaea* woodlands	1200–1800	1300	3
30901	East African halophytics	50–200	80	4
30902	Etosha Pan halophytics	30–200	80	3
30903	Inner Niger Delta flooded savanna	300–800	500	4
30904	Lake Chad flooded savanna	400–800	600	4
30905	Saharan flooded grasslands	900–1700	1300	4
30906	Zambezian coastal flooded savanna	700–1500	1100	4
30907	Zambezian flooded grasslands	1000–1900	1400	4
30908	Zambezian halophytics	50–200	80	4
31001	Angolan montane forest-grassland mosaic	1700–2500	2000	3
31002	Angolan scarp savanna and woodlands	1000–2000	1500	4
31003	Drakensberg alti-montane grasslands and woodlands	400–1200	800	3
31004	Drakensberg montane grasslands, woodlands and forests	3000–4500	3700	2
31005	East African montane moorlands	350–550	400	3
31006	Eastern Zimbabwe montane forest-grassland mosaic	1200–2600	1700	3
31007	Ethiopian montane grasslands and woodlands	1700–2500	2000	3
31008	Ethiopian montane moorlands	600–800	700	2
31009	Highveld grasslands	1600–2200	1900	2
31010	Jos Plateau forest-grassland mosaic	900–1600	1300	3
31011	Madagascar ericoid thickets	600–1500	1000	4
31012	Maputaland-Pondoland bushland and thickets	1800–3000	2100	3
31013	Ruwenzori-Virunga montane moorlands	350–550	400	3
31014	South Malawi montane forest-grassland mosaic	1500–2800	1900	3
31015	Southern Rift montane forest-grassland mosaic	1500–2500	1900	3
31201	Albany thickets	700–2000	1200	3
31202	Lowland fynbos and renosterveld	2500–3500	3000	3
31203	Montane fynbos and renosterveld	5500–7000	6300	2
31301	Aldabra Island xeric scrub	170–200	180	2
31303	East Saharan montane xeric woodlands	600–800	700	2
31304	Eritrean coastal desert	50–200	100	4
31305	Ethiopian xeric grasslands and shrublands	700–1000	850	3
31307	Hobyo grasslands and shrublands	600–1000	800	3
31308	Ile Europa and Bassas da India xeric scrub	40–250	80	4
31309	Kalahari xeric savanna	600–900	700	2
31310	Kaokoveld desert	300–800	500	3
31311	Madagascar spiny thickets	800–1500	1100	3
31312	Madagascar succulent woodlands	1000–1800	1400	3
31313	Masai xeric grasslands and shrublands	700–1300	900	4
31314	Nama Karoo	1000–1300	1100	2
31315	Namib desert	700–1800	1000	3

Appendix 1. continued

ID	Ecoregion Name	Species (range)	Species (working figure)	Underlying data
31316	Namibian savanna woodlands	900–1800	1100	3
31317	Red Sea coastal desert	200–500	350	3
31318	Socotra Island xeric shrublands	500–1000	750	2
31319	Somali montane xeric woodlands	1100–1800	1500	2
31322	Succulent Karoo	4800–5000	4850	2
31401	Central African mangroves	20–400	200	4
31402	East African mangroves	20–400	200	4
31403	Guinean mangroves	20–400	200	4
31404	Madagascar mangroves	20–400	200	4
31405	Southern Africa mangroves	20–400	200	4
60172	Trinidade-Martin Vaz Islands tropical forests	30–200	120	4
80425	Madeira evergreen forests	–	760	1
80513	Mediterranean conifer and mixed forests	1800–2800	2300	3
80904	Nile Delta flooded savanna	500–1100	800	3
80905	Saharan halophytics	50–200	100	3
81010	Mediterranean High Atlas juniper steppe	800–1200	1000	2
81203	Canary Islands dry woodlands and forests	1050–1200	1130	2
81212	Mediterranean *Acacia-Argania* dry woodlands and succulent thickets	1200–2000	1600	3
81213	Mediterranean dry woodlands and steppe	900–1400	1200	3
81214	Mediterranean woodlands and forests	1000–2000	1500	3
81304	Atlantic coastal desert	200–500	300	3
81321	North Saharan steppe and woodlands	1100–1200	1150	1
81327	Sahara desert	450–550	500	1
81329	South Saharan steppe and woodlands	400–700	500	3
81331	Tibesti-Jebel Uweinat montane xeric woodlands	570–620	580	2
81332	West Saharan montane xeric woodlands	500–700	550	2

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AFRICAN TREE SEED CONSERVATION RESEARCH: OPPORTUNITIES AND IMPLEMENTATION

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Abstract

Many tree seed conservation programmes have been initiated in Africa in recent decades, because of both the key role and the ever-increasing demand for seeds in reforestation efforts. However, national and regional capacity in the production, storage and uses of these seeds still need strengthening. To that end, 27 sub-Saharan African countries have identified about 62 priority tree species from 22 families for conservation, management and sustainable use. The urgent needs for research activities in collaboration with source countries are extended to identifying the optimum conditions for harvest (developmental studies), handling (germination and survival to drying) and storage longevity for seeds of all these species. Subsidised by Defra (UK), the Darwin Initiative (DIRECTS) project is developing seed research activities, as part of the *in-* and *ex situ* conservation programmes, together with 16 Tree Seed and Biodiversity Institutes in sub-Sahara Africa. The project aims to increase knowledge on the biology of all these seed species and share information among stakeholder institutes, over a three-year period (2003–2006). Already two regional research training workshops have been held in Burkina Faso (August, 2003) and Ethiopia (September, 2003) for scientists from nine (Benin, Burkina Faso, Cape Verde, Cote d'Ivoire, Ghana, Mali, Niger, Nigeria and Togo) and six (Botswana, Ethiopia, Kenya, Malawi, Tanzania and Uganda) countries, respectively. The project is supported at a technical level by both Millennium Seed Bank Project and IPGRI staff.

Résumé

Recherche sur la conservation des semences d'arbres africains: possibilités et amélioration. Beaucoup de programmes de conservation de semences d'arbres ont été initiés en Afrique au cours des dernières décennies en raison du rôle-clé et de la demande toujours croissante de graines dans les projets de reforestation. Néanmoins, la capacité nationale et régionale en matière de production, de stockage et d'utilisation de ces graines doit encore être renforcée. A cette fin, 27 pays de l'Afrique sub-saharienne ont identifié au sein de 22 familles, environ 62 espèces d'arbres prioritaires pour la conservation, la gestion et utilisation durable. Les besoins urgents en terme d'activités de recherche menées en collaboration avec les pays-sources sont prolongés de manière à identifier les conditions optimales de récolte (études de développement), de manipulation (germination et survie à la sécheresse) et de longévité de stockage pour les graines de toutes ces espèces. Subventionné par 'Defra' (UK), le projet 'Darwin Initiative' (DIRECTS) développe des activités de recherche sur les graines, dans le cadre de programmes de conservation *in-* et *ex situ*, avec 16 instituts de Semences Forestières et de Biodiversité d'Afrique sub-saharienne. Le projet a pour objectif d'augmenter la connaissance de la biologie de toutes ces espèces et de faire partager l'information entre les instituts partenaires au cours d'une période de trois ans (2003–2006). Deux séminaires régionaux de formation à la recherche se sont déjà tenus au Burkina-Faso (Août, 2003) et en Ethiopie (Septembre, 2003) pour des scientifiques de neuf (Bénin, Burkina Faso, Cap Vert, Côte d'Ivoire, Ghana, Mali, Niger, Nigeria et Togo) et six pays (Botswana, Ethiopie, Kenya, Malawi, Tanzanie et Ouganda), respectivement. Le projet est suivi d'un point de vue technique par le personnel du Millenium Seed Bank Project et de l'IPGRI.

Key words: conservation, Darwin Initiative, germination, storage, African tree seeds

1 Introduction

1.1 Background

Forests in sub-Saharan Africa are still disappearing at a rate of about 1% a year (FAO, 1997), despite the many reforestation and conservation programmes. Deforestation affects the daily life of millions of people. However, there is very little information available about the extent of the threat to tropical tree species. An attempt to categorise threats to about 2,000 tree species in sub-Saharan Africa (UNEP-WCMC, 2001; IUCN, 2002), shows that a wide range of these species is vulnerable as a result of the decline of their forest ecosystems (see Table 1). Raising trees and preserving their seeds is necessary to support reforestation, to combat desertification, to safeguard the environment and to conserve biodiversity. However, this is still an enormous challenge that requires the planting of large numbers of adapted species, which thus implies great demand for seeds.

TABLE 1. Estimated numbers of threatened tree species in sub-Saharan Africa by category of threat. The data were obtained from country reports from various sources (see IUCN 2002, http://www.unep-wcmc.org/trees/Background/africa.htm).

Type of threat	**Number of trees**
Critically endangered	113
Endangered	303
Vulnerable	1329
Lower risk, conservation dependent	27
Lower risk, near threatened	328

Most cultivated forests in sub-Saharan Africa are composed of only a handful of genera and families (Schmidt, 2000; FAO, 2001), such as Fabaceae (Leguminosae), Meliaceae, Myrtaceae and Verbenaceae, for which seed handling and storage are generally not major constraints. Many of these seeds are tolerant to desiccation and are easy to germinate and to store for periods of time. Because most developing African countries have often been obliged to rely on exotic fast growing tree species, the result has been the neglect of their own well-adapted natural resources. Furthermore, many tree species of socio-economic importance are still under-utilised because of poor seed handling techniques and lack of knowledge of seed storage physiology (Hong *et al.*, 1998) and their genetic conservation. There is, therefore, a great need to understand better the biology of indigenous species in order to promote their adaptive advantage for use in local conditions. In particular, methods for cost-effective collection and techniques for handling, germination and storage of seeds can help increase the number of indigenous tree species used in plantations, sustainable management and large-scale conservation efforts.

During the last two decades, symposia and workshops have been held on tropical forest seeds. Several proceedings of the International Union for Forest Resources Organisations (IUFRO) have been edited with special reference to seed problems (see Kamra & Ayling, 1987; Turnbull, 1990; Some & De Kam, 1993; Olesen, 1996; Marzalina *et al.*, 1999). Concurrently, technical books on tropical forest seeds were produced (Albrecht, 1993; Tompsett & Kemp 1996; IPGRI/DFSC project 1996; Poulsen *et al.*, 1998; Schmidt, 2000). However, there is still a need to adjust methods and procedures to particular species and conditions.

The will to set up collaborative programmes on the management of African forest genetic resources was expressed at recent meetings of environment and forestry experts. The capacities of National tree seed programmes still need to be strengthened in terms of availability and provision of seeds, handling and storing them as well as information diffusion and exchange. To that end, Sub-Saharan African countries in collaboration with various international and national agencies, got together (see IUFRO or IPGRI workshops in Kenya 1992, Madagascar 1994, Tanzania 1995, Senegal 1997, Burkina Faso 1992, 2001) to assess the status of their forest genetic resources and to discuss options for their preservation and regeneration. This framework is now known as the Sub-Saharan African Forest Genetic resources network, i.e. the SAFORGEN programmes. The International Plant Genetic Resources Institute (IPGRI, Rome) is playing a key role in implementing and co-ordinating SAFORGEN activities (Ouédraogo & Boffa, 1999, Eyog Matig pers. comm.). Here we review the SAFORGEN list of priority species, and identify the research needed to underpin the conservation, handling and utilisation of seed material.

1.2 Targeting priority species of value

Representatives of 18 countries, mostly from Western Africa (see Table 2), gathered in Dakar in April 1997 to discuss the management and sustainability of their Tree Seed Centres and Programmes (PRONASEF, 1997). A second regional group, of mainly the South African Development Community Tree Seed Centre Network met in Arusha, Tanzania in June 2000 for a sub-regional workshop on forest and tree genetic resources. These meetings proposed regional approaches for the sustainable management of forest genetic resources and selected species to be included in the SAFORGEN list for immediate priority actions (Ouédraogo & Boffa, 1999; Eyog Matig & Ouédraogo, 1999; Sigaud & Luhanga, 2000).

In consolidating these two regional programme lists, 62 species were identified for urgent attention for *in-* and *ex situ* conservation effort (see Table 3). The species fall into four key groups, based on socio-economic and ecological criteria: (i) producing edible fruits; (ii) forage species; (iii) species mostly used as timber and for amenities; and (iv) species used for crafts and other non-wood products. Because most of the species are distributed across national boundaries, co-operative actions have been agreed to avoid redundant effort and to promote the use of complimentary approaches. These species are now referred to as the core part of SAFORGEN programmes for detailed, regional research and development activities for the sustainable management and use of forest genetic resources. A full list of the SAFORGEN species, including uses, is given in Table 3.

TABLE 2. Countries that participated in SAFORGEN technical workshops in Burkina Faso and in Tanzania. (* = SAFORGEN countries (12) with formal signed agreement with IPGRI, including also Ethiopia, the Gambia and Uganda).

Countries at the Ouagadougou Workshop (1998)		**Countries at the Arusha Workshop (2000)**
Benin*	Guinea*	Botswana
Burkina Faso*	Kenya*	Malawi
Cameroon	Madagascar*	Mauritius
Cape Verde	Mali*	Mozambique
Central African Republic	Mauritania	Namibia
Chad*	Niger*	Swaziland
Congo*	Senegal*	Tanzania
Côte d'Ivoire	Sudan*	Zambia
Gabon	Togo*	Zimbabwe

TABLE 3. SAFORGEN priority list of forest tree species identified as highest priority for management and conservation actions in 27 sub-Saharan countries. Species produce edible fruits (Fruit) and African timber (Timber). Some are important forage species (Forage), and amenity and fuel-wood species (non-wood products). Species names authorities come from TROPICOS (http://mobot.mobot.org) or IPNI (http://www.ipni.org) and family names from the Angiosperm Phylogeny Group (APT searchable at http://www.systbot.uu.se/classification/APGclassification.html). The conservation status (vulnerable, endangered, critically endangered) is from IUCN (2002).

	Species	**Family**	**Main uses**	**Status: IUCN (threat)/CITES (concern)**
1	*Acacia nilotica* (L.) Willd. ex Delile	*Fabaceae*	Non-wood	
2	*Acacia raddiana* Savi.	*Fabaceae*	Forage	
3	*Acacia senegal* (L.) Willd.	*Fabaceae*	Forage; Non-wood	
4	*Adansonia digitata* L.	*Malvaceae*	Fruit; Forage; Timber; Non-wood	
5	*Afzelia africana* Sm.	*Fabaceae*	Forage; Timber	IUCN + CITES
6	*Afzelia quanzensis* Welw.	*Fabaceae*	Timber; Non-wood	
7	*Aningeria altissima* (A.Chev.) Aubrév. & Pellegr.	*Sapotaceae*	Timber	
8	*Anogeissus leiocarpus* (DC.) Guill. & Perr.	*Combretaceae*	Timber	
9	*Aucoumea klaineana* Pierre	*Burseraceae*	Timber	IUCN + CITES
10	*Baikiaea plurijuga* Harms	*Fabaceae*	Fruit; Forage; Timber	IUCN + CITES
11	*Balanites aegyptiaca* (L.) Del.	*Zygophyllaceae*	Fruit; Forage;	
12	*Bauhinia rufescens* Lam.	*Fabaceae*	Forage;	
13	*Borassus aethiopum* Mart.	*Arecaceae*	Fruit; Non-wood	
14	*Borassus flabellifer* L.	*Arecaceae*	Fruit	
15	*Carapa procera* DC.	*Meliaceae*	Fruit	
16	*Cola nitida* (Vent.) Sch. & Endl.	*Malvaceae*	Fruit	
17	*Colophospermum mopane* (J.Kirk ex Benth.) J.Léonard	*Fabaceae*	Timber; Non-wood	
18	*Combretum aculeatum* Vent.	*Combretaceae*	Forage; Timber	

TABLE 3. continued.

	Species	**Family**	**Main uses**	**Status: IUCN (threat)/CITES (concern)**
19	*Combretum* sp.	*Combretaceae*	Timber	IUCN
20	*Commiphora africana* (A.Rich.) Engl.	*Burseraceae*	Forage	
21	*Dacryodes edulis* (G.Don) H.J.Lam.	*Burseraceae*	Fruit	
22	*Dalbergia melanoxylon* Guill. & Perr.	*Fabaceae*	Fruit; Timber	IUCN
23	*Daniellia oliveri* Hutch. & Dalz.	*Fabaceae*	Timber	
24	*Detarium microcarpum* Guill. & Perr.	*Fabaceae*	Fruit; Timber	
25	*Diospyros mespiliformis* Hochst. ex A.DC.	*Ebenaceae*	Fruit; Timber	
26	*Entandrophragma* sp.	*Meliaceae*	Timber	IUCN + CITES (7 sp.)
27	*Faidherbia albida* (Del.) A.Chev.	*Fabaceae*	Forage; Non-wood	
28	*Garcinia afzelii* Engl.	*Clusiaceae*	Non-wood	IUCN
29	*Garcinia epunctata* Stapf	*Clusiaceae*	Non-wood	IUCN
30	*Garcinia kola* Heckel.	*Clusiaceae*	Non-wood	IUCN
31	*Gnetum africanum* Welw.	*Gnetaceae*	Non-wood	
32	*Grewia bicolor* Juss.	*Malvaceae*	Forage	
33	*Irvingia gabonensis* (Aubr.) Baill.	*Simaroubaceae*	Fruit; Non-wood	IUCN + CITES
34	*Isoberlinia doka* Craib & Stapf	*Fabaceae*	Timber	
35	*Khaya anthotheca* (Welw.) C.DC.	*Meliaceae*	Timber	IUCN + CITES
36	*Khaya ivorensis* A.Chevalier	*Meliaceae*	Timber	IUCN + CITES
37	*Khaya senegalensis* (Desr.) A.Juss.	*Meliaceae*	Forage; Timber	IUCN + CITES
38	*Lannea microcarpa* Engl. & Kr.	*Anacardiaceae*	Fruit	
39	*Lophira alata* Banks ex C.F.Gaertn.	*Ochnaceae*	Timber	IUCN + CITES
40	*Maerua crassifolia* Forssk.	*Brassicaceae*	Forage	
41	*Milicia excelsa* (Welw.) C.C.Berg	*Moraceae*	Timber	IUCN +CITES
42	*Nauclea latifolia* Blanco	*Rubiaceae*	Non-wood	
43	*Parinari curatellifolia* Planch.	*Chrysobalanaceae*	Non-wood	
44	*Parkia biglobosa* (Jacq.) R.Br. ex G.Don	*Fabaceae*	Fruit	
45	*Pausinystalia johimbe* (K.Schum.) Pierre ex Beille	*Rubiaceae*	Non-wood	
46	*Pentadesma butyracea* Sabine	*Clusiaceae*	Fruit	
47	*Prosopis africana* (Guill. & Perr.) Taub.	*Fabaceae*	Forage	
48	*Pterocarpus angolensis* DC.	*Fabaceae*	Forage; Timber	IUCN + CITES
49	*Pterocarpus erinaceus* Poir.	*Fabaceae*	Forage; Timber	
50	*Pterocarpus lucens* Lepr.	*Fabaceae*	Forage	
51	*Ricinodendron heudelotii* (Baill.) Pierre.	*Euphorbiaceae*	Fruit; Non-wood	IUCN
52	*Sclerocarya birrea* (A.Rich.) Hochst.	*Anacardiaceae*	Fruit; Forage; Non-wood	
53	*Spondias mombin* L.	*Anacardiaceae*	Fruit	
54	*Sterculia setigera* Del.	*Malvaceae*	Non-wood	
55	*Tamarindus indica* L.	*Fabaceae*	Fruit	
56	*Terminalia* sp.	*Combretaceae*	Timber	IUCN + CITES (2 sp.)
57	*Trichilia emetica* Vahl.	*Meliaceae*	Non-wood	
58	*Triplochiton scleroxylon* K.Schum.	*Malvaceae*	Timber	CITES
59	*Vitellaria paradoxa* Gaertn.	*Sapotaceae*	Fruit; Non-wood	IUCN + CITES
60	*Warburgia salutaris* (Bertol.f.) Chiov.	*Canellaceae*	Fruit; Non-wood	IUCN + CITES
61	*Ximenia americana* L.	*Olacaceae*	Fruit	
62	*Zizyphus mauritiana* Lam.	*Rhamnaceae*	Fruit; Non-wood	

2 Tree seed research for sub-Saharan Africa

Since the 1970s, efforts have been focussed on planting trees for fuel wood and to control desertification, and encouraged the establishment of national tree seed centres and the initiation of tree improvement work in some countries (Eyog Matig & Ouédraogo, 1999). Although they started small, many of these projects evolved into national and biodiversity centres or as seed stores within national forest departments. However, difficulties were soon experienced in handling and storing seeds of particularly many indigenous species.

Seed storage behaviour has been defined into three categories that are commonly used today, based on seed tolerance to desiccation (Roberts, 1973; Ellis *et al.*, 1990). Recalcitrant (or desiccation intolerant) seeds, e.g. *Vitellaria paradoxa* (shea butter tree) and *Mangifera indica* (mango), die after relatively little drying. Their storage longevity is rather short, lasting from weeks to a few months, although careful manipulation of seed water and cryopreservation provide the main (but challenging) long-term conservation option for such seeds. In contrast, orthodox (or desiccation tolerant) seeds survive desiccation to very low (<5%) moisture contents, e.g. *Acacia nilotica* (Egyptian thorn tree) and *Oryza sativa* (rice), and store well in the dry state for long periods of time. The longevity of such seeds in conventional seeds banks (-18°C) is predicted to be in the region of hundreds of years for many species (see Hong *et al.*, 1998). Finally, intermediate seeds are able to survive drying to relatively low water contents, between those of orthodox and recalcitrant seeds (Ellis *et al.*, 1990), but are sensitive to low temperature, e.g. -20°C storage. Because the characterisation of seed behaviour informs seed storage conditions, it is important to assess the seed storage features of these SAFORGEN priority trees.

The seed biology of a small number of species on the list has been investigated since 1996 as part of a project on “the handling and storage of recalcitrant and intermediate tropical forest tree seeds” [IPGRI/Danida Forest Seed Centre (DFSC), see Ouedraogo *et al.*, 1996]. These species are: *Khaya anthotheca*, *Khaya senegalensis*, *Lannea microcarpa*, *Pentadesma butyracea*, *Sclerocarya birrea*, *Trichilia emetica*, *Vitellaria paradoxa*, *Warburgia salutaris* and *Ximenia americana*. The project has built a strong global network on forest seed research and has trained scientists in using a screening protocol that has been developed to investigate seed storage physiology (see IPGRI/DFSC Newsletters 1996–2002). This work has advanced the understanding of seed storage behaviour of a number of species (Ouédraogo *et al.*, 1999).

3 Developing a seed science and technology agenda

Country reports and discussions at the recent Ouagadougou workshop on African tree seed Centres in March 2001, had particularly shown limits to investigating actions related to quality seed production, germination and storage longevity. Building on the modest achievements so far and expanding their research programmes, the African Tree Seed and Biodiversity Centres are now attempting to enlarge the range of local tree species in store, and seeking to better understand the factors that improve the life span of these seeds.

Choice of working species

Particular emphasis needs to be put on species that (i) lack comprehensive data for their germination and storage behaviour, and/or (ii) have high conservation status or belong to more than one category of use. Examples include *Aningeria altissima*

(Sapotaceae), *Baikiaea plurijuga* (Fabaceae), *Dacryodes edulis* (Burseraceae), *Garcinia afzelii* (Clusiaceae), *Gnetum africanum* (Gnetaceae), *Isoberlinia doka* (Fabaceae), *Lophira alata* (Ochnaceae), *Pausinystalia johimbe* (Rubiaceae) and *Ricinodendron heudelotii* (Euphorbiaceae). Other species for which more comprehensive data sets are in existence (Hong *et al.*, 1998; refs. in Poulsen *et al.*, 1998) are targeted for seed biology data improvement and modified seed handling, leading to better practical use in the implementation of *ex-* and *in situ* conservation activities. They include those that have recently been under investigation in the IPGRI/DFSC project (see Newsletters No 1, 1996 to No 10, 2002) or would exist in the grey literature in the participating institutes.

3.1 Investigations

Ex situ conservation via seeds can be used to support plant production and plantation programmes for species conservation and sustainable use. It is therefore important to identify the optimum conditions for harvest, handling and storage of seeds. In many species, mature seeds from ripe fruits germinate and store better than those from the other maturity stages (Poulsen *et al.*, 1998; CNSF, 2000; Hay & Smith, 2003). However, it is not always the case that fruit colour is a precise marker of physiological maturity of the embryos. For example, embryos of neem (*Azadirachta indica*) seeds from mature-green, yellow and brown fruits showed no significant differences in their initial germinability, but the storage longevity of those from yellow fruits was much superior (Sacandé, 2000). This indicates that physiological maturity of embryos is not only characterised by the attainment of maximum germination, but also by the seed's ability to withstand stresses. In this context, better characterisation of seed development and germinability in these tropical species is important. Developmental studies allow the identification of optimum collecting periods for quality seeds, and related field studies can reveal the contribution that dispersed seeds make to the natural regeneration of the species.

The germination of seeds is crucial to planting and storage programmes. However, there is a lack of detailed data on suitable conditions for germination of tropical tree seeds, in general (see Baskin & Baskin, 1998), and for the SAFORGEN species, in particular. The need for pre-treatments, including dormancy breaking, and the optimum temperatures for germination is usually unknown for SAFORGEN-listed species. In addition, optimisation of viability tests (ISTA, 1999), such as cutting, conductivity and tetrazolium chloride (TZ) vital staining, is not well established for this group of species.

Reviewing several recent references, and seed bank operations, has revealed that only about 60% of the species on the SAFORGEN list have confirmed desiccation tolerant seeds (Hong *et al.*, 1998; Tweddle *et al.*, 2003; RBG Kew and CNSF Seed Banks pers. comm.). For the other species listed, there is either insufficient information to be certain about the storage options for the seeds or they produce desiccation sensitive seeds. Thus the seed storage response for many SAFORGEN-listed species needs to be either confirmed or established for the first time. This can be achieved through seed drying and ageing studies and by checking the viability of seeds in stores across Africa in relation to the period of storage. In cases where the seeds are thought to be desiccation sensitive, in-depth work on their cryo-storage capability could be undertaken, as an alternative method of *ex situ* conservation. However, due to the relatively higher cost of such work compared with conventional seed storage, this type of study/effort should only be applied to species of considerable economic value (Pritchard, 1995).

The overall expected outcomes of the work are a better understanding of the biology of these seeds. This information will be fed into other SAFORGEN programmes, e.g. on production and recovery/restoration, and impact on long-term *ex situ* conservation efforts.

4 Darwin Initiative Research Exercise on Community Tree Seeds (the DIRECTS project)

Action to specifically address some of the issues raised above is underway through a Darwin Initiative project (2003–2006) supported by the Department of Environment, Food and Rural Affairs (Defra, UK Government). The project aims to increase seed biology knowledge for all 62 species (from 22 families), over a three year period. This will be achieved in collaboration with 40 scientists from institutes from about 16 African nations. Already two regional research workshops have been held in Burkina Faso (August, 2003) and Ethiopia (September, 2003) for scientists from nine (Benin, Burkina Faso, Cape Verde, Cote d'Ivoire, Ghana, Mali, Niger, Nigeria and Togo) and six (Botswana, Ethiopia, Kenya, Malawi, Tanzania and Uganda) countries, respectively. These workshops followed a planning meeting in the UK in July 2003 which was attended by 13 countries. Partners of this project will establish a network web presence, will publish co-authored research papers and cascade their experience to others in their institutes. The group will present their findings at a final research workshop in Kenya early in 2006. Both the Millennium Seed Bank Project and IPGRI staff supports the project at a technical level.

Completing this work programme will require a large amount of co-ordinated effort and collaboration. Institutes will need to share techniques and information related to the results and explore ways of exploiting/applying the findings. This can be achieved through enhanced interactions between institutes.

This project should considerably strengthen existing seed conservation and use activities in Africa, both reinforcing older collaborations and establishing new collaborations between the African biodiversity and tree seed centres. There are already some research partnerships between African Seed Centres and the Seed Conservation Department of the RBG Kew as a result of the IPGRI/DFSC (see Ouédraogo *et al.*, 1996, 1999) and the Millennium Seed Bank (see Pritchard & Linington, 2002) projects.

With the support of the Darwin Initiative, and the complementary support of the Millennium Seed Bank Project and IPGRI, it will now be possible to widen the seed scientific, technical and research capacity building activities in Africa to underpin the conservation effort on SAFORGEN tree species.

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SUSTAINABLE LAND USE AND CONSERVATION CONSIDERATIONS FOR EASTERN NIGERIA'S MONTANE FLORA

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Abstract

The Mambilla Plateau and Gotel Mountains of eastern Nigeria are part of a floristically unique montane archipelago that habours the most westerly forms of many Afromontane taxa. Our recent studies reveal that immense loss of native forest from this region has occurred in the past century due to increased livestock presence and resultant grazing pressure, soil compaction, and seasonal burns for maintaining grassland. Fuelwood and agriculture are also factors. Residual native forest in the region is fragmented and found only in areas that are relatively inaccessible to human use. At the same time, plantations and woodlots composed mainly of *Eucalyptus grandis* are increasing.

We conclude from this study that conservation and sustainable management by local communities are needed to help protect and maintain the region's natural biodiversity. Initial steps should investigate potential sustainable land use systems acceptable to local communities, as well as mechanisms by which natural restoration can assist the process. Some of these systems and mechanisms are explored in the paper. Successful biologically diverse land use systems will likely lessen human pressure currently placed on protected areas such as Gashaka Gumti National Park and surrounding forest reserves.

Résumé

Considérations sur l'utilisation durable et la conservation de la flore montagnarde de l'est du Nigeria. Le plateau Mambilla et les Monts Gotel dans l'est du Nigeria constituent une partie d'un archipel montagneux unique d'un point de vue floristique et qui héberge les formes les plus occidentales de nombreuses taxa afromontagnardes. Nos récentes études révèlent que la disparition importante de forêts natives dans cette région au siècle passé est à imputer à la présence croissante d'élevages et à la pression de pâturage qui en résulte, au compactage du sol et aux feux saisonniers destinés à maintenir la savane. Le bois de feu et l'agriculture ont également joué un rôle. Dans la région, la forêt native résiduelle est fragmentée et uniquement présente dans des endroits relativement inaccessibles à l'homme. Dans le même temps, les plantations et les lots boisés composés essentiellement d'*Eucalyptus grandis* sont de plus en plus nombreux. Nous concluons de cette étude que la conservation et la gestion durable par les communautés locales sont nécessaires pour aider à protéger et à maintenir la biodiversité naturelle de la région. Dans un premier temps, les démarches devraient consister à rechercher des systèmes durables d'utilisation des terres qui soient acceptables par les communautés locales, ainsi que des mécanismes par lesquels la régénération naturelle puisse aider ce processus. Certains de ces systèmes et mécanismes sont explorés dans cet article. Des systèmes d'utilisation des terres rencontrant un succès en matière de diversité biologique atténueront probablement la pression humaine visant actuellement des zones protégées comme le Parc national Gashaka Gumti et les réserves forestières avoisinantes.

Key words: Gotel Mountains, Mambilla Plateau, montane flora, Nigeria, restoration

1 Introduction

Mambila Plateau and the Gotel Mountains of Taraba and Adamawa States, eastern Nigeria, lie towards the northern end of the montane archipelago that extends from Bioko northeast to southern and western Cameroon.

This montane archipelago, comprising of grassland and fragmented forest, is some of the most threatened habitat in Africa today (Ezealor, 2002). The forests harbour westerly forms of many of Africa's montane taxa, as well as many endemic species (Maisels *et al.*, 2000; White, 1978). In addition to their rich biodiversity, these montane forests are an important water catchment for the river Benue (Bawden & Tuley, 1966), a chief tributary to the Niger River and a vital resource for a country of over 130 million people (CIA, 2003). Furthermore, the forests are traditionally a source of forest products. Remaining native forest is fragmented, varying in size from narrow streamside strips of less than one hectare to larger patches of up to 46 km^2 in the most remote, relatively inaccessible areas of the Gotel mountains. Much of the montane forest is afforded some protection from being within Gashaka Gumti National Park (GGNP).

Other forests are officially protected by being Local Authority Reserves, although in practice they are virtually unprotected. Other fragments, confined to streamsides or extremely inaccessable hillsides have no protection, and such fragments are now largely extinct.

People have continuously occupied the Mambila region for over four millennia (Zeitlyn & Connell, 2003), and in areas with very low human population levels, traditional methods of extracting resources have not exceeded the capacity of the resources to maintain themselves. However on Mambila Plateau, a shift of political authority from the majority agrarian society, the Mambila, to the minority pastoralist society, the Fulani, has resulted in a major increase in cattle numbers with very little emphasis placed on agricultural development (Hurault, 1998). Escalating cattle numbers have put immense pressure on the natural flora through the continual clearing of land for pasture, seasonal burns for grassland maintenance and new grass growth, soil compaction, and erosion of slopes and watersheds. Concurrently agricultural communities have been squeezed into pockets of land not required by the pastoralists.

Phytoanthropogenic uses of forests fall under the broad categories of food, nonwood products, medicine, fodder, utility and construction wood, fuelwood, spiritual value, shade, environmental protection, agroforestry, and amenity (Osemeobo & Ujor, 1999; Osemeobo, 2001b). Some of this local knowledge has been recorded for the Mambila region (Low, 1996), as well as for similar African montane flora from other countries such as Cameroon, Bioko, Uganda, and Ethiopia (Dijk *et al.*,

TABLE 1. Selected losers of forest cover in 1990–2000.

Country	Total forest	Total forest	Forest cover change (1990–2000)	
LOSERS	1990 ('000 ha)	2000 ('000 ha)	Annual change ('000 ha)	Annual rate of change (%)
Brazil	566,998	543,905	-2309	-0.4
Indonesia	118,110	104,986	-1312	-1.2
Zambia	39,755	31,246	-851	-2.4
Dem. Rep. of the Congo	140,531	135,207	-532	-0.4
Nigeria	17,501	13,517	-398	-2.6

Source: compiled from FAO (2001)

1999; Forboseh, 2002). Humans on Mambila have integrated certain useful plants (Table 1) into their traditional landuse systems. However, use of woody native species at the large woodlot or agroforest level on the Mambila and Gotel Mountains is rare or lacking. *Eucalyptus grandis* and *Cupressus lusitanica*, first trialed during the 1940's, were found to be the most suitable plantation species for the Mambila Plateau region (Fox, 1976). *Eucalyptus grandis* is now the major plantation species in the region.

The possibilities of integrating native flora into existing landuse systems are high as the people are already familiar with most native species and their uses. However, they are generally unfamiliar with the appropriate planting, propagation and management techniques for these species since, until recently, they have been widely available from nearby forests.

Recent research and development has provided valuable data on many useful African plant species. African community forestry projects that aim to build biological diversity into the existing landuse systems through integration of native species are likely to help maintain the floristic biodiversity in the future. These sorts of programmes will attempt to lessen human pressure on protected parks and reserves by increasing the availability of useful species in community forestlands, woodlots and agroforests.

1.1 A general overview of Nigeria's original native forest conditions

A study by the FAO shows that, from 1990 to 2000 the fastest rate of forest destruction for a country was recorded in Nigeria, not Brazil or Indonesia, at a rate of 2.6% annually (See table 1).

Various sources indicate Nigeria's remaining orginal forest cover to be as high as 20% to as little as 1% (Fonseca, 2002; Jensen *et al.* 2003). Considering these statistics and the current rate of deforestation, it will not be long before Nigeria's original native forest cover has all but disappeared from unprotected areas.

1.2 Status of the vegetation on Mambila and Gotel Mountain Plateaux

The Mambila Plateau and Gotel mountains have had, until recently, a relatively low human population, but a combination of high birth rates, recent road developments and enticement of people to the agricultural and grazing areas have significantly increased the population creating an acute deforestation problem in the region.

The landscapes on the plateaux of Mambila and the Gotel Mountains are largely human derived. Human conversion of forest to montane grassland has likely been occurring over several millenia by ancestors of the Mambila people (Zeitlyn & Connell, 2003), but within the last century a combination of frequent burning and cattle grazing has led to large expanses of *Hyparrhenia* and *Loudetia* dominated grassland on the plateaux (Chapman & Chapman, 2001; Hurault, 1998). This phenomenon is as common within the enclaves of GGNP (areas set aside within the Park boundaries for grazing and farming) as on Mambila Plateau and surrounding unprotected areas.

Where the forests have no protection, as on most of Mambila plateau, nearly all have been totally lost or reduced to minimal remnants and replaced primarily by grassland with some cassava and sorghum/maize farms or eucalyptus plantations. Constant grazing pressure and seasonal fires prevent the natural regeneration of woody forest species on these grasslands. The few forest remnants on Mambila today are almost always along streams, where locals protect them for their uses (for example *Raphia* is highly valued for its palm wine), or for sacred values (most village sites traditionally had a sacred grove). However these customary groves are dwindling as the traditional respect for sacred trees wanes. The original 1960's Mambila Afforestation Scheme favoured fast-growing exotics (Fox, 1976), and the present Taraba State Forest Service has followed suit, although there is some attempt to protect remaining native forests.

Native species occur in human settled areas of Mambila Plateau and the Gotel Mountains predominantly if they serve some function such as for live fences, shade, food, fibre, poles, fodder, and fetish trees (trees of a mystical nature). Only in the reserves and GGNP is the forest warranted "full" protection or managed use, but only to the extent that the State Forest and Park personnel can patrol and enforce forest use policies.

No evidence of sustainable management and conservation projects were noted for unprotected areas of Mambila Plateau and the Gotel Mountains. Inside Gashaka Gumti National Park, the Nigerian National Parks Service, the World Wide Fund for Nature (WWF) and the Nigerian Conservation Foundation (NCF) have been actively involved in promoting sustainable management of the human inhabited enclaves and have regulations related to the buffer zones. The State Forest Department is in charge of the forest reserves in the region, and allows limited use by the people, though corrupt relations often exist between forest officers and inhabitants of the local communities.

1.3 Main ethnobotanical uses and important plant species considered

Secondary data documenting the anthropogenic uses of African flora are widely available (Falconer & Koppell, 1990; Ambrose *et al.*, 1996; Mollet *et al.*, 2000; Sene *et al.*, 2002; Shackleton *et al.*, 2002; Ambrose-Oji, 2003), though there is little for Mambila Plateau and the Gotel Mountains. From observations and informal reports, it is known that many plant species are or were important to humans in the region prior to *Eucalyptus*. For example *Hallea stipulosa* and *Syzygium guineense* were used for timber and fuel and *Raphia mambillensis* for housing material (Chapman, 1973). *Prunus africana*, eminent in other afromontane areas for its prostate cancer therapeutic attributes (Cunningham & Mbenkum, 1994; Levin & Das, 2000; Liersch *et al.*, 2002), is found in the Gotel Mountains where locals say its bark cures stomach ailments. Unfortunately, because of overexploitation and poor management record to-date, it is among many of the montane flora of Africa that has been added to the list of endangered species (Cunningham *et al.*, 1997; Dawson, 1997; Dawson & Powell, 1999), though Cheek (2000) contests that it is actually endangered. In some afromontane forest such as in Cameroon, research is in place to manage *Prunus africana* for its valuable properties in hopes of protecting it from complete destruction (Acworth & Ewusi, 1999; Dawson 1997; Dawson *et al.*, 2001; Schaefer, 1990). Other Afromontane species observed or reported to be used in the Mambila and Gotel mountain region are shown in Table 2. Their uses fall into the

TABLE 2. Important uses of montane plant species. (Chapman & Chapman, 2001; Osemeobo & Ujor, 1999).

Category	Type and/or use	Species noted from surveys
Food	Fruits, nuts, edible roots and tubers, spices, edible oils, sauce leaves, juice, honey, palm wine	*Syzygium guineense* var. *macrocarpum*, *Annona senegalensis*, *Ficus* spp., *Afromomum* spp., *Phoenix reclinata*, *Raphia* spp.
Nonwood products	Gums, resins, oils, tannins, dye, bees wax	*Pterocarpus erinaceus*, *Harungana madagascariensis*
Medicine	Bark, leaves, roots for various bodily disorders, maternal applications	*Syzygium guineense* var. *macrocarpum*, *Prunus africana*, *Khaya grandifoliola*, *Harungana madagascariensis*, *Annona senegalensis*, *Macaranga* spp., *Hymenocardia acida*
Fibre	Rope, bark, cloth, mats	*Laportea mooreana*, *Phoenix reclinata*, *Raphia* spp., *Pandanus* spp.
Fodder	Grass, plants, leaves, pods and twigs for livestock	*Annona senegalensis*, *Gardenia* spp, *Ficus* spp.
Utility wood	Kitchen utensils, yogurt sticks, agricultural and hunting tool handles, walking sticks	*Syzygium guineense*, *Calamus* spp., *Prunus africana*, *Bridelia speciosa*, *Polyscias fulva*
Construction wood	Sawnwood, roundwood, poles, posts	*Newtonia buchananii*, *Cordia millenii*, *Entandrophragma angolense*, *Hallea stipulosa*
Fuel	Fuelwood and charcoal	*Syzygium guineense*, *Bridelia speciosa* and many others
Spiritual value	Sacred, ceremonial, fetish trees	*Elaeophorbia drupifera*, *Erythrina senegalensis*, *Stereospermum acuminatissimum*
Shade	Large crown	*Trema orientalis*, *Ficus* spp., *Croton macrostachyus*
Living fence	Hedge or live posts	*Erythrina senegalensis*, *Dracaena arborea*, *Dracaena fragrans*, *Ficus* spp, *Polyscias fulva*
Soil and water conservation	Hold soil in place, enrich soil	*Syzygium guineense*, *Tephrosia vogelii*
Amenity	Aesthetic, ethical values	*Dracaena arborea*, *Spathodea campanulata*
Agroforestry system	Park trees, enrich soil	*Tephrosia vogelii*, *Trema orientalis*, *Bridelia speciosa*

broad categories of food, nonwood products, medicine, fodder, utility and construction wood, fuelwood, spiritual value, shade, environmental protection, agroforestry, and amenity. These categories can be further subdivided by products types and/or uses.

1.4 Potential for native species in vegetative restoration

A number of the plant species found on the Mambila and Gotel mountain plateaux play an important role in the initial stages of natural forest restoration. Studies in Ethiopia show that various factors such as light, slope, moisture, plant density, and herbivory affect regeneration. The studies revealed that *Syzygium guineense* subsp. *guineense* generally exhibited healthier regeneration over *Olea capensis, Croton macrostachys* and *Prunus africana* (Getachew *et al.*, 2002). Species with appropriate regeneration characteristics will be most desirable for restoration purposes. Woody species recorded (by Chapman, 1993; Chapman & Chapman, 2001) as being light tolerant and moderate to very successful colonisers of open grasslands include: *Allophylus africanus*, *Antidesma vogelianum*, *Bridelia speciosa*, *Clausena anisata*, *Croton macrostachyus*, *Dracaena fragrans*, *Ficus exasperata*, *Maesa lanceolata*, *Pittosporum mambillae*, *Polyscias fulva*, *Psychotria succulenta*, *Solenecio mannii*, *Jasminum dichotomum.*

This list is far from exhaustive and needs more in-depth study. Additional native species on Mambila observed to be good colonisers include *Harungana madagascariensis* and *Syzygium guineense* subsp. *guineense*. Research on these and other species should reveal further information on their resilience and suitability for community forestry restoration projects. Important characteristics to consider would include their importance to the local people, their resistance to fire and grazing damage, and their soil and microclimatic enhancing properties favourable for ecological restoration efforts.

1.5 Restoration using native montane plants: the way forward

There are many opportunities to integrate useful native montane flora into the existing landuse systems on the Mambila and Gotel plateaux. An important initial step in this process is to understand and record historical and present knowledge of native plants as well as the local land use practices that incorporate native plant species. An in-depth participatory analysis with the local community to determine potentially acceptable land use practices is essential (Carter *et al.*, 1996; McDonald *et al.*, 2003). Ensuring that the local people's knowledge is included and that they have accepted a scrutinized system will largely determine a project's success (Mwihomeke, 1989). The production system's overview should not only examine human plant use and land use practices in the region, but also look at uses applied by societies from other African montane regions having the same, or similar, species, for example traditional land-use systems in Tanzania such as the Chagga home gardens (Smith, 1932; Fernandes *et al.*, 1985; Trapnell, 1997; Ya *et al.*, 2000). Additionally, science and technology have looked at the uses and management of quite a number of the same species for other regions in Africa (Trapnell, 1997). This information will be invaluable for the successful establishment of species whose propagation and silvicultural prescriptions are least or not at all known.

The ways that these species can be incorporated may be through a combination of means, 1) introducing a new agroforestry system with proven immediate benefits, 2) a gradual series of unthreatening reintroductions of anthropogenically and ecologically beneficial plant species. These would likely be applied in unison in a community forestry project, and 3) restoration with the assistance of natural agents of dispersal.

The first means, a new agroforestry system, must be socially acceptable and must not jeopardise the current means of livelihood. Immediate benefits that at least match those of the current production systems should be realised (Osemeobo, 2001a).

Initially it may be necessary to set up trial land-use systems with risk-taking farmers to illustrate their effectiveness. Incentives such as free seedlings, or paid labour may be necessary to help get these projects underway.

The second means, a gradual series of unthreatening reintroductions, would add useful native species to otherwise unused spaces and wastelands, providing the community with additional wood and nonwood forest products. These unused spaces would include rocky areas, barren lands, stream sides, road and walkway sides, private land boundaries and residential areas. Many exotic tree plantings, especially of *Eucalyptus* and *Cupressus,* are already in place, and trials to incorporate native species into these monocultures, such as the introduction of useful native understory plants, may be acceptable where they do not interfere with the overall production of the plantation. These will increase the biological diversity and add multiple benefits to the local community.

The third means compliments the second. Natural regeneration on restoration sites can occur with the assistance of wind, animal and coppice. Animal dispersal would require a mechanism to attract the seed dispersers e.g., birds, primates and bats to the desired sites. Sites might include tree rows or wind breaks, deteriorated corridors with remnant canopy trees, hill tops with remnant trees, and plantation understory or openings. A problem faced by many such sites is the exposure to livestock and fires and reduced seed dispersal (Holl, 1999). Some measure to lessen the exposure to grazing and fire as well as to increase seed dispersal would be required. Studies suggest that natural forest restoration may proceed very slowly on degraded lands (Duncan & Chapman, 1999) and is dependent on the connectivity and distance to forests (Harvey, 2000). It is likely that many degraded areas of today's tropics will require human assistance to recover forest structure, species composition, and species interactions typical of mature tropical forests (Chazdon, 2003; Holl *et al.*, 2000).

1.6 Barriers to the introduction of new innovative bio-diverse agroforest systems

While the reintroduction of native plant species into rural community landscapes on the Mambila and Gotel plateaux sounds relatively straightforward, past experience proves otherwise (Le Houerou, 2000; Omotayo, 2002) and a number of barriers are inevitable. People are one factor that present a barrier. They may be unwilling to participate in the reintroduction efforts if they see no immediate benefit and they may not be able to devote the time out of their busy farming lifestyle to protect and manage restoration sites, or to learn new agroforestry methods (Osemeobo, 2001a).

Another factor that is a barrier to restoration is domestic livestock. On the Mambila and Gotel plateaux, livestock, particularly cattle are the lifeline of the Fulani. If there is no incentive to prevent them from encroaching onto potential restoration areas, it will be extremely difficult to guarantee that they will not. So the success of any restoration project will require the investigation into what types of incentives will encourage the Fulani graziers to keep their cattle away from restoration sites.

2 Summary and conclusions

The biological diversity is still available in GGNP and the forest reserves and forest remnants of Mambila Plateau and Gotel mountains. This is the genetic source for potential projects that can reintroduce native species onto the landscape through both man-assisted and natural methods. The problem is how to get the people to incorporate native trees into their existing landuse systems. It will only be possible if they realise immediate and significant benefits from these systems. This will take innovative research and planning, but we believe it is possible.

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IDENTIFICATION DES AIRES PRIORITAIRES POUR LA CONSERVATION DES PLANTES A MADAGASCAR: UTILISATION DES DONNÉES BOTANIQUES POUR DÉFINIR LES PRIORITÉS EN MATIÈRE DE CONSERVATION

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Résumé

Les bases de données dérivées des étiquettes des spécimens déposés dans les musées et herbiers constituent un outil puissant pour la gestion et conservation de la biodiversité. Le développement des stratégies de conservation doit se baser sur une compréhension approfondie de la distribution et de l'écologie des espèces. L'évaluation de la distribution des espèces appartenant aux familles endémiques de Madagascar et l'estimation de leur risque d'extinction ont démontré que 26% des espèces sont absentes dans le réseau actuel des Aires protégées. De telles analyses SIG, ciblées sur des groupes dont le cadre taxinomique est à jour permettent d'évaluer des paramètres éco-géographiques afin de définir 1) des phytochorées (suivant le modèle développé par F. White pour l'Afrique Tropicale), 2) des schémas biogéographiques et 3) des aires d'une importance particulière pour la conservation (diversité exceptionnelle, concentration des espèces localement endémiques, rares ou menacées). L'objectif du projet que nous menons à Madagascar est de renforcer la conservation de la flore à travers une meilleure orientation des actions menées par différents organismes (l'Etat, des ONGs, etc…) afin d'améliorer la représentativité des aires protégées (ex. par l'addition de nouveaux sites importants pour la flore) et d'identifier les espèces les plus menacées qui nécessitent une conservation *ex situ* et *in situ*.

Abstract

Databases derived from herbarium specimen labels are a powerful tool for biodiversity conservation. Development of conservation plans should be based on an understanding of species distribution and ecology. The distribution of species (belonging to Madagascar's endemic families) and their extinction rate estimation show that 26% of the species are not present in the protected areas network.

GIS analysis, targeted on those important taxonomic groups allow us to evaluate new ecological and geographical parameters to define 1) phytochoria (according to

F. White's model for tropical Africa), 2) bio-geographical patterns, 3) important conservation areas (exceptional diversity, concentration of endemic, rare or endangered species). The aim of this project is to reinforce plant conservation through a better coordination between the different organisations (NGOs, State, etc), in order to improve the protected area's significance (by setting up new important sites for plants for example) and to identify the most endangered species in need of *ex situ* and *in situ* conservation.

Key words: conservation, database, Geographical Information System (GIS), phytochoria, Madagascar

1 Introduction

Les données systématiques incluant les données sur les collections, données phylogénétiques, classifications et données d'observations sur terrain peuvent ou doivent jouer un rôle important dans les études de la biodiversité et de la conservation biologique (Funk & Richardson, 2002).

Depuis quelques années, et à travers les différents projets de conservation, force est de constater l'utilisation accrue des informations/données sur les collections botaniques ou d'animaux à des fins de conservation si auparavant elles ont été souvent négligées du concept de la biodiversité. Dorénavant, il est admis que les connaissances principales de la diversité biologique découlent de l'étude des collections par les taxinomistes et notamment sur la définition et la délimitation ou « circonscription » des espèces, qui constituent l'unité de base de la biodiversité.

Les données primaires déterminent à la fois les cadres taxinomiques qui indiquent la délimitation des espèces par rapport aux espèces voisines, et également les distributions géographiques de ces espèces, sont préservés dans les 3,000 herbaria implantés par le monde (Schatz, 2002).

Selon Jorge *et al.* (2000), de larges bases de données sur les étiquettes des collections de plantes, géoréférencées, sont compilées par les nombreux musées et herbaria, aussi bien par des institutions gouvernementales. Non seulement de telles bases de données fournissent un accès rapide à une inestimable quantité d'informations qui intéressent les taxinomistes et systématiciens, mais elles peuvent également être utilisées pour les études écologiques et biogéographiques.

Il est indiscutable que de nos jours les synthèses et les analyses des données de base abritées dans les herbaria partout dans le monde, constituent un moyen efficace pour influencer directement la planification de la conservation, et de cette façon leur étude peut contribuer à une réduction des pertes de la diversité des plantes.

Cette étude présente alors un exemple d'utilisation des données primaires sur les collections botaniques à des fins de conservation adaptée à la réalité de la flore de Madagascar.

1.1 "TROPICOS": une base de données sur les plantes de Madagascar

A Madagascar, plusieurs herbaria aussi bien locaux, régionaux que nationaux ont été créés pour recevoir les collections botaniques effectuées dans toute l'île par différents chercheurs opérant dans la biodiversité. Mais la majeure partie des collections botaniques effectuées à Madagascar sont maintenues dans les deux herbiers nationaux TAN (affilié au Parc Botanique et Zoologique de Tsimbazaza) et TEF (affilié au Département de Recherches Forestières et Piscicoles). Ensemble, ces deux herbaria nationaux détiennent actuellement environs 150.000 spécimens d'herbiers de référence qui ont fait l'objet d'une élaboration de base de données botaniques en l'occurrence TROPICOS.

Initiée au début des années 80 par le Missouri Botanical Garden à travers ses multiples projets de collaboration dans divers pays et institutions partenaires, TROPICOS est l'une des plus grandes bases de données botaniques connues au monde. TROPICOS est mixte, et comporte trois composantes reliées: collections, taxons et bibliographie. Cette base de données est initialement utilisée à Madagascar en 1992 dans le cadre du projet «Conspectus des plantes vasculaires de Madagascar (1992–2000)» dont le but était de compiler les données sur toutes les plantes vasculaires de Madagascar en utilisant des sources diverses telles que littératures, les carnets de récolte mais principalement les étiquettes des spécimens d'herbier. Depuis, TROPICOS, disponible sur le site Internet du MBG (http://www.mobot.org/W3T/) s'est développé et comprend actuellement une grande quantité de données sur la flore malgache, à savoir 980.000 de noms de plantes en tout dont 26.000 noms de plantes de Madagascar avec 10.000 noms acceptés. Plus de 65.000 références bibliographiques compilés dont les 5000 traitent la flore malgache. Dans l'ensemble, 2 millions spécimens d'herbier dont 120.000 appartiennent à Madagascar sont enregistrés dans TROPICOS. La plupart de ces enregistrements sont géoréferencés.

1.2 Phytochorologie: un moyen efficace et fiable pour valoriser les donnees primaires

Van Wyk *et al.* (2001) définit la phytochorologie comme étant l'étude de la distribution des taxons de plantes et des régions floristiques ainsi que leur histoire. La diversité botanique n'est pas régulièrement répartie sur terre. En d'autres termes, chaque taxon végétal (allant de l'espèce au taxon de rang plus élevé) a une répartition géographique particulière qui détermine le modèle de distribution, un des caractères diagnostiques d'un taxon.

La géographie floristique des plantes consiste à définir et à décrire les aires ou régions floristiques (régions partageant les mêmes taxons) et les éléments floristiques. Elle tend à mettre en exergue aussi bien les endémiques que les espèces à large répartition. Les espèces ou taxons à rang élevé endémiques représentent l'élément géographique qui caractérise le plus naturellement l'unicité floristique d'une région particulière. Les importantes concentrations de ces espèces endémiques forment les centres d'endémisme des plantes qui sont d'un intérêt considérable pour les botanistes et les conservationistes.

De nos jours, nombreuses sont les nouvelles méthodes qui modélisent les données sur les collections de plantes en combinaison avec des données abiotiques et prédisent la distribution potentielle des espèces. Notons que le modèle de distribution d'une espèce peut être estimé soit par la technique de modélisation basée sur l'unique-présence, soit par la technique de statistique de modélisation basée sur les données absence-présence. De cette analyse spatiale prédictive peuvent être déduites des cartes de richesse spécifique, de centre d'endémisme, ou rareté et peuvent être sélectionnés des sites prioritaires pour une éventuelle conservation des espèces de plantes.

Toutefois, trois conditions s'avèrent nécessaires pour effectuer ce genre d'analyse spatiale.

La première condition concerne une analyse basée sur un échantillonnage de flore utilisant un cadre taxinomique à jour. Schatz (1994) confirmait qu'un tiers de la flore est encore à traiter et qu'un autre tiers doit être révisé car selon Morat et Lowry (1993) les familles dans la flore de Madagascar traitées avant 1960 doivent être révisées, la durée de vie d'une flore étant de 40 ans selon Polhill (1990). Selon Poncy *et al.* (1994), la flore de Madagascar a commencé à paraître en 1936 et 4 des 40 familles

(Euphorbiaceae, Fabaceae, Poaceae et Rubiaceae) qui restent encore à traiter représentent au moins 20% de la flore de phanérogames. Par conséquent, dans le cas de la flore malgache, l'analyse spatiale basée sur des taxonomies anciennes s'avère inadéquate et pourrait même induire en erreur.

La deuxième condition concerne une analyse basée sur des récoltes géo-référencées. Dans cette condition, la référence géographique doit se faire à une échelle significative pour la conservation. L'utilité des échantillons historiques dans la détermination de la distribution d'une espèce est souvent entravée par l'absence de coordonnées géographiques. (Schatz *et al.*, 1994).

Ainsi, un des aspects les plus importants dans l'élaboration de la base de données botaniques TROPICOS consiste à attribuer *post facto* au plus grand nombre d'échantillons historiques leurs latitude/longitude/altitude car pour la plupart d'entre elles, les informations sur les lieux de récolte sont imprécises ou vagues. Cette attribution *post facto* de coordonnées géographiques est facilitée par utilisation de l'Index Géographique ou gazetteer des localités des collectes botaniques à Madagascar compilé depuis 10 ans.

Par contre, la plupart des récoltes récentes par leur coordonnées géographiques issues par simple lecture de GPS sur le terrain sont à localisation précise.

La troisième condition concerne une analyse intégrant des données primaires récentes. La re-évaluation d'un cadre taxinomique existant nécessite l'examen de tous les spécimens disponibles dont les collections récentes qui peuvent fournir des données fiables sur la distribution de l'espèce.

Depuis quelques années le Missouri Botanical Garden a décidé de faire un effort concret pour chercher des moyens avec lesquels ses expertises sur la flore Malgache plus les données botaniques rassemblées dans la base de données TROPICOS, peuvent être mises à disposition pour une meilleure utilisation dans le cadre de la planification et de la gestion de la conservation à Madagascar.

1.3 Projet pilote Liste Rouge des familles endémiques de Madagascar

Les données primaires, souvent incomplètes et relativement anciennes fournissent les réponses aux trois questions «QUOI», «OU» et «QUAND» nécessaires pour caractériser la biodiversité. Ces données ont donc un rôle primordial dans la réalisation des programmes de conservation et de gestion durable et contribuent ainsi à l'effort global pour la diminution de la perte de la biodiversité. En 1998, pour intensifier le profil des plantes au sein de la communauté de la conservation à Madagascar, MBG en collaboration avec l'Université d'Antananarivo et l'Association Nationale pour la Gestion des Aires Protégées (ANGAP), a travaillé sur le projet Liste Rouge des espèces des familles endémiques de Madagascar. L'objectif principal de ce projet consiste à l'analyse globale des espèces appartenant aux sept familles des plantes endémiques malgaches, afin d'évaluer la distribution de chaque espèce et d'estimer leur risque d'extinction (Schatz *et al.*, 2000a).

Une première étape dans la méthodologie de ce projet est constituée par l'évaluation des cadres taxinomiques existants pour ces familles avec l'examen de toutes les données primaires sur les collections. Les révisions des cadres taxinomiques des 103 espèces appartenant aux familles endémiques Malgaches comprennent 36 espèces nouvellement reconnues avec 30 espèces nouvellement décrites et quatre espèces déjà reconnues auparavant (Schatz, présentation orale, Greece 2002). L'étape suivant est constituée par l'évaluation des statuts de conservation de chacune de ces espèces. Cette étape est basée sur l'analyse géographique avec l'aire d'occupation de l'espèce et les menaces. Pour chaque espèce, les mesures de surface basées sur la distribution primaire calculée directement avec l'outil SIG fournissent une estimation de la vulnérabilité des espèces. Les catégories de la liste rouge de l'IUCN (IUCN 1994, IUCN/SSC Criteria review Working group 1999) ont servi de directive dans la description hiérarchique des risques d'extinction des espèces. Ces études sur les familles endémiques de Madagascar ont permis d'identifier des sites de « richesse d'endémisme » important c'est-à-dire, avec une concentration d'espèces, dont un nombre important est vulnérable ou menacé (Schatz, 2002). Ainsi, la protection de ces sites permettra la conservation des quelques espèces vulnérables et menacées. A Madagascar, la protection d'une espèce dépend aussi de sa présence dans un type d'aire protégée. Ainsi, une superposition des polygones représentant les aires protégées actuelles et les polygones qui expriment l'occurrence primaire de l'espèce permet d'identifier les lacunes dans la protection existante.

TABLEAU 1. Tableau récapitulatif des résultats d'analyse sur l'étude des espèces appartenant aux familles des plantes endémiques Malgaches

Révision des cadres taxinomiques	Total des espèces: 108, Espèces nouvellement reconnues 36 (35%), Espèces nouvellement décrites 32 (30%) (Randrianasolo & Miller, 1999; Schatz *et al.*, 1998, 1999a, b, 2000b, 2001; Lowry *et al.*, 1999, 2000, 2002)
Analyse des lacunes existantes dans la conservation de la diversité des plantes à Madagascar	24 espèces (26%) sur 93 sont absentes dans le réseau actuel des aires protégées donc ne possèdent aucune protection (Schatz, 2002)
Analyse de la distribution des espèces	Identification des sites 1) «irremplaçables»: relatif au concept de l'unicité permettant de définir des sites qui contiennent des espèces existant uniquement dans une localité, 2 localités,… 2) «richesse d'endémisme» important: sites avec une concentration d'espèces dont la distribution est fortement restreinte. Un concept fortement lie avec la notion de «complémentarité». Les sites irremplaçables et/ou présentant une richesse d'endémisme important deviendront «Aires Prioritaires pour la Conservation des Plantes»

Un autre but de l'analyse préliminaire de ces espèces appartenant aux familles endémiques malgaches est d'explorer des méthodologies d'analyse potentielles pour le projet d'évaluation des aires prioritaires pour la conservation des plantes. Ainsi, cette méthode qui utilise les critères de représentativité et de complémentarité des espèces et des sites, a été retenue.

1.4 Projet d'evaluation des aires prioritaires pour la conservation des plantes (APAPC)

Les résultats des études sur les familles des plantes endémiques Malgaches ont démontré que le réseau actuel d'aire protégé est inadéquate pour conserver la flore malgache dans son ensemble et suggèrent que la même situation pourrait être constatée avec certains groupes de faune. Ainsi, pour renforcer cet effort déjà initié avec les familles endémiques Malgaches, le MBG a démarré, au début de l'année 2002, le projet

APAPC qui utilise un échantillonnage représentatif de l'ensemble de la flore malgache. Le projet utilise plus de 1000 espèces sur les 12,000 à 13,000 espèces présentes à Madagascar soit les 10% de la totalité de la flore malgache. Cet échantillonnage servira de base objective pour identifier les Aires Prioritaires pour la Conservation des Plantes, évaluer leur contribution à la conservation des plantes et servir les gestionnaires de la conservation dans leurs planifications régionale et nationale.

Pour assurer la conservation de toutes les aires les plus importantes pour les plantes, le projet APAPC contribue à la mise en oeuvre de la Stratégie Globale pour la Conservation des Plantes (GSPC) adoptée en 2002, dans le cadre de la Convention sur la Diversité Biologique (CDB). En effet, le projet APAPC identifie les aires prioritaires pour la conservation des plantes à l'échelle nationale et participe de façon significative au défi de la communauté de la conservation mondiale pour arrêter le déclin de la biodiversité vers 2010.

Les pricipaux objectifs du projet d'évaluation des Aires prioritaires pour la Conservation des Plantes à Madagascar sont, d'une part, augmenter le nombre de sites protégés pour assurer la conservation des espèces de plantes menacées, ceci a contribué à l'identification des aires les plus importantes pour les plantes (IPAs) décrites dans, l'objectif 5 de la Stratégie Globale de la Conservation des Plantes. Et d'autre part, de renforcer la conservation de la flore malgache par le biais de l'amélioration des actions menées par les différents opérateurs nationaux et internationaux. Ces objectifs contribuent à l'effort national pour la mise en œuvre de la déclaration du President Malgache pour tripler la totalité de la surface des Aires protégées à Madagascar dans 5 ans (World Parc Congress, Durban, Septembre 2003).

A long terme, toutes les aires importantes pour les plantes devront être protégées en utilisant les méthodes les plus appropriées concernant la mise en place des réseaux d'aires protégées, l'application d'une gestion adéquat, l'implication des communautés locales et de toutes les parties prenantes.

Cette nouvelle initiative suit une approche logique dans son ensemble en utilisant les méthodes rigoureuses et dont l'efficacité est déjà prouvée dans l'exécution du projet Liste Rouge des familles endémiques Malgaches.

1.5 Base de donnees pour la conservation des plantes (Plant Conservation Database/PCD)

De nos jours, les chercheurs botanistes taxonomistes et systématiciens mettent l'accent sur les activités liées à la conservation, cherchant l'application des données botaniques et leurs expertises pour mieux servir la gestion et la planification de la conservation. Avec cette nouvelle orientation de la recherche pour la conservation de la biodiversité, une amélioration de TROPICOS s'impose. Ainsi, avec les modifications par rajout des valeurs ajoutées sur les données écologiques et biologiques du spécimen, plus les metadonnées sur le degré de précision des coordonnées géographiques et l'altitude, TROPICOS devient une base de données utile pour la conservation dénommée «Base de données pour la Conservation des Plantes (PCD, Plant Conservation Database)».

Les données de base comprennent des taxinomies à jour jointes à des cadres taxonomiques fiables et des enregistrements géo-référencés des spécimens représentatifs. En élargissant l'échantillonnage pour inclure les enregistrements disponibles appartenant aux groupes de plantes soigneusement sélectionnés, il est possible d'évaluer les paramètres tels que la distribution géographique ou des paramètres écologiques pour clarifier les modèles de distribution géographique et ensuite identifier les sites d'importance pour la conservation.

La base de données contient des informations botaniques globales, provenant des récoltes récentes et des collections historiques, pour plus de 600 taxons prêts pour l'analyse de la conservation. En effet, pour l'identification de ces taxons cibles, le projet collabore avec les spécialistes des plantes malgaches partout dans le monde et avec le Groupe des Spécialistes des Plantes Malgaches (GSPM) créé pour représenter l'autorité scientifique de l'IUCN pour la validation des espèces de la Liste Rouge à Madagascar.

1.6 Aires prioritaires pour la conservation des plantes (Priority Areas for Plant Conservation/APAPC)

Les données primaires compilées dans la Base de données TROPICOS serviront à la production des cartes de distributions des espèces. Ces cartes permettront la délimitation des grandes régions floristiques définies comme aires présentant des groupes de base similaires d'espèces. Lorsque les distributions des espèces sont cartographiées, l'étape suivante consiste à la modélisation bioclimatique des espèces et l'analyse des influences des paramètres environnementaux sur la biodiversité. Les techniques usuelles de SIG permettront les calculs des différents aspects de la biodiversité et par la suite, on peut distinguer des aires surnommées «centre d'endémisme» déterminées par une haute concentration d'espèces et à distribution très restreinte. Le processus d'analyse du projet fait intervenir le concept d'irremplaçabilité, qui se réfère à la mesure "d'unicité" de telle sorte que la valeur d'irremplaçabilité d'un site reflète l'importance relative de ce site dans l'atteinte d'un objectif de conservation. La forte corrélation entre richesse des espèces et la richesse d'endémisme permettra la prédiction de la richesse des espèces à partir des espèces rares. Les résultats de ces analyses formeront des bases objectives pour l'évaluation de l'importance de la conservation dans le réseau actuel d'aires protégées. En effet, le projet prévoit l'analyse des lacunes pour le réseau actuel des aires protégées avec une superposition des résultats du projet avec la carte des aires protégées existantes. D'une part, la conservation de ces centres d'endémismes pour les plantes permettra la sauvegarde de nombreuses espèces vulnérables. Et d'autre part, ces aires détiennent la clé de l'origine et de l'évolution de la diversité botanique dans une région particulière et elles sont considérablement importantes pour les botanistes/ taxonomistes et les conservationistes.

1.7 Aires prioritaires clés

Après avoir identifié les aires prioritaires pour la conservation des plantes, un nombre limité d'aires prioritaires sera sélectionné en utilisant les critères suivant: 1) Importance du site vis-à-vis de l'augmentation de l'ensemble de la conservation des plantes à Madagascar, plus précisément par le degré de complémentarité de sa composition en espèces par rapport au réseau actuel d'aires protégées; 2) Compatibilité aux priorités actuelles et stratégies définies par les organismes de conservation à Madagascar; et 3) des considérations logistiques qui pourraient influencer l'accessibilité. Les aires prioritaires clés seront évaluées en terme d'étendue de la végétation primaire et présence d'espèces végétales critiques. Des études sur le terrain prévoient des enquêtes concernant les activités des populations locales dans les aires prioritaires pour estimer l'intensité des activités qui ont des impacts sur ces aires prioritaires. Cette partie de l'étude prévoit la production de cartes sur l'occupation des sols, localisation et nombre approximatif de la population, et des pistes aux alentours et à l'intérieure des aires prioritaires. Ces informations seront présentées aux gestionnaires de la conservation et décideurs sous formes de recommandations de conservation pour chacune des aires prioritaires pour servir à la réalisation des différents plans de gestion et des programmes de conservation locale, régionale et nationale.

1.8 Partenariat et collaboration

Les informations sur les processus biologiques et les activités humaines peuvent constituer des outils extrêmement précieux pour les gestionnaires des sites de conservations (White *et al.*, 2001). Des informations mises à jours et collectées de façon rigoureuse donnent une idée des forces en présence dans un endroit donné. Ainsi, les décideurs devront disposer des informations fiables (conforme à l'objectif 14 du GSPC), sur les sites de conservation prioritaires, qui abritent les plus grandes concentrations d'espèces à conserver, et il faut que ces informations soient basées sur des analyses objectives et pas seulement sur l'avis de quelques experts.

En effet, une étape clé pour la réalisation de tout projet d'identification des aires prioritaires de conservation est la mise en œuvre du processus participative avec «Consultation-Réalisation-Evaluation par retour d'information» avec les partenaires. Ce n'est pas nécessairement un processus facile, mais beaucoup d'efforts doivent être focalisés pour construire un partenariat et une collaboration efficace entre les parties prenantes.

Que ce soit pour les étapes de collecte des données (taxons cibles) ou pour les étapes d'analyse des données permettant l'identification des aires prioritaires pour la conservations des plantes, ou que ce soit pour enchaîner sur les recommandations concernant des stratégies de conservation et les propositions d'actions prioritaires, les différentes parties prenantes ont l'opportunité de s'exprimer.

En définitive, cette approche a permis:

Premièrement, les implications des acteurs d'intérêt différents: scientifiques (taxinomistes, biologistes, ...), décideurs (bailleurs, politiciens, ministres, ...), Institutions et Organismes de conservation de l'environnement (OGs, ONGs, Institutions/Centres de recherches, Herbiers nationaux et internationaux, et Universités, ...).

Deuxièmement, les implications des acteurs du début jusqu'à l'obtention des résultats attendus par des réunions, ateliers, consultations individuelles, rapport d'avancement des activités et des articles publiés dans notre bulletin Ravintsara. Ravintsara est un bulletin trimestriel sur les plantes malgaches et leur Conservation, édité par le MBG de Madagascar depuis décembre 2002.

(www.mobot.org/MOBOT/Research/africaprojects.html).

Afin d'assurer que les espèces absentes ou insuffisamment représentées dans le réseau actuel d'aires protégées seront conservées dans des nouveaux sites, nous espérons à la fin du projet de délimiter les principales phytochorées et d'évaluer la représentativité du réseau actuel des aires protégées avec 1) identification d'au moins 10 nouveaux sites prioritaires de conservation pour augmenter le nombre des espèces conservées et 2) la définition des mesures de conservation *in situ* et *ex situ* pour au moins 50 espèces fortement vulnérables ou menacées.

2 Conclusion

Les méthodologies développées dans ce travail permettent une approche globalement satisfaisante dans l'exercice de définition de priorité pour la conservation. Les trois points suivants méritent d'être retenus:

Meilleure approche pour appliquer les données botaniques à la conservation, et notamment à la planification et l'identification des priorités. Avec les expériences acquises par le projet APAPC, les données botaniques issues des collections botaniques récentes ou historiques contribuent à l'identification des aires prioritaires pour la conservation des plantes. L'utilisation des informations botaniques dans l'étude de la biodiversité ajoute une dimension aux résultats utilisés pour la prise de décision concernant la conservation.

Approche faisable avec un échantillonnage représentatif qui valorise les travaux des spécialistes de la flore d'un pays, mais aussi opportunité de compléter la flore surtout d'un pays comme Madagascar où la connaissance sur la flore est loin d'être complète. Etude repliquable pour la priorisation des aires de conservation dans les hotspots en Afrique. Cette étude nécessite une condition *sine qua non*: avoir une taxonomie fiable et distribution bien définie. Comprendre le modèle de la biodiversité est un moyen pour arriver à la conservation des espèces menacées et les habitats uniques, en particulier à Madagascar et en général dans les hotspots en Afrique.

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THE SIGNIFICANCE OF IMPORTANT BIRD AREAS FOR CONSERVATION OF PLANTS IN UGANDA

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Abstract

Plant diversity surveys in Uganda are still far from complete. The limited availability of resources for conservation of biodiversity has made it imperative to design strategies aiming at prioritizing areas for conservation. The Important Bird Area (IBA) programme and process is an effort to this end and it is here assessed to evaluate the significance of these areas (known to be important for birds) for the conservation of plants. The diversity and distribution of vascular plants in selected areas in Uganda were examined with a view of assessing the extent to which they conserve plants. These were seven drylands and 10 wetlands. Over 2000 species (37% of the national total) were recorded. Four of the species recorded are globally threatened, and two are endemic to the country. New records to the country, which are accordingly nationally rare, were 34, three of which are also new to the whole Tropical East Africa Flora area. It is apparent that the IBAs have a significant role to play for the conservation of plants in Uganda on account of species richness, global threat and endemism. It is however necessary to survey the non-IBA areas to establish the latter's comparative contribution.

Résumé

Le rôle des zones de protection des oiseaux dans la conservation des plantes en Ouganda. Les inventaires de la flore en Ouganda sont loin d'êtres finis. Les budgets limités pour la conservation de la biodiversité ont rendu impérative la création de stratégies favorisant certaines zones de conservation. Le programme de zones de protection des oiseaux (IBA Important Bird Area) est ici une aide, et évalué dans ces zones (renommées importantes pour la conservation des oiseaux), pour la conservation des plantes. La diversité et distribution des plantes vasculaires dans des zones sélectionnées en Ouganda furent examinées en relation avec leur rôle dans la conservation des plantes. Sept zones sèches et dix zones humides furent choisies. Plus de 2000 espèces (37% du total national) furent comptées. Quatre de ces espèces sont globalement menacées, et deux sont endémiques au pays. 34 nouveaux rapports de plantes furent enregistrés pour le pays, trois de ces espèces sont aussi nouvelles pour tout l'Est de l'Afrique tropicale. Il est évident que ces zones de protection des oiseaux ont un rôle significatif à jouer dans la conservation des plantes en Ouganda par rapport à la richesse en espèces, menace globale et endémisme. Il est cependant nécessaire d'inventorier les zones autres pour établir une prochaine étude comparative.

Key words: biodiversity conservation, drylands, Important Bird Area (IBA), Uganda, wetlands

1 Introduction

The conservation of biodiversity in Uganda has historically hinged on the protected area system which includes National Parks, Forest Reserves, Wildlife Reserves, Community Wildlife Reserves and Wildlife Sanctuaries. The existing protected area system was designed without much scientific consideration as many of them were only gazetted to evacuate people from areas of epidemics such as yellow fever and sleeping sickness. This was the driving force for eviction of people and thus for the areas' declaration as protected areas. There is therefore bound to be a number of areas outside the protected area network that are important for biodiversity conservation. Plant diversity in Uganda, like elsewhere in the tropical world, is highest in the forest areas and much research has been concentrated in these habitats. Wetlands are potential candidates but not a single one is gazetted. Drylands also do support a very rich flora but less attention has been accorded to them. The vegetation types and the floral regions in the country are shown in Fig. 2.

Conservation efforts in Uganda are taking shape and both planning and resource management strategies are being developed based on a more firm foundation than they were in the past. There is, however, a need to review how well they capture the country's biodiversity and whether they protect the key species. To this end, the existing protected area network has been re-examined (Pomeroy *et al.*, 1999) in light of its effectiveness in protecting the rich biota of the country. The Important Bird Area (IBA) programme is one of the efforts in this direction though only based on birds.

Nature Uganda (East African Natural History Society), the Ugandan partner of BirdLife International, carried out bird surveys and identified 30 IBAs in Uganda. Of these, 20 fall within the country's protected area categories such as National Parks, Forest Reserves and Wildlife Reserves and the remaining 10 are unprotected (Fig. 1). The unprotected ones are either open water areas, wetlands or a combination of the two. All these areas qualified on the basis of at least one of the four set criteria: a) areas with species under global threat, b) those with range-restricted species, c) those with biome-restricted

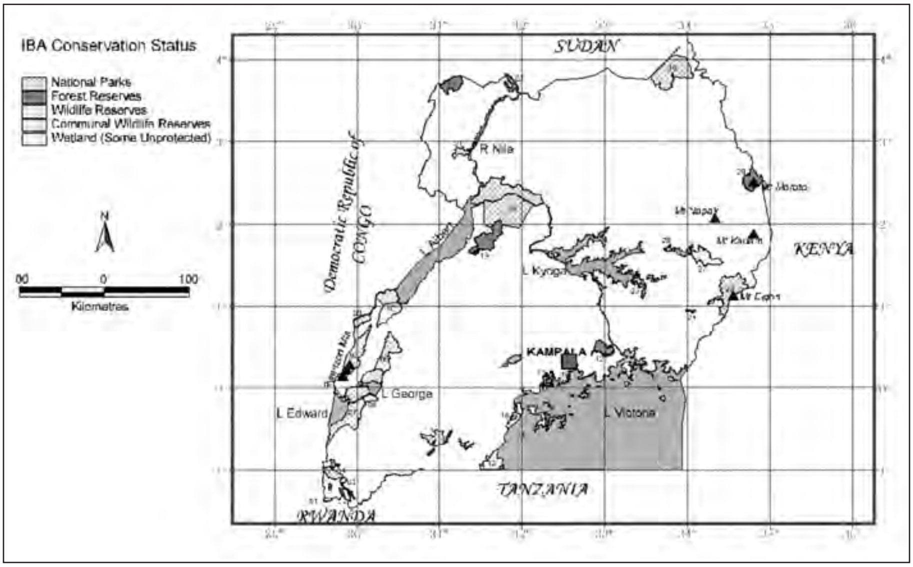

FIG. 1. Location of the IBAs in Uganda.

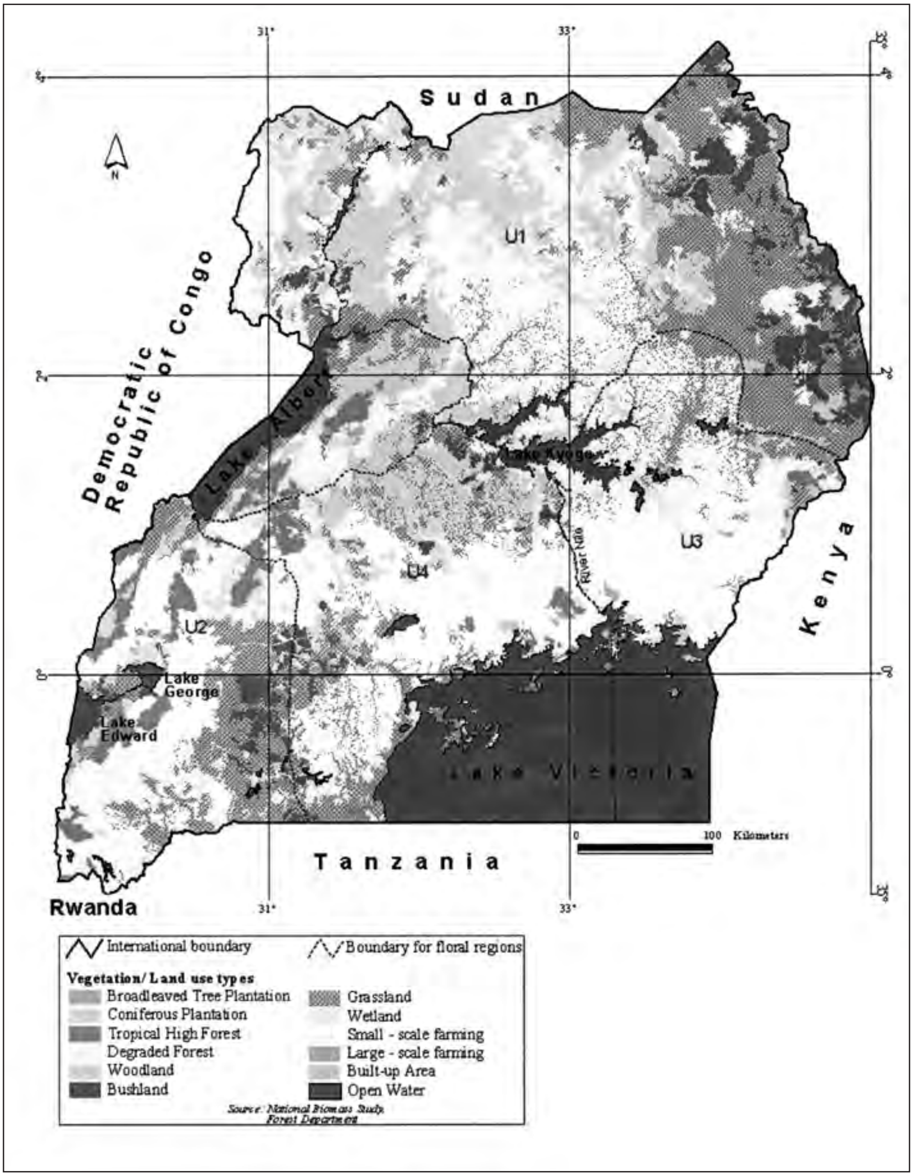

FIG. 2. Map of vegetation types in Uganda with floral regions U1–U4.

species, and d) areas that support congregatory species (Stattersfield *et al.*, 1998). It must be observed here that some of these criteria are not applicable to plants or are not the most appropriate.

Since habitat modification and destruction, and introduction of alien species (Stadler *et al.*, 2000) are the most important cause of biodiversity loss (Ehrlich, 1988; Ehrlich, 1992; WCMC 1992; Lovejoy *et al.,* 1993; Canaday, 1996; Turner, 1996; Mendoza & Dirzo, 1999; Lyaruu *et al.*, 2000), the identification of candidate habitats where conservation efforts may be especially focused has become crucial in the contemporary world (Davis *et al.*, 1994; Kerr, 1996; Kitching, 1996; New, 1997; van Jaarsveld *et al.*, 1998; Tshiguvho *et al.*, 1999; Koch *et al.*, 2000; Lovett *et al.*, 2000; Myers *et al.*, 2000; Rodrigues *et al.*, 2000). The identification of such hotspots has been variously based on number of species, rarity and level of endemism, level of threat, congruence and complementarity between habitats, all of which are of vital significance in biodiversity conservation (Myers, 1988; 1990; Balmford *et al.*, 1996; Mittermeier *et al.*, 1998; Reid, 1998; Sluys, 1999; Balmford *et al.*, 2000; Peterson *et al.*, 2000). Here, the significance of the IBAs in Uganda has been evaluated on the basis of species richness, rarity, endemism, and threat level. Their contribution to the conservation of Uganda's flora was assessed in light of the proportion of species richness they capture, numbers of endemic and threatened species they harbour

2 Methods

Both the data collected by myself and that collected by others were used for the analysis. The survey of plants in the 13 forested IBAs was conducted during the period 1993–1994 by the Forest Department. That of the 10 wetland and seven savanna IBAs began August 2000 and continued through December 2001 by the author. The areas of the IBAs were quite variable (ranging from 0.8 km^2 in the case of Musambwa Island to over 3800 km^2 for Murchison Falls National Park). This variation had to be controlled for based on the species-area relationship: $S = cA^z$ where S is the number of species, A is the sampled area, c is the slope of the graph and z is the y-intercept (for details see Rosenzweig, 1995). This relationship was used as a guide in allocating the number of sites, and subsequently the number of sampling days, to the IBAs. The areas of collection were marked using a GARMIN 45 GPS navigator by taking their Universal Traverse Mercator (UTM) kilometric coordinates.

All the vascular plants encountered were identified to species or subspecies level and recorded. Repeat visits were made for each IBA so that each was visited once in the drier and once in the wetter seasons of the year. This was intended to enable capturing of variation in floral assemblage due to seasonality. The plants were identified using the published floras of the Tropical East Africa region (FTEA), and guides such as Hamilton (1991), Agnew & Agnew (1994) and Beentje (1994). Species that were not easy to identify in the field were collected for subsequent identification and deposition at the Makerere University Herbarium (MHU).

3 Results

The areas of wetland and dryland surveyed together covered an area of 10,628 km^2 representing only 4.5% of the country's total area. Nonetheless, 1038 taxa were encountered in the wetlands and 1448 in the drylands. The combined total for both habitat types was 2011 representing 37% of the national total number of vascular plants. This is an indication of the floral richness of these areas.

A total of 31 (41%) taxa endemic to Uganda were captured in the IBAs (Table 1). The vast majority of these (75%) came from floral region U2. This is essentially the western part of the country and also where the biotically significant Albertine Rift area is located. Most of the endemic species in Uganda also occur in this floral region. It is worth noting that many of these endemics occur in only one floral region and have only a very limited range of occurrence within the floral region. They are therefore quite vulnerable to extinction. Of the 31 endemic plant taxa represented in the IBAs, one is Critically Endangered – *Afrothismia winkleri* Schlechter var. *budongensis* E.J.Cowley (Burmanniaceae) and three Endangered – *Brazzeia longipedicellata* Verdcourt (Scytopetalaceae), *Dialium excelsum* J.Louis ex Steyaert and *Lovoa swynnertoniii* Bak.f. (Meliaceae) (Table 2). Table 2 shows the globally threatened species recorded from the IBAs. Among these are eight species of the family Meliaceae – the mahoganies – and *Milicia excelsa* (Welw.) C.C.Berg, all of which are under tremendous overexploitation pressure because of their commercially desirable good timber. *Prunus africana* (Hook.f.) Kalkm. is threatened because of its medicinal and good timber value.

Table 3 shows the taxa that were recorded for the first time in Uganda. These were a total of 34. Their distributions by floral region and by IBA are shown in Fig. 3 and Fig. 4 respectively. Three of these (C*hasmopodium caudatum* (Hack.) Stapf, *Dyschoriste multicaulis* (A. Rich.) O. Kuntze and *Ochna leucophloeos* Hochst. ex A. Rich.) were first records for the whole flora area of Tropical East Africa. Ajai and Kidepo, both from U1, registered the highest proportion of new distribution records followed by Murchison and Queen Elizabeth from U2. It should be noted that the summation of the individual numbers for all the IBAs is higher than the actual number of taxa (34) because some of the taxa are shared between some IBAs. The new records from Doho i.e. *Nicandra physalodes* (L.) Gaertn. (Solanaceae), *Acmella uliginosa* Cass. (Asteraceae) and *Xanthium strumarium* L. (Asteraceae) are all weeds of cultivation and probably introduced. They therefore are a potential conservation threat to the indigenous species especially if they become invasive. Doho is a rice growing area with large fields under cultivation.

The main habitat types in the country, i.e. forests, wetlands and drylands, are all represented in the network of the IBAs and so are the six phytochoria according to White (1983). This reflects coverage of the various climatic, edaphic, altitudinal, topographical and other physical features and patterns in the country all of which have a bearing on the flora.

4 Conclusion

The IBAs are important for plant conservation in Uganda on account of the levels of richness, threat and rarity of the species that were registered in them. The range of habitat type they encompass also adds to their conservation value. However, there is not sufficient evidence to suggest that they are the most significant for plant conservation in the country. There is need to develop an Important Plant Area (IPA) approach based on criteria suitable for plants and assess the extent to which they overlap with the IBAs. This would also capture other areas that may not necessarily be IBAs.

TABLE 1. Plant taxa endemic to Uganda that were captured in the IBAs. LBK=Lutoboka, BGO=Budongo Forest Reserve, ELG=Mt. Elgon National Park, KIB=Kibale National Park, SNP=Semuliki National Park, MOR=Mt. Moroto Forest Reserve, LMP=Lake Mburo National Park, BINP=Bwindi Impenetrable National Park, RWE=Rwenzori Mountains National Park, QEP=Queen Elizabeth National Park and Lake George, MAR=Maramagambo Forest, MGL=Mt. Morongole Forest Reserve.

Family	**Species**	**IBA**	**Floral Region**
Annonaceae	*Uvariodendron magnificum* Verdc.	LBK	U4
Burmanniaceae	*Afrothismia winkleri* Schlechter var. *budongensis* E.J.Cowley	BGO	U2
Caryophyllaceae	*Melandrium syngei* Turrill	ELG	U3
Convolvulaceae	*Ipomoea* sp. C	KIB	U2
Euphorbiaceae	*Euphorbia bwambensis* S.Carter	SNP	U2
Poaceae	*Snowdenia microcarpha* C.E.Hubbard	ELG	U3
Poaceae	*Stipa tigrensis* Chiov.	MOR	U1
Papilionaceae	*Erythrina* sp. C	BGO	U2
Papilionaceae	*Erythrina* sp. D	SNP	U2
Papilionaceae	*Rhynchosia crispa* Verdcourt	LMP	U2
Papilionaceae	*Trifolium masaiense* J.B.Gillett ssp. *morotoense*	MOR	U1
Menispermaceae	*Triclisia* sp. B	KIB	U2
Orchidaceae	*Aerangis jacksonii* J.Stewart	KIB	U2
Orchidaceae	*Angraecopsis macrophylla* Summerhayes	BGO	U2
Orchidaceae	*Cynorkis kassnerana* Kraenzel. ssp. *tenuior*	BINP	U2
Orchidaceae	*Diaphananthe cuneata* Summerhayes	BGO	U2
Orchidaceae	*Diaphananthe eggelingii* P.J.Cribb	BINP	U2
Orchidaceae	*Diaphananthe schimperiana* (A.Rich.) Summerhayes	MGL	U1
Orchidaceae	*Distylodon comptum* Summerhayes	BGO	U2
Orchidaceae	*Habenaria buettneriana* Kraenzel.	BGO	U2
Orchidaceae	*Liparis caillei* Finet	BGO	U2
Orchidaceae	*Polystachya doggettii* Rendle & Rolfe	RWE	U2
Orchidaceae	*Polystachya meyeri* P.J.Cribb & A.Podzorski	BINP	U2
Orchidaceae	*Polystachya nyanzensis* Rendle	QEP	U2
Orchidaceae	*Polystachya poikilantha* Kranzlin. var. *poikilantha*	BINP	U2
Orchidaceae	*Rhaesteria eggelingii* Summerhayes	BINP	U2
Orchidaceae	*Tridactyle* sp. A	KIB	U2
Rubiaceae	*Chassalia ugandensis* Verdcourt	Kayonza (BINP)	U2
Rubiaceae	*Oldenlandia duemmeri* S.Moore	NBG	U4
Rubiaceae	*Oxyanthus ugandensis* D.M.Bridson	SNP, BGO	U2
Rutaceae	*Balsamocitrus dawei* Stapf	MAB, MAR (QEP)	U4, U2

TABLE 2. The globally threatened plants in Uganda's IBAs. CR=Critically Endangered, EN=Endangered, VU=Vulnerable, LR/nt=Low Risk/Near-Threatened. Key: AJA = Ajai Wildlife Reserve; SBY = Sango Bay complex; MAB = Mabira Forest Reserve; KID = Kidepo National Park; KEI = Mt. Kei Forest Reserve; OTZ = Mt. Otzi Forest Reserve; MFP = Murchison Falls National Park; LTB = Lutembe Bay. The other abbreviations are as in Table 1.

Family	**Species**	**Global threat category**	**IBA**	**Floral Region**
Burmanniaceae	*Afrothismia winkleri* Schlechter var. *budongensis* E.J.Cowley	CR	BGO	U2
Caesalpiniaceae	*Afzelia africana* Sm.	VU	BGO, MFP*, KEI, SNP, OTZ	U2, U1
Caesalpiniaceae	*Afzelia bipindensis* Harms	VU	SNP	U2
Mimosaceae	*Albizia ferruginea* Benth.	VU	MAB, BGO, SNP, KIB,	U4, U2
Anacardiaceae	*Antrocaryon micraster* A.Chevalier & A.Guillaumin	VU	BGO	U2
Lauraceae	*Beilschmiedia ugandensis* Rendle var. *ugandensis*	VU	LTB	U4
Scytopetalaceae	*Brazzeia longipedicellata* Verdcourt	EN	BINP	U2
Sterculiaceae	*Cola bracteata* De Wild.	VU	BINP, KIB	U2
Papilionaceae	*Cordyla richardii* Planch.	VU	OTZ	U1
	Dalbergia melanoxylon Guill. & Perr.	LR/nt	MFP, OTZ, KID, MOR, BGO, KEI, AJA	U1, U2
	Dialium excelsum J.Louis ex Steyaert	EN	BGO, KIB. SNP	U2
Meliaceae	*Entandrophragma angolense* (Welw.) C.DC.	VU	SNP, BGO, MAB, KIB, QEP, SBY, BINP	U2, U4
Meliaceae	*Entandrophragma cylindricum* Sprague	VU	BGO, MFP, KIB, SNP, BINP, KEI	U1, U2
Meliaceae	*Entandrophragma utile* Sprague	VU	MAB, BGO, RWE, BINP, SNP	U2, U4
Euphorbiaceae	*Euphorbia bwambensis* S.Carter	VU	SNP	U2
Meliaceae	*Guarea cedrata* Pellegr. ex A.Cheval.	VU	BGO, SNP	U2
Meliaceae	*Guarea mayombensis* Pellegr.	VU	BINP	U2
Rubiaceae	*Hallea stipulosa* (DC.) Leroy	VU	MFP, BGO, SNP, RWE, MAB, BINP, KIB	U2, U4
Irvingiaceae	*Irvingia gabonensis* Baill. ex Lanen	LR/nt	BGO, MAB, SBY, SNP, BINP	U2, U4
Annonaceae	*Isolona congolona* Engl. & Diels	LR/nt	SNP, BGO, KIB,	U2
Cupressaceae	*Juniperus procera* Hochst. ex Endl.	LR/nt	ELG, MOR	U1, U3
Meliaceae	*Khaya anthotheca* C.DC.	VU	BGO, MAB, SNP	U2, U4
Meliaceae	*Khaya grandifoliola* C.DC.	VU	MFP, BGO, OTZ	U1, U2
Meliaceae	*Khaya senegalensis* A.Juss.	VU	OTZ, KEI	U1

TABLE 2. continued

Family	**Species**	**Global threat category**	**IBA**	**Floral Region**
Meliaceae	*Lovoa swynnertoniii* Bak.f.	EN	SNP, KIB, QEP, BINP, MAB	U2, U4
Meliaceae	*Lovoa trichilioides* Harms	VU	MAB, BGO, QEP, SBY, BINP, KIB	U2, U4
Melastomataceae	*Memecylon bequaertii* De Wild.	VU	BINP	U2
Moraceae	*Milicia excelsa* (Welw.) C.C.Berg	LR/nt		U3, U4
Rubiaceae	*Nauclea diderichii* Merrill	VU	KEI, OTZ, SNP, BGO	U1, U2
Lauraceae	*Ocotoea kenyensis* (Chiov.) Robyns & Wilczek	VU	BINP	U2
Rubiaceae	*Pavetta intermedia* Bremek.	VU	KIB	U2
Sapotaceae	*Pouteria altissima* (A.Cheval.) Baehni	LR/cd	KIB	U2
Rosaceae	*Prunus africana* (Hook.f.)Kalkm.	VU	ELG, BGO, RWE, KID, MAB, BINP, KIB, SBY, QEP, MOR	U1, U2, U3, U4
Asclepiadaceae	*Rhynchostigma racemosum* Benth.	VU	BINP	U2
Meliaceae	*Turraeanthus africanus* Pellegrin	VU	KIB, SNP	U2
Sapotaceae	*Vitellaria paradoxa* Gaertn.f.	VU	AJA	U1

TABLE 3. Taxa recorded for the first time in Uganda.

Family	Taxon	Location where species found (FTEA region)	FTEA countries/regions where species is known	Countries outside FTEA where species is known
Poaceae	*Chasmopodium caudatum* (Hack.) Stapf	Murchison Falls National Park (U2); Namukongo-Nakasongola District (U4)	None	Nigeria, Sud, Belg Congo
Acanthaceae	*Dyschoriste multicaulis* (A.Rich.) O.Kuntze	Kidepo Valley National Park (U1)	None	Eth, Sud
Ochnaceae	*Ochna leucophloeos* Hochst. ex A.Rich.	Ajai Wildlife Reserve (U1)	None	Horn of Africa
Asteraceae	*Nicolasia nitens* (O.Hoffm.) Eyles var. *nitens*	Kidepo Valley National Park (U1)	K1,3,4,6,7; T1,2,5,7	Zam, Zim, Bot, Nam
Araceae	*Stylochiton borumensis* N.E.Br.	Kidepo Valley National Park (U1)	K1,2,4,7; T1,3-8	Zam, Moz
Cucurbitaceae	*Kedrostis leloja* (Forssk.) C.Jeffrey	Kidepo Valley National Park (U1), Queen Elizabeth National Park (U2)	K7; T3,6,8	Som, Arabia
Amaranthaceae	*Pupalia lappacea* (L.) A.Juss. var. *glabrescens* C.C.Townsend	Ajai Wildlife Reserve (U1)	K7; T6,8; Z; P	Moz
Euphorbiaceae	*Caperonia stuhlmannii* Pax	Ajai Wildlife Reserve (U1)	T1-6,8; Z	Moz, Mala, Zam, Zim, S. Afr
Caryophyllaceae	*Polycarpaea linearifolia* (DC.) DC.	Ajai Wildlife Reserve (U1)	T4, 8	Trop. Afr.
Oleaceae	*Jasminum stenolobum* Rolfe	Ajai Wildlife Reserve (U1)	T5,6,8	Zim, Mala, Bot, S. Afr
Lamiaceae	*Plectranthus longipes* Baker	Lake Mburo National Park (U2)	K; T	Eth, Rwa

TABLE 3. continued

Family	Taxon	Location where species found (FTEA region)	FTEA countries/regions where species is known	Countries outside FTEA where species is known
Papilionaceae	*Indigofera tenuis* Milne-Redh.	Kidepo Valley National Park (U1)	T1,2,4,7,8	Zam
Papilionaceae	*Indigofera vicioides* Jaub. & Spach var. *rogersii* (R.E.Fries) Gillett	Kidepo Valley National Park (U1)	K4; T1,2,4,7	DRC, Moz, Mala, Zam, Zim, Ang, S.Afr
Papilionaceae	*Tephrosia subtriflora* Bak.	Murchison Falls National Park (U2); Queen Elizabeth National Park (U2)	K1,4,6,7; T2,3,5,7	Cape Verde Is., Niger, Sud, Arabia, Pak, Indi, Burma, Eth, Eri, Som, Ang, Mada
Papilionaceae	*Aeschynomene pfundi* Taub.	Lake Opeta wetland (U3)	K1,3; T2,4,5	Sud, Mala, Zam
Celastraceae	*Maytenus putterlickioides* (Loes.) Exell. & Mendonca	Murchison Falls National Park (U2)	K1,3,4,6,7; T3-5,7,8	DRC, Eth, Moz, Mala, Zam, Zim, Ang
Poaceae	*Panicum phragmitoides* Stapf	Murchison Falls National Park (U2)	T1, 4-8	Guinee, Zam, Ang
Poaceae	*Panicum pole-evansii* C.E.Hubbard [a]	Luweero (U4)	Tanz.	DRC, Zam
Anthericaceae	*Chlorophytum occultum* A.D.Poulsen & I.Nordal [b]	Budongo Forest (U2)	None	Ituri Province of DRC
Anthericaceae	*Chlorophytum hirsutum* A.D.Poulsen & I.Nordal [b]	Albertine rift (U2)	None	DRC, Bur
Zingiberaceae	*Aframomum uniflorum* Lock & A.D. Poulsen [b]	Budongo (U2)	None	Ituri Province of DRC
Zingiberaceae	*Aframomum spiroligulatum* A.D.Poulsen & Lock [b]	Kasyoha-Kitomi (U2)	None	Rwa

TABLE 3. continued

Family	**Taxon**	**Location where species found (FTEA region)**	**FTEA countries/regions where species is known**	**Countries outside FTEA where species is known**
Costaceae	*Costus foliaceus* J.M.Lock & A.D.Poulsen [b]	Kasyoha-Kitomi (U2)	None	None
Poaceae	*Sporobolus tenuissimus* (Schrank) O.Ktze	Ajai Wildlife Reserve (U1)	K7; T3,4,6,8; Z;P	From East Africa westwards to Sen & Trop. Am., eastwards to Burma
Poaceae	*Urochloa setigera* (Retz.) Stapf	Queen Elizabeth National Park (U2)	K1,7; T?1,3,6,8; Z; P	DRC, Eth, India, Sri Lan, Burma, Thai
Asteraceae	*Flaveria trinervia* (Spreng.) Mohr*	Queen Elizabeth National Park (U2)	K; T; Z	None
Solanaceae	*Nicandra physalodes* (L.) Gaertn.*	Doho (U3)	K; T	NE and southern Afr, Mad
Asteraceae	*Acmella uliginosa* (Sw.) Cass.*	Doho (U3)	K; T	Pantropical
Asteraceae	*Xanthium strumarium* L.*	Doho (U3)	K; T	Pantropical
Papilionaceae	*Aeschynomene Americana* L. var. *glandulosa* (Poir.) Rudd*	Lutembe (U4)	K (Cultivated)	S. Am.
Caryophyllaceae	*Silene lynesii* Norman[c]	Mt. Elgon National Park (U2)	None	Central Sahara, Sud
Moraceae	*Ficus katendei* Verdc.[c]	South Kyambura River (U2)	None	None
Menispermaceae	*Syrrheonema fasciculatum* Miers [d]	Kibale National Park (U2)	None	Belgian Congo, Came, Gab
Thymelaeaceae	*Craterosiphon scandens* Engl. &Gilg [d]	Budongo Forest Reserve (U2)	None	Came

TABLE 3. continued

Family	**Taxon**	**Location where species found (FTEA region)**	**FTEA countries/regions where species is known**	**Countries outside FTEA where species is known f**
Sterculiaceae	*Cola pierlottii* Germain [e]	Bwindi Impenetrable National Park (U2	None	DRC
Orchidaceae	*Stolzia cupuligera* (Kraenzl.) Summerh. [e]	Bwindi Impenetrable National Park (U2	None	DRC
Orchidaceae	*Angraecopsis* sp. nov.? [e]	Kasyoha-Kitomi Forest Reserve (U2)	None	Probably none
Orchidaceae	*Angraecopsis elliptica* Summerh. [e]	Bwindi Impenetrable National Park (U2	None	West Tropical Africa
Begoniaceae	*Begonia subscutata* De Wilde [e]	Kasyoha-Kitomi Forest Reserve (U2)	None	DRC, Came
Aspleniaceae	*Asplenium* sp. nov.? [e]	Bwindi Impenetrable National Park (U2	None	Probably none
Verbenaceae	*Clerodendrum welwitschii* Guerke	Bwindi Impenetrable National Park (U2	None	?
Annonaceae	*Friesodielsia enghiana* (Diels) Verdc.[d]	Budongo Forest Reserve (U2)	None	?
Apocynaceae	*Landolphia foretiana* (Pierre ex Jumelle) Pichon[d]	Bwindi Impenetrable National Park (U2)	None	?
Celastraceae	*Loeseneriella apiculata* (Welw. ex Oliv.) R.Wilczek[d]	Bwindi Impenetrable National Park (U2)	None	?
Convolvulaceae	*Neuropeltis velutina* Hall.f.[d]	Budongo Forest Reserve (U2)	None	?

TABLE 3. continued

Family	**Taxon**	**Location where species found (FFTEA region)**	**FTEA countries/regions where species is known**	**Countries outside FTEA where species is known**
Cucurbitaceae	*Momordica jeffreyana* Keraudren[d]	Bwindi Impenetrable National Park (U2)	None	?
Rubiaceae	*Tricalysia anomala* E. A.Bruce var. *montana* Robbrecht [e]	Bwindi Impenetrable National Park (U2)	None	?
Rubiaceae	*Tarrena eketensis* Wernh. var. *auricluna* N.Halle	Bwindi Impenetrable National Park (U2)	None	?
Sapotaceae	*Chrysophyllum welwitschii* (Engl.) Pierre ex Aubr. & Pellegr.	Budongo Forest Reserve (U2)	None	?
Lamiaceae	*Aeollanthus buchnerianus* Briq. [e]	Bwindi Impenetrable National Park (U2)	?	?
Lycopodiaceae	*Huperzia gnidioides* (L.f.) Trevisan [e]	Kasyoha-Kitomi Forest Reserve (U2)	?	?
Hymenophyllaceae	*Trichomanes (Vandenboschia) radicans* Sw. [e]	Bwindi Impenetrable National Park (U2)	?	?
Hypericaceae	*Garcinia* L. sp. nov.? [e]	Bwindi Impenetrable National Park (U2)	?	?
Menispermaceae	*Cissampelos truncata* Engl.[d]	Kibale National Park (U2)	?	?
Plantaginaceae	*Plantago lanceolata* L. [c]	Rwenzori Mountains National Park (U2)	K3; T3	Global weed

[a] Source: Namaganda, M 2003. Lidia **6**: 1–12

[b] Source: Poulsen, A. D. & Lock, J. M. 1997. Kew Bulletin **52**: 601–616.

[c] Source: Katende, A.B & Lye, K.A 1997. Lidia **4**(1) 3–12

[d] Source: Eilu, G. 1999. Lidia **4**(4) 93–120

[e] Source: Eilu, G. *et al.* (in prep.)

[*] introduced; weedy

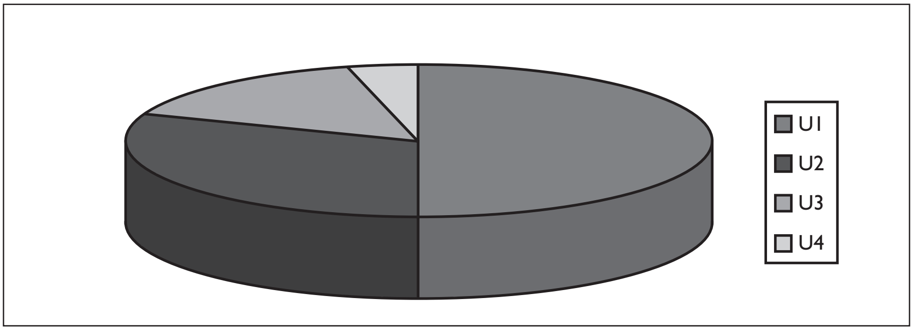

FIG. 3. Distribution of new records in Uganda by FTEA region.

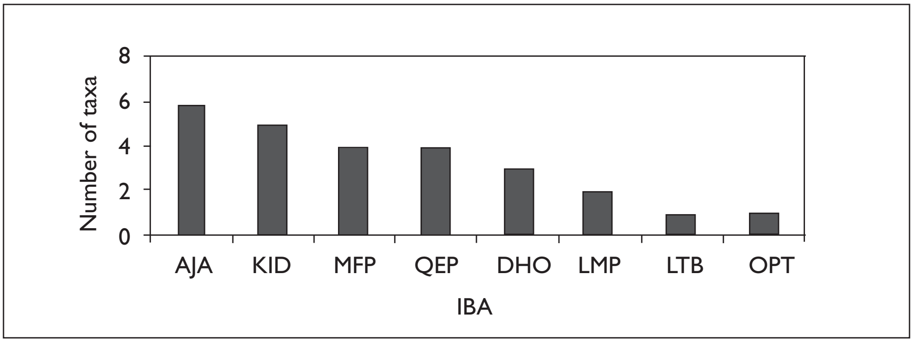

FIG. 4. Distribution of new records for Uganda by IBA.

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A LOCAL BOTANICAL GARDEN AS A TOOL FOR SUSTAINABLE USE: CONSERVATION OF PLANTS AND INDIGENOUS KNOWLEDGE IN NORTHERN BENIN

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Abstract

In most West African regions, phytodiversity is under great threat due to increasing human impact and changing climatic conditions. Numerous plant species are noticeably becoming rarer, and the shortage of species used in traditional medicine may become a problem for local traditional health systems. During an ethnobotanical study on the utilisation of plants, environmental classification and environmental-change perception of Fulani groups in West Africa, it was revealed that local populations in north-west Benin are very conscious of this problem, and they expressed a need to take measures. Together with these villagers the concept of a local botanical garden was developed in order to conserve species richness as well as the traditional knowledge linked to numerous threatened species. In 2001, a species-rich savannah area of about 14 ha, including different ecological sites, was protected against human impact. The garden area contains more than a hundred woody plants and several hundreds of herbaceous species, many of them traditionally used. An educational infrastructure (e.g. nature trail) for field visits and the sensitisation of visitors (pupils, students, tourists, villagers) was installed. A tree-nursery was created in order to multiply rare species for distribution and to reintroduce them into the garden. Knowledge transmission from older to younger generations is encouraged, and monitoring of vegetation dynamics is also affected in permanent plots. Up to now, there have been many positive side-effects for the local community, most of all an increasing ecological awareness in the village and its neighbourhood. This project demonstrates the efficiency of sustainable, participatory-based management of plant resources at a local scale.

Résumé

Un jardin botanique local, outil de développement durable: conservation de plantes et connaissances indigènes au nord du Bénin. Dans la plupart des régions ouest-africaines, la phytodiversité est grandement menacée par l'impact croissant de l'homme et les changements climatiques. De nombreuses espèces végétales se sont de toute évidence raréfiées et la diminution du nombre d'espèces utilisées en médecine traditionnelle peut constituer un problème pour les systèmes de santé locaux. Au cours d'une étude ethnobotanique sur l'utilisation des plantes, la classification environnementale et la perception des changements de l'environnement chez des groupes de Fulani en Afrique occidentale, il s'est avéré que les populations locales du nord-ouest du Bénin étaient très conscientes de ce problème et qu'elles exprimaient le souhait que des mesures soient prises à ce propos. En collaboration avec ces villageois, le concept de jardin botanique local a été développé de manière à conserver tant la richesse spécifique que l'usage traditionnel lié à de nombreuses espèces menacées. En 2001, une zone de savane d'environ 14 ha, riche en espèces et incluant différents sites écologiques, a été protégée contre l'impact humain. La zone du jardin contient plus d'une centaine de plantes ligneuses et plusieurs centaines d'espèces herbacées dont un grand nombre sont utilisées de manière traditionnelle. Une infrastructure éducative (notamment un sentier nature) a été installée pour les visites de terrain et la sensibilisation des visiteurs (élèves, étudiants, touristes, villageois). Une pépinière a été créée pour multiplier les espèces rares en vue de les distribuer et de les réintroduire dans le jardin. La transmission des connaissances des personnes plus âgées vers les jeunes générations est encouragée et un suivi de la dynamique de la végétation est également effectué dans des parcelles permanentes. Jusqu'ici, on a relevé plusieurs effets positifs pour la communauté locale et surtout une prise de conscience écologique grandissante dans le village et aux alentours. Ce projet démontre l'efficacité de la gestion durable et participative des ressources végétales à l'échelle locale.

Key words: Botanical Garden, North Benin, phytodiversity conservation, sustainable use, traditional knowledge

1 Introduction

In most West African regions severe vegetation changes have become obvious during the last few decades. Numerous plant species are noticeably becoming rarer due to increasing human impact and changing climatic conditions. As the use of plants in these regions is of major importance for various purposes in everyday life, the loss of species is seriously affecting the quality of life for local people (Guinko, 1984). In particular, the shortage of species used in traditional medicine is becoming a problem for the local traditional health system. Throughout West Africa, a large proportion of the population still regularly uses traditional medicinal methods and medicines (Neuwinger, 1996; Sofowora, 1982; Iwu, 1993). This is due to factors such as cost, accessibility and cultural acceptability. High cost modern medicine is therefore primarily used for severely affected patients. Despite the importance of traditional methods, particularly for healing common, widespread diseases, medical knowledge, which has been verbally passed on from generation to generation, is currently in danger of falling into oblivion (Burkill, 1985). The reason for this is the increasing modernisation of daily life, resulting in a lack of interest in traditions, especially amongst the younger generations (Burkill, 1985). In addition, many plants used in traditional medicine are increasingly difficult to find due to demographic growth, which results in more and more land being used as fields and pastures. Habitat loss and the overexploitation and degradation of remaining habitats are resulting in a noticeable decrease in species diversity. The use of plants for medicinal purposes is also a factor, because the traditional methods call for particular species, those species are harvested more frequently and gradually become rarer (Pushpangadan & Thomas, 1998).

In an ethnobotanical study investigating the environmental perception of different Fulani groups in Burkina Faso and Benin and their knowledge and utilisation of plants (Demira *et al.*, 2000; Demira & Krohmer, 2004; Krohmer, 2004) it appeared that villagers in Northern Benin felt very concerned about declining species richness and were eager to participate in protection measures. Together with these villagers, the concept of a local botanical garden was developed, inspired by two (ethno)botanical gardens already existing in the region. The aims of the garden initiative have been elaborated conjointly by villagers and scientists and are as follows:

1) Conservation of phytodiversity (*in situ* and *ex situ*); providing protection for threatened species, including the possibility to reintroduce rare or locally extinct species
2) Conservation of traditional knowledge by documentation of all kinds of traditional plant uses, especially medical use
3) Establishment of training possibilities, in order to promote the economic value, and the transmission (in some cases the revival) of traditional plant knowledge to younger generations
4) Using the garden as a tool and a resource for environmental education, i.e. for school children, students, non-governmental organisations (NGO), local, national and international public
5) Protection of natural resources by sustainable production of the plants used in traditional medicine
6) Creation of new income possibilities for the local population
7) Improvement of the state of knowledge of biodiversity dynamics in utilised and protected areas by long term monitoring, and leading to development of management plans
8) Establishment of permanent test sites designated for research into sustainable utilisation methods and the reintroduction of threatened species, at the same time promoting awareness amongst the population.

2 Establishment of the botanical garden

In 2001, a species-rich savannah area of about 14 ha, which had not been cultivated for many years due to its poor soil, was protected from all human impact. It includes different ecological sites, and is situated close to several Fulani farmsteads. In addition to the ecological and geographical requirements necessary to include a maximum of different habitats, the following social conditions had to be respected to guarantee the long-term existence of such a local garden:

1) Integration of all local communities in the garden-planning, especially the different ethnic groups present in the region and affected by the protection measures, in order to avoid local conflicts
2) Integration of traditional (e.g. council of the elders) and modern authorities
3) Sensitisation, by means of workshops, excursion etc., of all villagers affected directly by exploitation restrictions
4) Community-elaborated code of conduct, the protection measures being agreed by all members of the local community

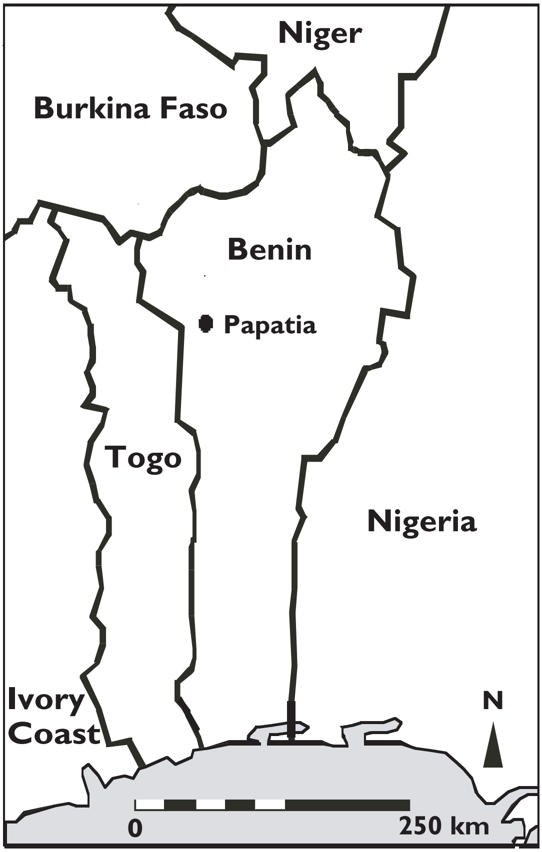

FIG. 1. Location of the garden.

After the very efficient co-operation of the local population of Papatia and neighboring villages as well as partners from universities (Frankfurt, Cotonou) and NGOs (Potal-Men, Pro Benin, ASA-Foundation), the garden was inaugurated in the presence of many traditional and modern authorities at the end of 2001.

2.1 The garden

The garden is situated in the north of Benin near the small village of Papatia (Fig. 1). The area is part of the southern Sudanian zone with two contrasting seasons: a rainy season from April to October and a dry season from November to March. Mean annual precipitation is 1184 mm and the mean annual temperature 28°C. The typical vegetation of this area consists of various woodland types, grass, shrub and tree savannahs, fallow as well as very small islands of dry forests and gallery forests. The whole region is pastured by cattle and small ruminants, and the vegetation is strongly influenced by annual bush fires.

The garden area is divided into a partly protected outer area, the buffer zone (approximately 9 ha), and a totally protected core zone with a size about 5 ha. In the buffer zone, moderate pasture influence is allowed and annual early fires (at the end of the rainy season) are lit as a protection measure to avoid the much more destructive accidental bush fires in the late dry season. The core zone, including different ecological sites, is surrounded by a 10 m wide fire break and an *Acacia senegal* hedge. To enable natural growth without any human influence, wood-cutting, pasture, hunting and bush fires are forbidden in this core zone. In 2002, a species-rich gallery forest of a nearby small river was also declared as totally protected. The biodiversity of such water-accompanying formations is particularly high. Long term, the integration of the area between the two parts, which now consists of fields and fallow, is planned.

A one kilometre long educational nature trail enables the visitors to discover the variety of the garden. The trail leads through the different soil zones (laterite, sand, rock, damp zone) and to the gallery forest. Along the nature trail, representative individuals of all trees and bushes are labelled with the scientific species and family name and the names in the local languages Fulfulde and Bariba. The herbaceous species, which are to be seen only during and after the rainy season, are documented in the herbarium at the information centre.

To date, over 100 different woody species and 150 herbaceous species have been inventoried in the core and buffer zones. Nearly all of the woody species and a significant number of the herbs and grasses are utilised in traditional medicine.

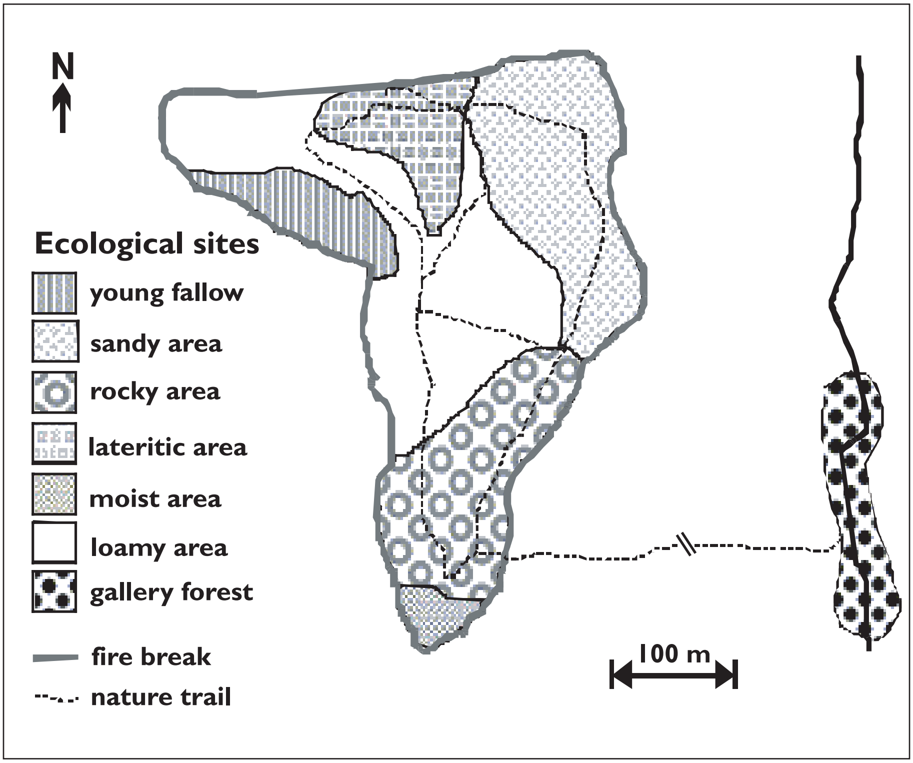

FIG. 2. Map of the core zone and the gallery forest.

2.2 Activities

Various activities have been undertaken so far. Some of them are directly related to the aims of conservation, awareness and promotion of traditional knowledge. Others refer more to the necessity of developing additional income sources for the local population in order to guarantee the long-term maintenance of the garden, even though the activities seem not to always match directly the idea of protection of indigenous species and vegetation. The tree nursery for example is producing plants according to the demands of clients, and as there is a high demand for exotic fruit trees (*Anacardium occidentale*, cashew nut tree); more than 3000 saplings of cashew been produced instead of local species, which can not easily be sold at the moment. As a consequence, the tree nursery has become well-established and is now in a good position to produce and promote local species.

In detail, the following activities have been (and continue to be) undertaken:

1) Training of guides for guided visits for all kinds of visitors (e.g. tourists, school classes) along the nature trail which crosses the different ecological sites
2) Publication of a booklet containing the Fulani's traditional medicinal knowledge about the woody species. It is intended to be completed for all herbaceous species and to include the knowledge of other ethnic groups of the region
3) Collection of herbarium specimens to document the abundance of the herbaceous species
4) Creation of a regional network of traditional healers in order to provide information on their specialization
5) Opening of a pharmacy where their medical products are sold
6) Establishment of an information centre for educational purposes for visitors (general information about the garden, herbaria, sale of the booklet on the medical use of plants etc.)
7) Establishment of a plant nursery, watered by a new well, for the sale of seedlings of woody species (additional income) and propagation of endangered trees and shrubs (enrichment planting)
8) Horticultural training
9) Beginning of apiculture activities for additional income: bee hives have been placed in the garden area
10) Monitoring research in permanent plots has been started in the core area to evaluate vegetation dynamics. These works are conducted by botanists of the University of Abomey-Calavi (Cotonou).

2.3 Garden management and maintenance

All decisions concerning the botanical garden, like management measures, financial questions, codes of conduct (such as interdiction of pasture, woodcutting, bush-fires, hunting), control measures of the codes of conduct and the decisions about further activities are made by a local Fulani-Committee, the Walde jangoobe of Papatia, which is part of the regional Fulani NGO POTAL MEN ("Our Union").

To ensure that the Botanical garden can attain its education, conservation and scientific goals, maintenance work such as regular clearing of the fire break, reliable fire protection measures, maintenance of the path leading to the garden and of the nature trail and maintenance and eventual replacement of plant labels must be undertaken regularly .

So far the garden has been run as a low budget project with limited funding from several donors (NGOs, IUCN, individuals). In order to ensure maintenance activities, the management committee has to secure further funding as well as the continuous motivation of the participating local community.

3 Outlook

So far, many positive effects and side-effects for the local community have been noticed, most of all an increasing ecological consciousness in the neighbourhood and in other villages in the area. The garden seems to be very well accepted by the local population, and up to now no human disturbance (pasture, bush fires) has occurred, which demonstrates the effectiveness of participatory-based management of plant resources at the local scale. It also clearly reveals that additional income for the village population is an important factor for the maintenance of the garden in the long run. As pointed out before, pure conservation purposes have to be combined with income improvements. In this regard, further activities are planned for the future. The garden will be integrated into eco-tourism projects, and the apiculture activities as well as the sale of nursery plants will be enlarged. Moreover, the potential for income creation for women is substantial (e.g. market gardening, fabrication of local soap), as they perform important functions in the local community and are frequently referred to as the “engine of progress”, without whose involvement no project would persist in the long-term (United Nations, 1999). Furthermore, it is planned to intensify the botanical research activities (germination and growth tests for threatened woody plants, experiments for more sustainable production of plant material, e.g. substitution of bark products by leaves) and to start zoological research. Involvement in research activities will also provide additional income for the local people, and serve at the same time to demonstrate the importance of replanting local species. It is to be pointed out that the exceptional situation of a natural botanical garden enables scientists to explore completely new paths, especially with regard to the practical relevance of their scientific work.

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ASSESSMENT OF SESAME AND ITS WILD RELATIVES IN AFRICA

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Abstract

Sesame presents a paradox: popular enough to be labeled ‘Queen of Oilseeds’ yet disregarded completely by agencies involved with agricultural improvement. Its wild relatives are established beneficial weeds. They contribute to food and medicine, particularly during famine. Leaves and seeds are eaten across the Sahel zone and in Central and Southern Africa. Their relative importance may vary by location, but subsistence farmers use most taxa in strikingly similar ways.

Each wild *Sesamum* species occupies a distinct ecological zone, and all seem to tolerate poor soils. *Sesamum alatum* Thonn. thrives under arid conditions – throughout the Sahara, near Kenya’s Lake Turkana, and on severely degraded abandoned cultivation in northern Tanzania. *Sesamum angustifolium* Engl. occupies a wider and moister band of marginal and abandoned lands in heavier soils. *Sesamum angolense* Welw. reaches heights exceeding 2 m in impoverished, well-drained soils at higher elevations. *Sesamum latifolium* Gillett is an excellent colonizer, growing on degrading rock, but also on heavy clay soils subjected to seasonal water-logging. The closely related *Ceratotheca sesamoides* Endl. is weedy in old cultivation, and favours sands, while *Rogeria adenophylla* J.Gay prefers the driest zones across the Sahara.

Résumé

Evaluation du sésame et de ses parents sauvages en Afrique. Le sésame présente un paradoxe: à la fois tellement populaire qu’il est appelé ‘reine des oléagineux’ et complètement délaissé par les agences impliquées dans l’amélioration de l’agriculture. Ses parents sauvages sont des adventices utiles. Ils contribuent à l’alimentation et à la médecine, particulièrement au cours des famines. Les feuilles et les graines sont consommées à travers toute la zone sahélienne ainsi qu’en Afrique centrale et australe. Leur importance relative peut varier en fonction de la région mais les paysans vivant de l’agriculture de subsistance utilisent la plupart des taxons de manière similaire. Chaque espèce sauvage de sésame occupe une zone écologique distincte mais toutes semblent tolérer les sols pauvres. *Sesamum alatum* Thonn. se développe dans des conditions arides – à travers le Sahara, près du lac Turkana au Kenya et dans des friches sévèrement dégradées dans le nord de la Tanzanie. *Sesamum angustifolium* Engl. occupe une bande plus large et plus humide de terres marginales et abandonnées, sur des sols plus lourds. *Sesamum angolense* Welw. atteint des hauteurs dépassant 2 m, sur des sols appauvris et bien draînés et à plus haute altitude. *Sesamum latifolium* Gillett est un excellent colonisateur qui dégrade les sols pierreux mais qui pousse également sur des argiles lourdes sujettes à des inondations saisonnières. *Ceratotheca sesamoides* Endl. est une proche parente qu'on retrouve dans les anciennes cultures, de préférence sur sables, alors que *Rogeria adenophylla* J.Gay préfère les zones plus sèches du Sahara.

Key words: famine, medicine, selection, *Sesamum*, vegetable

1 Introduction

Sesamum and *Ceratotheca* are very closely related African genera (Endlicher, 1836–1840; Bernhardi, 1842; Bentham & Hooker, 1873–1876; Baillon, 1888; Hooker, 1888; Staph, 1906; Bruce, 1953; Abels, 1975; Ihlenfeldt & Grabow-Seidensticker, 1979; Stevels, 1990). Both are much appreciated food sources for their oily seeds and edible leaves. Nowadays these species are sliding into disuse, due to emigration from rural areas, and the introduction of exotic vegetables, although indigenous knowledge about these taxa still exists in rural areas. These species tolerate dry conditions and do not require fertilizer supplements, unlike hybrid maize, for example, which creates problems for cash-poor farmers. Sesame provides a glimpse into the transitional phase of the farming way of life and still remains a appreciable part of the diet in some African regions today.

1.1 Habit and selection factors in *Sesamum* spp.

Cultivated *Sesamum indicum* L. has a highly variable genotype (Bedigian *et al.*, 1986), and as a result of Africa's wide variation in habitats, as well as the cultural variation and geographic isolation among its growers, there is an enormous diversity of sesame landraces on the continent compared with Asia. Local cultivars remain confined to their narrowly specialized habitats. Diverse demands bring about specialized adaptations, e.g. *hirehir* has a short maturity growing on the hot dry *qoz* soils across Sudan, while the *dinderawi* landrace has the longest capsules ever studied (Bedigian & Harlan, 1983).

Sudan's diversity alone is enormous, and is especially visible in the cultivars planted in the isolated Nuba Mountains, where over 50 distinct dialects are spoken among isolated populations (Bedigian, 1988; 1991; Bedigian & Harlan, 1983; Nadel, 1947). In this area farmers planted mixtures, particularly near the southern villages, a strategy often employed in situations of uncertainty, e.g. scarce rainfall, unrelenting heat. Under these conditions, unpredictable, non-deterministic behaviour can be advantageous for maximizing outcomes. Knowledgeable farmers may have adopted this strategy to successfully achieve some modicum of yield regardless of the conditions by planting cultivars that differ in maturity, branching, ability to withstand water-logging and drought. Mortimore (1998) incorporated this 'uncertainty-as-norm,' as opposed to 'uncertainty-as-aberration,' into an understanding of the dry lands as suggested in the concept of the unstable, resilient ecosystem.

Another noteworthy example is a local landrace found in northern Uganda (Acholi region) and western Kenya (region of the ethnically related Luo) that has tetracarpellate capsules, an unusual trait usually seen in collections from East Asia (Bedigian, Smyth & Harlan, 1986). The corolla has a dark purple lower lip and an intense purple flake in the interior of the corolla. Local names of this cultivar are *latino* (Acholi) and *ojimo* (Lango).

Sudan's common commercial cultivar grown in the central rain lands originated with a simple selection begun by W. M. Tahir and continued by Mahmoud A. Mahmoud named 'Ziraa A.1.10'. It has white seed, few branches, and is relatively short, ca 1 m, vastly different from the distinct red-seeded high oil-containing cultivar of the Nuba Mountains of Kordofan, and the robust brown-seeded form grown throughout Darfur, which is more than 2 m tall, woody, and is impressively drought resistant.

The local landrace grown in Morocco is one of a kind, with a deep yellow seed color not seen elsewhere in the world collection. Yellow is a popular colour for other goods in Morocco too. *Zafran* is the name and characteristic colour of Berber rugs, and a popular dye colour applied after tanning leather for handmade Moroccan shoes; it originates with the saffron crop itself, a common colouring and flavouring agent gathered by Berber villagers in the High Atlas Mountains, that enhances many couscous and other dishes.

Plants in the Pedaliaceae family are covered with characteristic mucilage glands. After contact with water, the outer cell walls of the four cells forming the head of each gland are thought to swell up and burst (Burger, 1967; Abels 1975), producing an enormous amount of mucilage. That product is occasionally used as an emollient and lubricant (Beille, 1909; Bedigian & Harlan, 1986; Bedigian, 2003b, 2004b; Bedigian & van der Maesen, 2003) and can partially explain the dietary popularity of species of *Sesamum.*

Wild *Sesamum* species including *S. latifolium* and *S. malabaricum* Burm., have strongly dormant seeds (Bedigian *et al.*, 1985). But the year 1999 was superb for field study in Eastern Africa, because heavy downpours brought by El Niño enabled the germination inhibitors on seed surfaces to be washed away. Boulders and erosion had badly reconfigured the roads, but the 'seed bank' of each *Sesamum* species germinated, presenting this author with a spectacular view – in some places *Sesamum* spp. were the dominant flowering plants, emergent over acres.

Most *Sesamum* species are described as annuals, although van Epenhuijsen (1974) described *S. radiatum* as perennial and Grabow-Seidensticker (1988) considers perennial *S. rigidum* the progenitor of the entire *S. calycinum* complex. This author observed regeneration from the previous year's woody dried stalks in *S. alatum, S. angolense, S. angustifolium* and *S. latifolium.* As a group, the species show good colonizing ability, on degrading rock or living in sand, without demanding nutrients or requiring much moisture.

Pedaliaceae is a tough family, with species that have woody capsules and stems, and the capsules of several genera are protected with needle-sharp spines, hooks, barbs or horn-like appendages (Burger, 1967), possibly to prevent predation as well as to promote dispersal.

1.2 Appraisal of fitness and environmental adaptation: habitat selection and expansion

The distribution of *Sesamum* species is based on environmental opportunities. The wild species can become weedy, expanding to new habitats. Since the advent of agriculture in Africa, they have migrated into sites created by humans in a dynamic coevolution with humans, because woodlands and savanna cleared for agriculture and roads have created opportunities for wild *Sesamum* species too. Human use, such as gathering and tolerating these particular species sprouting in cultivated fields, provided additional opportunity for their expansion.

Sesamum and all other Pedaliaceae show supreme flexibility and adaptability due to their plastic genetic backgrounds. Variable, irregular functioning can be advantageous for maximizing outcomes, and these parameters have been selection factors in evolution. Cultivated sesame is highly variable in developmental traits such as days to maturity, and in morphological features: seed colour, plant colour, height, leaf morphology, capsule size/number per node, number of carpels, number of branches, and branching arrangement.

1.3 Famine food and folk medicine

Many authors (Portères, 1950; Dalziel, 1955; Watt & Breyer-Brandwijk, 1962; Busson 1965; Dokosi, 1969; David, 1976; Fabregues & Lebrun, 1976; Seignobos, 1982, Boudet *et al.*, 1986, Smith *et al.*, 1996; von Koenen; 1996, Maundu *et al.*, 1999) report that wild species of *Sesamum* are cultivated across Africa. This may be due, in part, to their physical resemblance to cultivated *S. indicum*, but also because they are independently recognized as acceptable foods for their leaves and oil-containing seeds. Manlove (1932, cited by Dalziel, 1955) reported that *S. radiatum* seed contain 32.3% oil, and *Ceratotheca sesamoides*, 37.3% oil. *S. alatum*, *S. angolense*, *S. angustifolium* and *S. radiatum* are consumed as potherbs and used for medicine (Bedigian, 2003b, 2004b; Bedigian & van der Maesen, 2003). The leaves are added to soups and sauces, and may be used fresh or dried. Since the dried leaves can be stored, families routinely dry and stockpile the leaves of *Sesamum* and *C. sesamoides* for emergencies during the 'hungry' season, before the next year's harvest is ready.

1.3 Sorrows of sesame: 'queen of oilseeds' yet orphan crop

Herein lies a conundrum: sesame seeds are so popular that the plant is often dubbed "the Queen of Oilseed crops" (Eckey, 1954; Al-Yemeni *et al.*, 2000; Bedigian, 2000). Plants in the genus *Sesamum* produce chemical constituents not found in other edible oils that enable the oil to resist oxidative rancidity (Ikeda, 2001). These antioxidant compounds, sesamin and sesamolin, belong to a category of phenylpropanoid lignans that occur in few other plant groups (Bedigian *et al.*, 1985; Bedigian, 1988, 2003a, 2003b). The seeds are rich in the limiting amino acid methionine, and are nutritionally excellent, containing 25% protein by weight, unsaturated fat, and are rich in vitamins and minerals, especially calcium. The oil is versatile, used as emollient, lamp oil, lubricant, ink and insecticide, exceptionally synergistic with pyrethrin (Haller *et al.*, 1942).

Yet sesame receives no mandated research support from any international CGIAR center), leading Mahmoud *et al.* (1995) to label sesame an 'orphan crop.' There seems to be no financial/institutional support for research into sesame's diverse landraces and indigenous 'unimproved' cultivars concentrated largely in Africa, nor support for investigation into its wild relatives. Since it has widespread use, sesame does not fit into a depiction as an "Underutilized and Underexploited Crop" and was consequently dropped from the IPGRI list (Bedigian, 2003a).

Sesame was reviled by French and British colonial-era governments. Question du Sésame (1843), was a petition protesting against sesame cultivation. It predicted the "immediate and complete ruin of the southeast and north of France by the introduction of Egyptian sesame competing with the French olive trade." It described the introduction of sesame onto the French market as an invasion, pushing out the prosperity of the French via their local rapeseed oil industry. Drastic measures were necessary to discourage planting sesame. While simultaneously portraying much about sesame that is commendable, this Manifesto warned that sesame was a change agent leading to many troubles, including bankruptcy of olive oil merchants, disruption of navigation, and destruction of the local soap-manufacturing industry.

Similarly, a century ago the British attempted to discourage sesame cultivation among Kenyan farmers and immigrants from India and Pakistan, in order to increase maize production for reimportation to Britain as livestock feed. Records at the Kenya National Archives reveal that early in the 20th century, rail shipping rates to Mombasa's seaport were deliberately increased for sesame, vis a vis maize, as a disincentive against sesame.

1.5 Sesame and its wild relatives are neglected research subjects

Attention to sesame and its close relatives remains neglected despite sesame's clear cultural and dietary importance in Africa and Asia (Bedigian, 2000). While its use as an oil and food source has diminished in the last century due to the introduction of exotic cash crops such as cassava, cocoa, cotton, maize and peanut, sesame is still broadly used across Africa. The accessibility of exotic collards, cabbages and peas has eroded use of *Sesamum* spp. as leaf vegetables, although they still contribute substantially to dietary needs in more out of the way places (Bedigian, 2004b).
Neither *Sesamum* spp. nor *C. sesamoides* were included among a list of 23 'Key species of African leafy vegetables' (Maundu *et al.*, 2003). They were not considered to be a priority by five country representatives the authors questioned when preparing an evaluation for Plant Resources of Tropical Africa (Patrick Maundu pers. comm.). Similarly, wild *Sesamum* spp. were dropped from a list of Priority Species in the 1996 IPGRI Leafy Vegetable study (Maundu *et al.*, 1999).

One bystander (Ashri, 1990, 1994, 1998) followed Bedigian (1981) and van Rheenen (1981) in urging that special efforts be devoted to the exploration, collection, evaluation and conservation of wild *Sesamum* species. Decades earlier, the author of this paper had already begun work towards that goal. Fieldwork in India (August-September 1979), Sudan (October 1979–January 1980), Kenya (1993, 1994), Uganda, Kenya, Tanzania and Sudan (June–December 1999) and Mali (December 2000–January 2001) resulted in collections of *S. alatum*, *S. angolense*, *S. angustifolium*, *S. latifolium*, *S. malabaricum* and *S. radiatum*, as well as cultivated sesame landraces. Two other species of Pedaliaceae: closely related and much prized *Ceratotheca sesamoides*, and the desert dwelling *Rogeria adenophylla* were also included. Accounts of these explorations were published (Bedigian, 1981, 1988, 1991, 2003a, 2003b, 2004b; Bedigian & Harlan, 1983; Bedigian *et al.*, 1985, 1986; Bedigian & van der Maesen, 2003) and are ongoing. A key West African species, *S. radiatum*, is of some significance to the local economy, particularly in Nigeria, where it may substitute for *S. indicum* (Dalziel, 1955). Other less familiar wild species occur in Southern Africa, and are the subject of this author's forthcoming fieldwork.

1.6 Early exploration – geographic coverage and species investigated

A study of the collections of *Sesamum* and *Ceratotheca* in the world's herbaria seems akin to a 'Who's Who' of early African exploration. Theodor Kotschy's (1813–1866) groundbreaking travels in Sudan and Ethiopia (1837–40) brought him into early contact with the genus *Sesamum*, particularly with *S. alatum*, *S. latifolium*, *S. indicum* and *C. sesamoides*. Kotschy's collection of *S. alatum* (*Kotschy* 106, K) and *C. sesamoides* (*Kotschy* 101, BR, HUH, K, MO, W, WAG) are designated type specimens. Grant and Speke's travels 1860–1863 (Speke, 1863) yielded a type specimen of *S. angustifolium*, K.

Auguste Chevalier explored the Sahara in the late 19th and early 20th century, and recorded precise observations (1952) about the early use of *S. alatum*, *S. indicum*, *Ceratotheca sesamoides* and *Rogeria adenophylla*. His collections of *S. alatum* (*Chevalier* 624, 1293 (K), *Chevalier* 5520 (BR)) provide early documentation from West Africa.

1.7 Re-examination of misinformation about *Sesamum* spp. perpetuated in literature

1.7.i *Quest for the earliest historical report about Sesame in Africa*

Authorities writing about early sesame in Africa, including Burkill (1997), Busson (1965), Lewicki (1974) and Mauny (1953) state that sesame was observed by the Arab traveler al Zouhri in 1150 AD at Gao (Mali). That notion has persisted in the literature because each commentator has relied upon a previous well-respected compiler. It was even recently presented by this author (Bedigian & van der Maesen, 2003) and by Fuller (2003). When this author later attempted to verify that well-established report by examining the original Arabic source (Zouhri, 1968), there was no mention of sesame or Gao in those pages (Elsiddig M. At-Taras and Mark T. Day, Associate Librarian, Reference Librarian for Middle Eastern Studies, Indiana University, translators 2002). No English translation of al Zouhri (1968) has been published, but this author's careful study of the Spanish edition (Zuhri, 1991) reveals that Mauny's (1953) report was quite certainly incorrectly rendered, and that subsequent authors have simply repeated the mistaken interpretation. Al Zouhri referred to sesame grown at a place called Kawlam, also known as Quilon, on the Malabar coast of India, and not to Kaw Kaw (Gao). Mauny or the authority upon whom he relied, mistook Quilon, southwest of Madurai (Webster's New Geographical Dictionary 1997), for Gao.

1.7.ii *Seeking the origin of sesame*

The issue of the domestication of cultivated sesame, *S. indicum* L., continues to be misrepresented by reviewers even now (e.g. Namiki, 1995; Ashri, 1989, 1998; Weiss, 2000; Weiss & de la Cruz, 2001; Morris, 2002). Bisht *et al.* (1998), incorrectly reporting this author's published work, stated that … "Bedigian feels that it is appropriate to consider Africa as the primary centre of origin…" Some authors relying on secondary sources may not be aware of work published in the past. Evidence from genetic crosses (Bedigian, 1988, 2003a; Hiremath & Patil, 1999), chemical constituents (Bedigian *et al.*, 1985) and molecular studies (Bhat *et al.*, 1999; Nanthakumar *et al.*, 2000) show that wild *Sesamum malabaricum* Burm. (2n=26) is very likely the progenitor of the oilseed crop (2n=26). This species occurs on the Indian subcontinent. Observant of the aforementioned persistent misinterpretations, all the evidence was recently thoroughly reviewed and updated again (Bedigian, 2003a).

Ihlenfeldt & Grabow-Seidensticker's (1979) proposal of *S. latifolium* as the progenitor of cultivated sesame is dubious in light of these more recent studies. They failed to perform the requisite reciprocal crosses, and their record of its distribution is incomplete (Bedigian, 2003a).

1.7.iii *Misidentification and authentication of* S. latifolium

Gillett (1953) described the new species, *Sesamum latifolium.* It occurs in Ethiopia, Kenya, Sudan, Uganda, and Tanzania. This author visited Abim's old growth forest region in Kotido district of northern Uganda where the type specimen was collected in 1940 (*Thomas* 3708 EA, HBG, K) and confirms that it still grows there (*Bedigian* 7, MO).

Correspondence about *S. latifolium* and direct communication with Gillett at the Kew herbarium in 1980 immediately after fieldwork in Sudan convinces this author beyond any doubt that the prevalent species in central Sudan is *S. latifolium.* Gillett sent this author a letter from Kenya dated June 16, 1980, answering several questions about *S. latifolium,* and a copy of Gillett's letter has been retained within the *S. latifolium* folder at the East African Herbarium. *S. latifolium* is encountered throughout central Sudan on granitic outcrops south of Gedaref along the Ethiopian border (*Bedigian* 46, 47, 48, MO), in the Nuba Mountains as far south as Talodi, near Agadi and El Obeid (Bedigian & Harlan, 1983) and as far west as Zalengei, in Darfur (*Bedigian* 59, MO). The species occurs widely in Kenya too: Kendu Bay on Lake Victoria (*Bedigian* 36, MO), a dry riverbed near the Nguruman Escarpment (*Bedigian* 38, MO), as well as along roadsides near Lakes Bogoria and Baringo (*Bedigian* 39, 40, 42, 43, 45, MO).

It is unfortunate that Andrews (1956) overlooked the species *S. latifolium* in his *Flowering Plants of Sudan* (1956). In its place, he published another vaguely described species, *S. radiatum*, listing its sole distribution as Equatoria province. Andrews (1956) retained a name *S. radiatum* previously recorded by Broun & Massey (1929) who gave a similarly unclear description, and they specified another Southern province, Bahr al Ghazal (Jur). Political circumstances in recent years have prevented this author from travelling to southern Sudan to confirm whether *S. radiatum* occurs there, and no herbarium specimens are available from that area. Therefore we have insufficient data to know whether *S. radiatum* actually occurs in Southern Sudan, although it is widespread in neighboring Zaire and areas westward (Bedigian, 2003b, 2004a, 2004b; n.d.). Since Andrews (1956) omitted *S. latifolium*, an erroneous name: *S. radiatum* has been adopted. Despite published corrections (Bedigian & Harlan, 1983; Bedigian, 1988) recent reports e.g. Mahmoud *et al.* (1995) still use the incorrect name. Salih sent seeds to this author in 1992 requesting a correct identification of the taxon, but disregarded that advice and retained the wrong name in all her publications (1993). Chromosome counts, too, were attributed to the wrong species (Khidir, 1962), a mistake that is problematical because *S. radiatum* has 64 chromosomes (John & Rao, 1941) whereas Ihlenfeldt & Grabow-Seidensticker (1979) reported the number for *S. latifolium* as 32.

2 Conclusions and outlook

Wild *Sesamum* and *Ceratotheca* spp. are exceptionally valuable wild sources of food and medicine, yet like cultivated *S. indicum* they remain neglected, and research about them, unfunded. These genera contribute to food security because early maturing sesame cultivars help smallholder farming due to reduced risk of crop failure; sesame escapes end-of-season drought and ensures adequate food most years, even in risky environments; harvesting wild leaves provides food during the traditional 'hungry period' (Bedigian, 2004b). These taxa protect fragile environments because they thrive in dry lands, efficiently using soil, water and nutrients while arresting and even reversing land degradation.

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INVENTORY OF *ALLANBLACKIA FLORIBUNDA* IN THE SANAGA MARITIME DIVISION, LITTORAL PROVINCE, CAMEROON

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Abstract

This paper gives an account of the inventory of *Allanblackia floribunda* in the Sanaga Maritime Division of the Littoral Province of Cameroon, and was necessitated by the lack of information on its distribution, density, habitat preference, phenology and occurrence of other species, accessibility, and local uses. A total of 25 sites/villages were investigated. The results showed that there was no clear correlation between this tree and the vegetation types investigated: *A. floribunda* densities are more or less randomly distributed. The study showed that *Allanblackia* is found in three main land use types: farms (14.0%), fallows (63.7%), and forest (22.3%). Despite the different shapes of the fruits, *A. floribunda* was the only *Allanblackia* species found in the entire area. The results showed that most of the trees (97%) were found within a range of 3 km from the villages. Regeneration of the species appears to be only natural and is observed in particular in fallows and in open forest.

Résumé

Inventaire de *Allanblackia floribunda* dans le département de la Sanaga Maritime, Province du Littoral, Cameroun. Cet article décrit l'inventaire de *Allanblackia floribunda* mené dans le département de la Sanaga Maritime, Province du Littoral, au Cameroun, et était rendu nécessaire par le manque d'information sur la distribution, la densité, les préférences en matière d'habitat, la phénologie et la présence d'autres espèces, l'accessibilité et les utilisations locales de cette espèce. Au total, 25 sites/villages ont été étudiés. Pour chacun d'eux, un transect de 5000 m × 100 m a été échantillonné. Les résultats ont montré qu'il n'y avait pas de corrélation claire entre cet arbre et les types de végétation étudiés: les densités de *A. floribunda* sont plus ou moins distribuées au hasard. L'étude a montré que *Allanblackia* existe dans les trois principaux types d'occupation des sols: les fermes (14,0%), les jachères (63,7%) et la forêt (22,3%). Malgré les différentes formes de fruits observés chez cette espèce, *A. floribunda* était la seule espèce d'*Allanblackia* trouvée dans toute la zone. Les résultats ont montré que la plupart des arbres (97%) étaient présents dans un rayon de 3 km autour des villages. La régénération de l'espèce semble être naturelle et est observée particulièrement dans les jachères et en forêt ouverte.

Key words: Inventory, *Allanblackia floribunda*, Sanaga Maritime Division, Cameroon

1 Introduction

The main aim of GTZ and the Unilever Research Laboratories, Vlaardingen, Holland, together with a number of national businesses, is to promote biodiversity conservation and poverty alleviation in the African tropical forest belt in general and Cameroon in particular. In order to achieve this they want to develop a new, profitable and internationally recognised sustainable raw material that can be obtained from these forests. Only limited knowledge is available concerning the ecology, distribution, habitat, phenology, uses and trade of *Allanblackia floribunda* (Clusiaceae), based on past studies and inventories across Africa (Bamps, 1969; Hall & Swaine, 1981; Hawthorne & Abu-Juam, 1995; Tchouto *et al.*, 1999; van Rompaey, 2003). *A. floribunda* constitutes a potential source of oil and can be used in medicine and for biodiesel production (van Rompaey, 2003). *A. floribunda* has the largest fruits of all plants in the African rainforest. The seeds are known to contain edible fat, but have scarcely been used on a commercial scale. Although *A. parviflora* is reported to be common in West African forests, *A. floribunda*, discovered near Cameroon river "wouri" by Gustav Mann (Benth. & Hook., 1867), seems to be the most abundant *Allanblackia* species in the Central African forest. However, more detailed knowledge of its distribution is needed if its exploitation is to be envisaged. It is therefore on the basis of all these gaps that Unilever and GTZ have chosen the Sanaga Maritime Division as a pilot area for the study of this species.

The Limbe Botanical and Zoological Gardens (LBZG), working to become the Mount Cameroon Biodiversity Conservation Centre (MCBCC), has proven experience and expertise in environmental assessment and monitoring, specifically in the fields of botany, wildlife, socio-economics and Geographic Information Systems (GIS)/Mapping. LBZG has carried out similar studies in many areas within Cameroon (Ndam *et al.*, 2001) and was selected for this project based on this experience.

Named after Allan Black, 19th century Kew botanist, *Allanblackia* is a small genus with nine species confined to tropical Africa, from Sierra Leone to Congo, and upland eastwards to Tanzania (van Rompaey, 2003). It is centred mostly in the lowland rainforests existing in areas up to 800 m above sea level. It is most abundant in the Atlantic forest to the west and less abundant in the Congolese forests in the South. It is rare or absent from the semi-deciduous and montane forests of Cameroon. Due to extensive deforestation, this genus is becoming rare and even extinct in some humid regions. *A. floribunda* is commonly known as the "Tallow tree" and from time immemorial it has had various uses to communities in forest areas where it is found (Figs. 1, 2). Cultivation appears desirable and is certainly practicable, although in managed forests, it is considered a weed-species and is eradicated (Burkill, 1994).

The main objective of the inventory was to quantify the number and size distribution of *Allanblackia* spp., in the Sanaga Maritime Division, Littoral Province of Cameroon, with main emphasis on: 1) the distribution of *A. floribunda* within the division, 2) a list of sensitive/fragile ecological niches, 3) habitat preference, 4) recording phenological data of the species at recording time, paying special attention to flowering and fruiting, 5) providing accessibility of the species to the people as well as to the markets, 6) occurrence of other *Allanblackia* species, 7) local uses of the species, and 8) its natural regeneration.

FIG. 1. *Allanblackia floribunda* tree with fruits. (Photo by Gonnermann)

FIG. 2. Fruits of *Allanblackia floribunda*. (Photo by Nkeng)

2 Methodology

In order to assess the distribution and density of *Allanblackia*, the sampling design was put in place after analysis of Landsat TM images. The survey used 100 × 5000 m (50 ha) transects as suggested by Unilever. Transects were laid perpendicular to topography and through pilot villages. Transects cut across farmland, fallow land, forest and other land use types. The intention of this stratification was to ensure that the full range of vegetation land use types were included in the transects. The bearing for each transect was measured using a compass. Once transects were laid out, the enumeration or tree counting team followed. The tree counting was carried out by moving slowly and carefully searching a 100 m band (50 m on either side of the central line) for *Allanblackia*. The 50 m distances were periodically checked for borderline trees. Once spotted and checked by the field botanists, each tree was measured, and stem diameter recorded for stems with dbh (diameter at breast height) greater than 10 cm. Information on habitat, land use type and phenology (fruiting or not) were also recorded in the field data sheet. Information was also noted on the natural regeneration status as well as the uses by local people.

3 Results and discussion

3.1 Land cover and spatial distribution map

Fig. 3 shows the spatial distribution of stem density of *Allanblackia*. Apparently, there doesn’t seem to be any trend or correlation between stem density and land cover type: the densities are more or less randomly distributed.

3.2 Diameter distribution and tree density

A total of 25 transects were surveyed in 25 sites/villages. A total of 515 stems were recorded. The diameter distribution (Fig. 4) is skewed showing a decreasing inverted J or negative exponential pattern with most trees (482 or 93.6%) in the 10–35 cm dbh classes. There are few stems above 35 cm dbh. The modal class is 15–20 cm dbh. No trees were found with a diameter above 60 cm dbh. This could be due to the fact that most of the *Allanblackia* species, especially *A. floribunda*, do not grow very large (Hutchinson & Dalziel, 1954; Keay, 1984; Burkill, 1994).

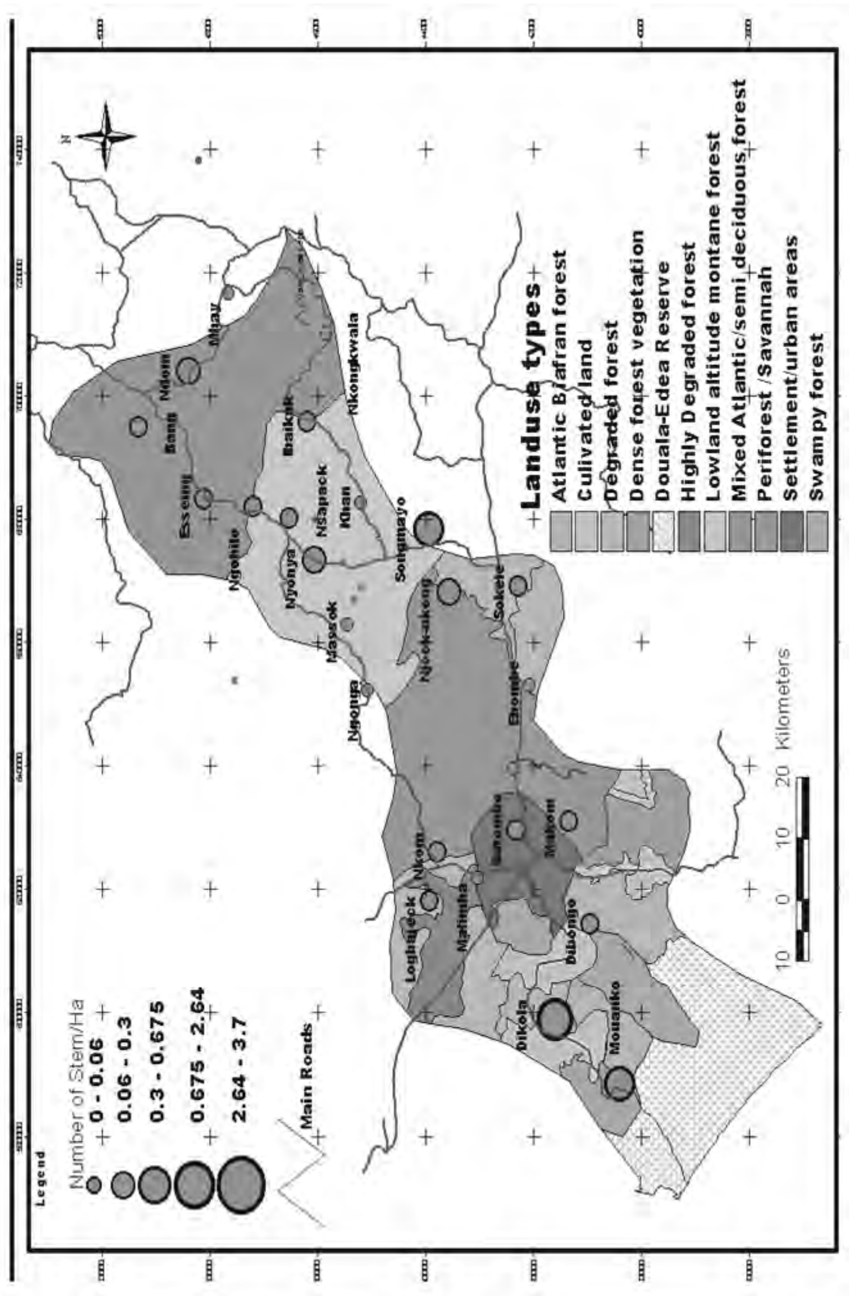

FIG. 3. Land cover and spatial distriution map for *Allanblackia floribunda* in the Sanaga Maritime Division.

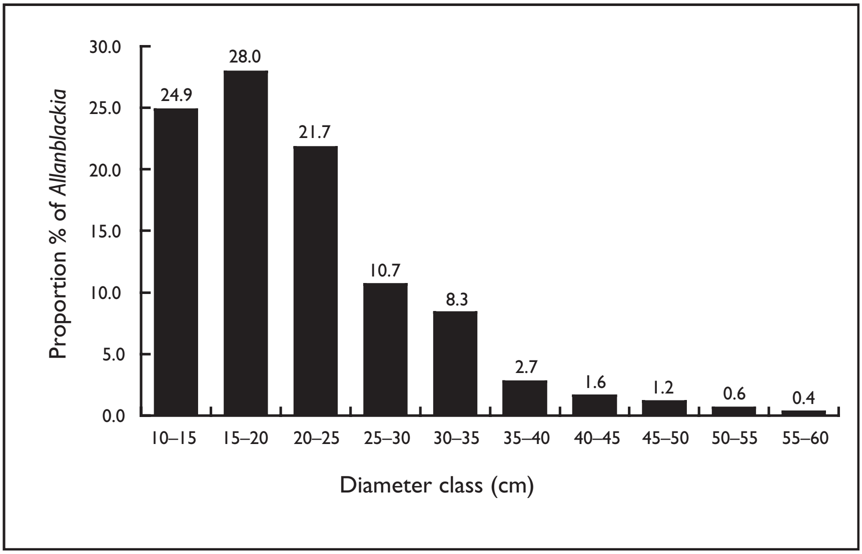

FIG. 4. Diameter distribution for *Allanblackia floribunda* in the Sanaga Maritime Division.

3.3 Expected number of *Allanblackia floribunda* trees in the Sanaga Maritime Division

From the spatial distribution map (Fig. 3), transect data were grouped into the different land cover types and stem densities extrapolated. Approximate surface areas for each land cover type were estimated from a GIS database (Arcview 3.2) and used with the densities to produce approximate number of trees per land cover type. These stems were further distributed into fruiting (FR) and non-fruiting (NF) trees based on the 35.9: 64.1 ratio. (See section 5.5 below). The final results (Table 1) excluding the Douala-Edea reserve, gives 298,159 trees of which 104,655 had fruits and 193,274 had no fruits.

TABLE 1. *Allanblackia floribunda* densities in Sanaga-Maritime (excluding the Reserve). FR= Fruiting trees; NF= Non-fruiting trees.

Land cover Type	**Area(ha)**	**Density**	**Standard error**	**Stems**	**FR**	**NF**
Periforest Savanna	141,627	0,144	0.106	20,394	7,158	13,236
Mixed Lowland Bamboo	110,341	0,249	0.147	27,475	9,644	17,831
Low Altitude Montane	107,075	0,270	0.208	28,910	10,148	18,532
Degraded Biafran	94,900	2,147	1.068	203,750	71,516	132,234
Highly-Degraded Forest	86,158	0,128	0.065	11,028	3,871	7,157
Urban Settlement Edea	29,735	0,222	0.000	6,601	2,317	4,284
Swamps	46,001	0	0	0	0	0
Industrial Plantations	33,809	0	0	0	0	0
Total	**649,646**			**298,159**	**104,644**	**193,274**

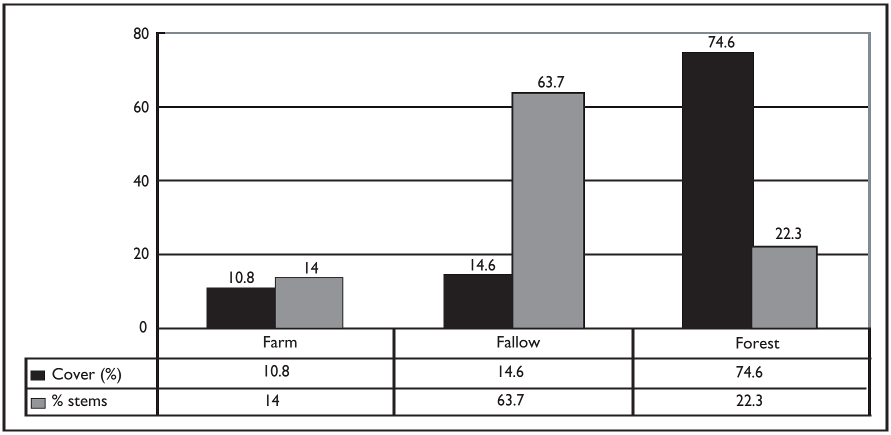

FIG. 5. Proportion (%) of *Allanblackia floribunda* in different land use types.

3.4 Distribution of *Allanblackia floribunda* by land use types

During the survey, all land use types traversed by transects were recorded. It was observed that *Allanblackia floribunda* is mainly found in three main land use types, i.e. fallows, forest and farmland (Fig. 5). The figure shows that 63.7% of trees were found in the fallows, 22.3% in the forest, and 14.0% on farmland. This tendency was observed irrespective of study zone or vegetation cover. The high proportion of *A. floribunda* in fallows implies that the species is probably a pioneer there. Hutchinson & Dalziel (1954), Keay (1989) and Burkill (1994) consider *Allanblackia* to be an evergreen forest tree, while Cable & Cheek (1998) considered it to be a shade-bearing species. However, our observations in this study showed that this plant is highly light demanding (heliophytic). Examples were observed in Dibongo village where many stems were seen along the road around houses but none were seen in the transect, which was predominantly forest. Most of the stems recorded in the forest were in open forest and within and around forest gaps. Very few or none were recorded in dense, close canopy forest. Trees found in the forest were taller than those in the other land use types, perhaps indicating more suitable conditions or less disturbance. Further evidence was provided by some villagers who indicated that *Allanblackia* was more abundant around human settlements than in the high forest. The fact that *Allanblackia* was not found in the plantations (Oil Palm, Rubber) was due to the total clearance of the area for plantation establishment, and savanna seems not to be the natural habitat for this genus. One hunter in Nyouya village even declared that "*Allanblackia* is among the first trees to colonise an area after it has been cleared."

The entire survey covered a distance of 105,750 m. Of this total distance, 11,450 m (10.8%) of transect distance covered farmland, and 67 stems were found on it; 78,850 m (74.6%) of forest were covered and 108 stems found; and finally 15,450 m (14.6%) of fallow land was covered, and 316 stems counted. On a linear scale, this gives a frequency of 5.9 or 6 stems per km covered on farmland; barely 1.4 stem per km on forest land, and as much as 20.5 stems per km on fallow land. This further confirms the fact that more *Allanblackia floribunda* trees grow in fallow land than in closed canopy forest (Fig. 5).

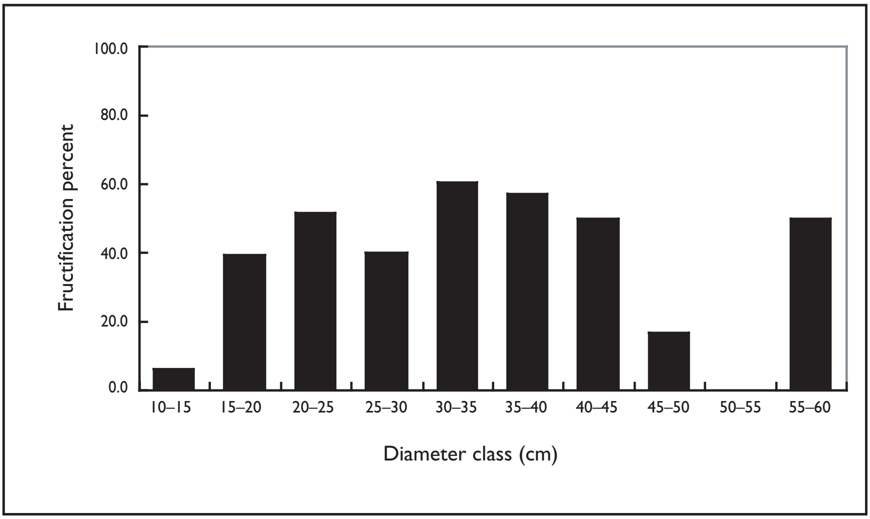

FIG. 6. Variation of fructification with diameter classes.

Plots of variation of stem density against transect land use (Figs. 8–11) show a negative trend or tendency as the forest area in the transect is increased. The tendency is positive with fallow land and slightly positive with farmland. It is negative with altitude, and this may suggest that *Allanblackia* prefers low altitude fallows or open forest to high altitudes. At close to 800 m altitude, we found very low densities of *A. floribunda*, confirming the information obtained from the literature that *Allanblackia* is mostly found in lowland rain forests up to 800 m above sea level, and absent from the semi-deciduous and montane forests of Cameroon. However, given that this study is only exploratory, more research needs to be conducted to confirm some of these assertions.

3.5 Phenology

From our survey, 185 (35.9%) trees out of 515 were bearing fruits and 330 (64.1%) had no fruits at the time of the enumeration. Fructification sets in when *Allanblackia* stems are at least 15 cm in diameter and remains more or less constant until 60 cm (Fig. 6).

Our survey period did not coincide with the flowering period of *Allanblackia*. No trees were seen in flower within the transects or elsewhere within the survey area. Keay (1989) states that the male and the female flowers are all borne on the same tree with some branches having only male flowers and others having only female ones. Interviews made in the field confirmed the hypothesis of Thikakul (1985) who proposed that fruiting of the species is almost all year round.

3.6 Accessibility of *Allanblackia*

About 97% of the *A. floribunda* trees were found within 3 km of villages; and about 90% within 2.5 km. Any search for *Allanblackia* should therefore be within a 2.5 km to 3 km radius of most villages (Fig. 7). This radius corresponds to the area of farmland and fallow land in most villages on which *A. floribunda* is mostly found. This habitat preference has a positive consequence as it eases the exploitation of this useful species by villagers.

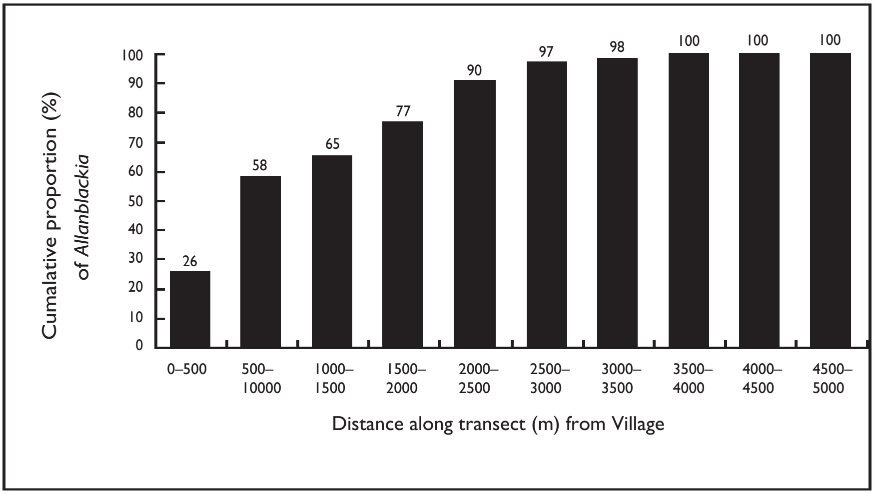

FIG. 7. Cumulative proportion (%) of *A. floribunda* along transect from village.

3.7 Occurrence of other *Allanblackia* species

Despite the different shapes of the fruits encountered, *Allanblackia floribunda* was the only *Allanblackia* found in the entire area. However, *Allanblackia* seems to be a problematic genus, and thus there is an urgent need of its revision.

3.8 Uses

According to informal interviews made, *Allanblackia* fruits were commonly used as bait for trapping of rodents. Like in Congo (Burkill, 1994), a decoction of the bark was reported to be used for cough, bronchitis, and other bronchial affections.

3.9 Natural regeneration

Contrary to our expectations from looking at the number of fruits produced per tree, the rate of regeneration of *Allanblackia* seems low. This might be due to the fact that rodents immediately eat up the fallen fruits. Few seedlings were recorded in the old fallow and forest under the parent-tree or a few meters away. Considering the high proportion of *Allanblackia* in the fallows and farms and given the practice of shifting cultivation, regeneration may be reduced by the farmers who clear everything during the planting period. Forest cleared along the road to Ibaikak village is a good example of this; many trees including *Allanblackia* were felled, despite the fact that its fruits were collected some years back and sold to one American company. Most people cannot explain this, other than through ignorance; hence the usual statement "…*if I had known it was valuable, I wouldn't have felled it*".

4 Conclusion and recommendations

The results and observations made during the inventory show that the southern part of the division is very rich in *Allanblackia floribunda*. It is therefore recommended that exploitation should start from that part (Mouanko, Dikola etc…)

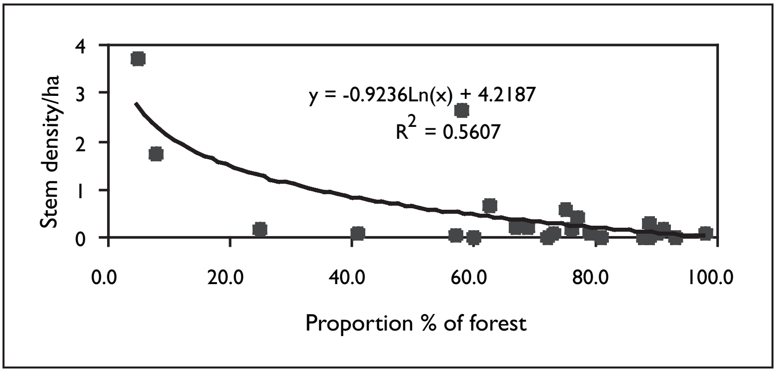

FIG. 8. Variation of stem density with forest area.

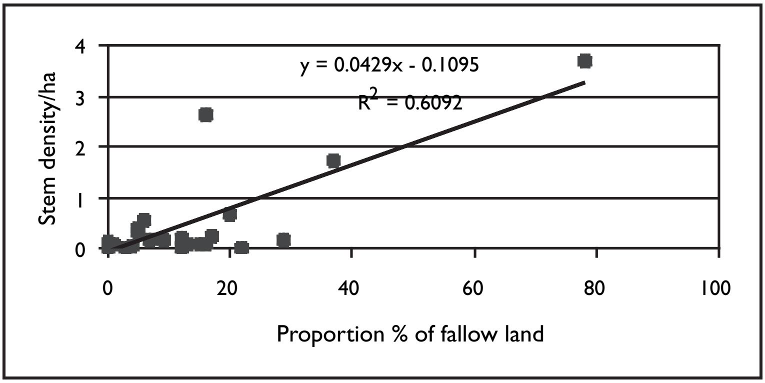

FIG. 9. Variation of stem density with fallow land area.

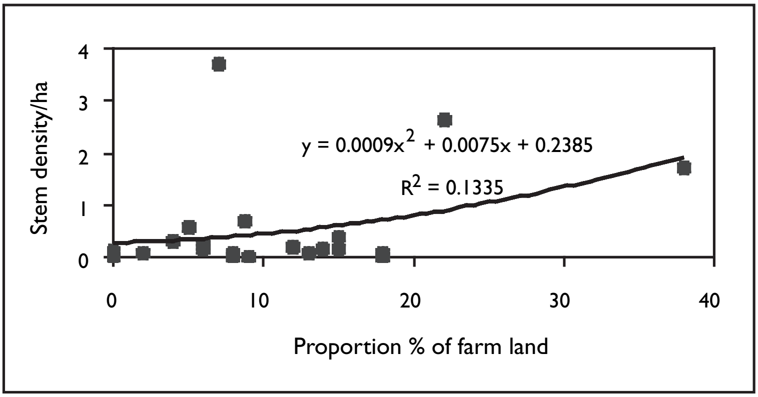

FIG. 10. Variation of stem density with farm land area.

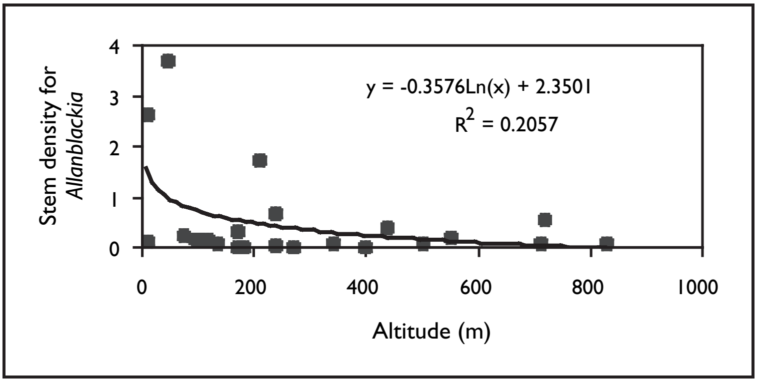

FIG. 11. Variation of stem density with altitude.

The total number of stems of the species is estimated at 303,834 in the exploitable sites of Sanaga-Maritime, i.e. excluding the reserve, (Table 1) comprising 106,646 (35.9%) fruiting and 197,188 (64.1%) non-fruiting trees.

It is recommended that a more detailed study be carried out to clarify whether *A. floribunda* is monoecious (male and female sexual organs on different trees) or dioecious (male and female sexual organs on the same tree). Given the fact that this study is only exploratory in nature, more research need to be conducted to confirm some of the assertions. Considering its eventual importance in poverty alleviation, *A. floribunda,* although not exploited yet should be encouraged in agro-forestry systems. Education of the farmers will be necessary to prevent felling of tall trees during harvesting of fruit. Agro-forestry practices should be developed prior to exploitation. It is also recommended that any search for *A. floribunda* should be within a 2.5 to 3 km radius of most villages in the area survey.

Acknowledgements

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MEDICINAL PLANT USES IN NYABUSHOZI COUNTY, MBARARA DISTRICT, WESTERN UGANDA

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Abstract

An ethnobotanical study conducted in Nyabushozi to explore medicinal plants used among the Banyankore people recorded 68 species from 35 families. Data collection involved informal interviews, direct observation, field walks in three parishes and semi-structured questionnaires of 47 respondents. The study showed that preparation and administration of medicinal plants include several methods. Taxa commonly used belong to three families in particular: Asteraceae (20.6%), Fabaceae (16.2%), Lamiaceae (7.4%). Shrubs formed a major component (36%) of harvested material, while herbs formed 31% and trees 15%. Leaves (72%), roots (16.2%), and bark (8.8%) are used in most concoctions. Diseases treated include malaria, stomachache and cough – commonest in Nyabushozi County; and, dysentery, syphilis, headaches/migraine, snakebites, skin rash, anaemia, splenomegaly, measles, tapeworms, and pneumonia. All those interviewed hold traditional knowledge about treatment of common diseases. Elderly women hold TK about complicated diseases such as convulsions/epilepsy.

Résumé

Usages des plantes médicinales à Nyabushozi, district de Mbarara, Ouest de l'Ouganda. Une étude ethnobotanique menée à Nyabushozi afin d'explorer les plantes médicinales utilisées par la population Banyankore a permis de recenser 68 espèces parmi 35 familles. La collecte de données consistait en des entrevues informelles, l'observation directe, des randonnées sur le terrain dans trois paroisses et des questionnaires semi-structurés adressés à 47 personnes sondées. L'étude a montré que la préparation et l'administration de plantes médicinales peuvent résulter en des méthodes diverses. Les taxons communément utilisés appartiennent à trois familles en particulier: Asteraceae (20,6%), Fabaceae (16,2%), Lamiaceae (7,4%). Les arbustes constituaient la plus grande part (36%) du matériel récolté, alors que les herbacées représentaient 31% et les arbres 15%. Les feuilles (72%), les racines (16,2%) et les écorces (8,8%) sont utilisées dans la plupart des potions. La liste des maladies traitées comprend la malaria, les maux de ventre et le rhume – les plus communes dans le Nyabushozi; ainsi que la dysenterie, la syphilis, les maux de tête/migraines, les morsures de serpent, les écorchures, l'anémie, la splénomégalie, la rougeole, les vers et la pneumonie. Toutes ces entrevues ont révélé l'existence de connaissance traditionnelle du traitement des maladies fréquentes. Les femmes âgées avaient également des connaissances sur les convulsions/épilepsie.

Key words: ethnobotany, medicinal plants, Nyabushozi, traditional knowledge, Uganda

1 Introduction

Traditional medicine (TM) occupies a special place in health care systems in Uganda (Kamatenesi Mugisha, 2002, Tabuti *et al.*, 2003). The World Health Organisation (WHO) estimates 80% usage of TM in developing countries (Farnsworth & Soejarto 1991), and in Uganda extensive use of TM for day-to-day health care in rural areas is close to 90% (Kakudidi, 1999, Kamatenesi *et al.*, 2000). About 80% of the population live in rural areas, where the distances involved to reach health centres (HC) at parish headquarters range between 5–10 km or more for over 70% of the population, and it takes a healthy person approximately 2 hours to walk 10 km; a sick person or a mother carrying a child requires twice as long (Adkisson 1989).

The orthodox health care delivery system in Uganda is generally underdeveloped and resources are scarce. Nyabushozi County is no different, with three HC; one of which at Rushere can be classified as a small hospital, in that it can carry out operations, admits few patients and has a maternity ward, as well as having a trained doctor and nurses. Although the number of patients attending Rushere hospital is on the increase as it also serves patients from neighbouring counties, the distance traveled as well as lack of funds to reach the hospital mainly influence the decision by many to seek biomedical health care. The HC are inadequately stocked with drugs, so people resort to use of medicinal plants. Many of the plants, as well as the knowledge of their uses, may be lost before they are documented.

The lifestyle in Nyabushozi County has changed from the traditional nomadic type, where local long-horned cattle breeds utilized the natural pastures. Recent developments, mainly involving the introduction of exotic dairy breeds in the area, have necessitated pasture improvement and bush clearing. The plant community structure is changing as a result, coupled with loss of indigenous knowledge that is associated with use of the plants once the plants disappear. This knowledge will not be there for long to salvage. As the ecosystem in Nyabushozi has been subject to seasonal fires, cultural change, overgrazing and at one time massive cutting of trees and burning to control tsetse fly spread, some valuable plant species may already have been lost, while knowledge about others is threatened through migrations of youths to towns where they can no longer learn about medicinal plants, as well as death of older custodians of indigenous knowledge. Therefore, the aim of this study is to explore medicinal plants used by the Banyankore people and document the indigenous knowledge about these plants.

2 Study area

Nyabushozi County is located in the eastern part of Mbarara District of Uganda, between 0°05'N–0°18'S and 30°41'E–31°06'E (Fig. 1), about 200 km west of Kampala, the capital city. It lies in the "cattle corridor" – a pastoral area in the eastern semi-arid area of the district. Within the county are six sub-counties, namely Kinoni, Kenshunga, Kashongi, Kikatsi, Sanga/Kanyaryeru and Nyakashashara. Each sub-county has several parishes that consist of a number of villages. Nyabushozi county has an estimated population of about 96,617 people and a population density of 30–140 people/km^2 based on the population census of 2001 (UBS, 2001). Historically the events of pestilence, tsetse flies infestation, ranching schemes and wildlife conservation kept the population in the area low, but recently there has been a sharp increase in population through migration from densely

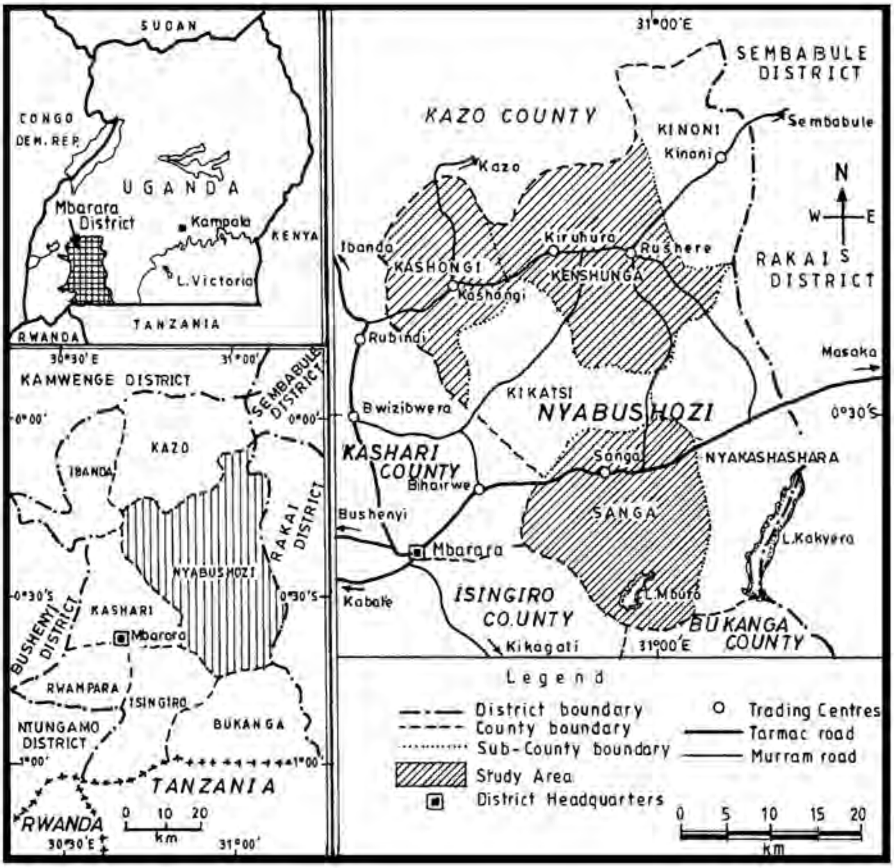

FIG. 1. Location of Nyabushozi County in Western Uganda.

populated parts of the district, the 1986 Lake Mburo resettlement scheme in Kanyaryeru of 1986 and the ranch restructuring programme of 1991. This population increase has caused conversion of more land for agriculture, bush clearing and pasture improvement, all in the name of development. Economic activities in the area include pastoralism and agriculture as the main source of livelihood for the local population, as well as fishing and tourism in Lake Mburo National Park and retail trade.

The vegetation is mainly dominated by *Acacia* spp./*Themeda triandra* Forssk. associations. The tree layer is dominated by *Acacia hockii* de Wild., the poorly drained valley bottoms are characterized by *Sporobolus pyrimidalis* P. Beauv. and various sedges, while the rocky hillsides with poor shallow soils are dominated by *Loudentia kagerensis* (K.Schum.) Hutch. *Cymbopogon afronardus* (L.) Rendle is common in ranches adjacent to Lake Mburo. Nevertheless, the county has a diverse flora and fauna.

3 Methods

An ethnobotanical study was carried out between March and May 2001 in three sub-counties (Kenshunga, Kashongi and Sanga/Kanyaryeru) employing transect walks, free listing, direct observation and semi-structured questionnaires. Kenshunga was chosen because it is the home sub-county of one the researchers, while Kashongi and Sanga/Kanyaryeru were selected by a simple lottery method. The information is partly derived from the authors' experience as residents of Nyabushozi and Kazo counties of Mbarara District and from interviewing a total of 47 respondents: 28 women and 19 men, with 15, 14 and 18 respondents from Sanga/Kanyaryeru, Kanshongi and Kenshunga sub-counties, respectively. Interviews were conducted orally in the local language of Runyankore, but were guided by the questionnaires to solicit information on use for treating various diseases affecting humans. After the interviews, the respondents were asked to accompany the authors for a walk through the village bushes so that the plants mentioned could be identified and collected. The walk enhanced recall of additional information not provided earlier.

4 Results

A total of 69 medicinal plant species were identified by local people as sources of medicine (Table 1) belonging to 35 plant families. The highest number of species used as medicine belong to Asteraceae (20.6%) followed by Fabaceae (16.2%), and Lamiaceae (7.4%). The large number of medicinal plants recorded within a period of 3 weeks of the study shows a substantial amount of knowledge among the community. Of the 69 species, women mentioned 43 while men identified 26.

Most herbal medicine plants grow wild (79.5%); only 13.2% are cultivated, 2.9% are semi-wild, while 2.9% are either cultivated or semi-wild. Thus medicinal plants are mainly harvested from the wild. Rare plants are often cultivated in banana plantations, except for the introduced *Allium cepa* L., which is cultivated as a spice, while *Cleome gynandra* L. occurs in newly opened gardens and/or abandoned cow dung heaps, and is often left in gardens when weeding since it is used as a vegetable. *Senna spectabilis* H.S.Irwin & Barneby and *Spathodea campanulata* Beauv. are often planted in compounds for shade.

Overall, shrubs (36%) form a major component of harvested material, followed by herbs (31%) and trees (15%). Different parts of medicinal plants are used when preparing concoctions, a significant proportion of which are made from various parts (Fig. 2): leaves (72%) followed by roots (16.2%) and bark (8.8%). The rest of the other parts are used in small proportions of below 6%. In some cases the whole plant is used (4.4%).

Diseases/medical conditions recorded during this study that are treated by plants include malaria, stomach-ache and cough, which are commonest in the area. Other cases are sinus infection, dysentery, fevers, syphilis, palpitations/hypertension, headache, gingivitis, nose bleeding, splenomegaly, measles, snake bites, skin rash, anaemia, pneumonia, polio, false teeth, wounds, whitlow, tapeworms, bee stings, mild cases of epilepsy/convulsions due to high fever [ebirezi as contrasted with epilepsy (ensimbo)] and sex determination. Although the local people claimed that any disease could be treated and cured by herbal medicine, this does not appear to be true for HIV/AIDS, cancer and tuberculosis.

TABLE 1. Catalogue of medicinal plants used the study area.

Taxon	Local name	Growth habit	Part used	Application	Uses and conditions treated
ACANTHACEAE					
Acanthus pubescens Engl. & Turrill	Matojo	S	R	Leak ash	Sinus infection
Asteracantha longifolia Nees	Kihwa	H	Lv	Drink infusion	Dysentery
Thunbergia alata Bojer ex Sims	Wankuula	C	Sd	Swallow two seeds	Sex determination
Monochma subsessile C.B.Clarke	Erazi	H	Lv	Drink infusion	Stomachache
ALLIACEAE					
Allium cepa L.	Butungulu	H	Bulb	Smear on affected area	Stop wasp and bee stings swelling
ALOACEAE					
Aloe wollastoni Rendle	Rukaka	S	LV	Drink infusion	Malarial fever
AMARYLLIDACEAE					
Crinum kirkii Baker	Kinyabarecu	H	Bb	Drink infusion	Malaria; induction of vomiting
ANACARDIACEAE					
Rhus natalensis Bernh. ex Krauss	Musheeshe	S	Lv	Bathe body with infusion	Remove bad omen or evil spirits
APOCYNACEAE					
Carissa edulis Vahl	Muyoonza	S	R	Rub powder into incision	Painful nerves (Omuziga)
ASCLEPIADACEAE					
Sopubia sp.	Shagama-nungi		St	Keep on body	To bring good luck
ASPARAGACEAE					
Asparagus africanus Lam.	Bushebashebe/ Nyarwehungura	S	Fr, Lv	Rub on	Sex determination, treatment of wounds
ASTERACEAE					
Aspilia africana (Pers) C.D.Adams	Ekarwe	H	Lv	Chew	Gingivitis
Bidens pilosa L.	Nyabarashana/ Murashe	H	Lv	Tie on wound	Stop bleeding after injury

TABLE 1. continued

Taxon	Local name	Growth habit	Part used	Application	Uses and conditions treated
Crassocephalum crepidioides (Benth.) S.Moore	Ekinami	H	Lv	Drink infusion	Heart palpitations
Crassocephalum vitellinum S.Moore	Mushunuunu/ Eshunuunu	H	Lv	Drink infusion	Fever during pregnancy
Dichrocephala integrifolia Kuntze	Mubuza	H	Wh	Drink & bathe with infusion	Syphilis
Microglossa angolensis Oliver & Hiern	Muhe/Kashoha/ Kavuga-nkaande	S	R, Lv	Chew root; drink infusion	Cough; malaria
Senecio sp.	Muziraanfu	H	Lv	Bathe with infusion	Fever during pregnancy
Senecio sp.	Mukunda/ Mwanga	S	Lv; R	Enema; chew roasted roots	Malaria; cough
Solanecio angulatus (Vahl) C.Jeffrey	Kizimya-muriro	S	Lv	Bathe with infusion	Malaria
Tagetes minuta L.	Mukazi-murofa	H	Lv, Fl	Rub on forehead	Headache
Vernonia amygdalina Delile	Mubiriizi	S	R, B, Lv	Drink infusion	Malaria fever
Vernoia lasiopus O.Hoffm.	Nyakajuma	S	Lv	Drink infusion	Malaria
Vernonia smithiana Less.	Enyaweera	H	Lv	Wash body or sprinkle around home	To bring good luck
BASELLACEAE					
Basella alba L.	Enderema	C	Lv	Infusion as enema	Malaria (reduce temperature)
BIGNONIACEAE					
Spathodea comparnulata Beauv.	Munyaara	T	B, LV	Drink infusion	Vaginal dryness
CAESALPINIACEAE					
Senna didymobotrya (Fresen.) H.S.Irwin & Barneby	Mugabagaba	T	Lv	Boil with salt, drink infusion	Malaria; stomachache
CAPPARIDACEAE					
Capparis sepiaria L.	Mutahatsi/ Mukorokoombe	S	R	Drink infusion	Nose bleeding

TABLE 1. continued

Taxon	Local name	Growth habit	Part used	Application	Uses and conditions treated
Cleome gynandra L.	Eshogi	H	Lv	Eat cooked leaves	Improve appetite
CHENOPODIACEAE					
Chenopodium opulifolium Schrad.	Mweetango	H	Lv	Rub over stomach, skin, drink infusion	Splenomegaly, measles and cough
CUCURBITACEAE					
Momordica foetida Schum.	Mwihura	C	Lv/St	Drink/ bathe infusion	Measles
Zehneria scabra Sond.	Kabindiizi		Lv	Enema	Stomachache
EUPHORBIACEAE					
Tragia benthami Baker	Engyenyi	C	Lv/Fl	Put little on genitals	Wetting beds
Ricinus communis L.	Kashoga akakye	S	Lv/F	Drink little infusion; put on wound	Stomachache; snakebite
MIMOSACEAE					
Acacia hockii De Wild.	Rugando	T	R	Drink infusion	Anemia
Albizia coriaria Welw.	Musisa	T	B	Bathe with hot infusion	Scabies
FABACEAE					
Desmodium repandum DC.	Kanyanshagama	H	Lv	Boil with milk, drink	Cough
Erythrina abyssinica DC.	Muko	T	B, F	Drink infusion;	Splenomegaly; dysentery/ stomachache
Indigofera dendroides Jacq.	Akaryabuzimba	S	Lv	Pound, mix with ghee, rub on area	Swelling
Indigofera arrecta Hochst. ex A.Rich.	Musorooza	S	Lv	Pound, mix with ghee, rub on area	Bone fracture, sprains
Rhynchosia resinosa Hochst. ex Baker	Kashaka-karibyooya	S	Lv	Boil, wash body	
				Rub under pits	Baby skin rash; body odour
Sesbania sesban (L.) Merr.	Munyeganyegye	T	Lv	Rub powder into incision on head	Cerebral/high malaria fever (Ebirezi)

TABLE 1. continued

Taxon	**Local name**	**Growth habit**	**Part used**	**Application**	**Uses and conditions treated**
Tephrosia linearis Pers.	Nyakarimi-kamwe	S	Lv	Eat /drink infusion	Love charm
Vigna unguiculata (L.) Walp.	Kaihabukuru	C	Lv	Rub on head; chew roots	Headache; afterbirth pain
HYDNORACEAE					
Hydnora abyssinica A.Braun	Mutima gw'ensi	P	R	Drink infusion	Heart palpitations
LAMIACEAE					
Hoslundia opposita Vahl	Esitaimwe	S	Lv	Bathe infusion	Birth wounds
Leonotis nepetifolia (L.) R.Br.	Kicumucumu	S	Lv	Crush, rub on ribs	Pneumonia
Leucas martinicensis (Jacq.) R.Br.	Kacumucumu	H	L	Chew	Vomiting, colic
Ocimum sauve Willd.	Mwenyi	S	Lv	Chew	Stomachache
Tetradenia riparia (Hochst.) L.E.Codd	Muravunga	S	Lv	Chew; drink infusion	Cough, high fever with shivering
MALVACEAE					
Hibiscus acetosella Welw.	Eshagama	S	Lv	Drink infusion	Anemia
Hibiscus aethiopicus L.	Mugona-mpiri	S	Lv	Bandage on area	Wounds
MYRTACEAE					
Eucalyptus sp.	Kalitusi	T	Lv, B	Chew; drink infusion	Cough
PHYTOLACCACEAE					
Phytolacca dodecandra L'Hér.	Muhoko	S	Lv	Drink; wash body with infusion	To induce abortion; to treat scabies, skin rash
POACEAE					
Brachiaria brizantha (A.Rich.) Stapf	Ejubwe	H	Lv	Okujumburira	Celebral/high malaria fever (Ebirezi)
Cynodon dactylon Pers.	Rucwamba	H	Wh	Chew and tie on	Injury wounds
POLYGALACEAE					
Polygala sp.	Bwoomi	H	R	Chew	Whooping cough

TABLE 1. continued

Taxon	Local name	Growth habit	Part used	Application	Uses and conditions treated
POLYGONACEAE					
Oxygonum sinuatum Dammer	Bucumita-mbogo	H	Lv	Wilt over fire, crush, tie on area	Whitlow
RUTACEAE					
Fagara chalybea Engl.	Entare y'eirungu	T	B	Drink infusion	Epilepsy
SAPINDACEAE					
Allophyllus africanus Beauv.	Mutete	T	Lv, R	Drink infusion	Stomachache
Cardiospermum grandiflorum Sw.	Ruzibira	C	Lv, St	Boil in milk, drink	Cough
SCROPHULARIACEAE					
Rhamphicarpa montana N.E.Br.	Ensheko y'ensi	S	Wh	Put in new house	To bring good luck
Rhamphicarpa tubulosa Benth.	Encwa-bugufu	S	Lv	Rub into incision	Polio
SOLANACEAE					
Nicotiana tabacum L.	Etaabe	H	Lv	Chew	Stomachache
TILIACEAE					
Triumfetta rhomboidea Jacq.	Ruhigura	S	Sd	Pocket/tie around body	To bring good luck
VERBENACEAE					
Lantana trifolia L.	Muhuuki	S	Lv	Boil in milk, drink; squeeze into nose	Cough; headache
VITACEAE					
Cyphostemma adenocaule Descoings ex Wild & R.D.Drumm.	Kimara/ Kibombo	C	R	Drink infusion; rub on gums	Anthelminthetic for tape worms; false teeth
ZINGIBERACEAE					
Zingiber officinale Rosc.	Ntagahuuzi	Ge	R	Chew, drink infusion	Cough

Abbreviations used: H herb; S shrub; C climber; T tree; Ge geophyte; Fr fruit; Fb fiber; Sd seed; St stem; Fl flower; Wh whole plant; Lv leaves; B bark; R root.

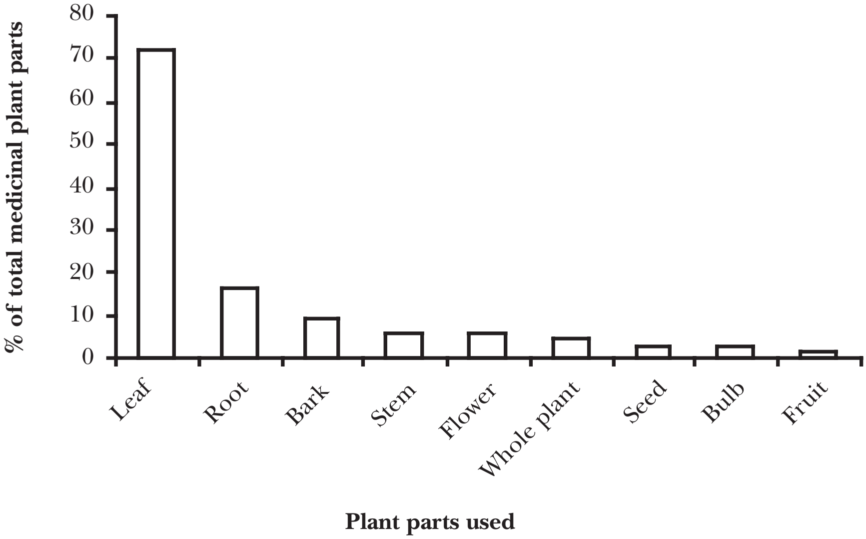

Fig. 2. Plant parts used to make concoctions.

Most people interviewed confessed their belief in the existence of the spiritual world and in the value of consulting traditional healers. So medicinal plants in this regard do not only treat conditions which can be clinically tested, but also bring good luck, cleanse bad omens, protect against witchcraft, and appease the spirits of the ancestors, which are all believed to bring either mental or physical imbalance.

4.1 Specially held traditional medical practice

Traditional knowledge about medicinal plants is generally held for common diseases such as malaria and cough, and even children know what plants to use. Nevertheless, for complicated cases such as high malaria fever in children (Ebirezi, a mild case of epilepsy), this kind of information is held only by old women. Also there are cases where a particular group of people share some specialized knowledge, for instance the Abararira clan, who are known for treating snakebite. Sometimes one person or one family hold the knowledge, such as bonesetters and a known polio-healer, both of whom were not willing to disclose their cures. Bonesetters are few and the practice is inherited.

4.2 Methods of treatment

Plants are used either in combination of varying numbers from 2 to 5(+) and quantities, or singly as in the highly potent *Cyphostemma adenocaule*, which is used as an anthelmintic. The methods of preparation of medicinal plants vary depending on the raw material used, on the age of the patient, and/or the disease. They include chewing, squeezing in water, boiling in water or milk, roasting, burning, or pounding (especially the bark). The administration methods were also varied and include:

a) the squeezed concoction or boiled material in water or milk is drunk

b) the material is crushed or made into powder and tied on wounds/injury (okwomoora)

c) the pounded material is rubbed externally for headache, sprains and broken bones (okubunga)

d) the concoction is given as enemas (entego), where the liquid is applied through the rectum, especially in cases of constipation or stomachache

e) the ash or powder is rubbed in an incision made on the affected area (okushandaga)

f) chewing as first aid by adults, while mothers often chew the herbs and give the resultant decoction to the infant(s) by mouth or through the nose (okujumburira)

g) the material is burnt and the ash is leaked

h) the plant part is pocketed or tied on the body as good luck charm or for protection.

5 Discussion

Traditional medicine is generally conceived to involve both seen and unseen forces – it is holistic in approach. Traditional medicine addresses both the causes that are of concern to biomedicine, as well as underlying causes such as witchcraft, aggravated ancestors and many others that are not apparent. While plants provide many necessities for life such as food and medicine, they are also central in ritual rites, taboos, social ceremonies, material culture and religion and beliefs, all shaped through experience and long historic association of humans with the plant world (Sofowara, 1993; Katende *et al.*, 1999; Tabuti *et al.*, 2003).

Anokbonggo (1992) recorded at least six major categories of traditional practitioners, although Muller & Balagizi (2001) recognize mainly two types, that is, popular medicine and medicine of traditional healers. The greatest part of therapy involves the use of plant extracts. Traditional medicinal practitioners in Uganda include about 43% pure herbalists and 41% herbalist-spiritualists, followed by mixed activity healers (14.3%) who use all types of traditional medicine including invoking the spirits; diviners and magicians constitute 1.4% and rely exclusively on their spiritual practical skills and experience, while bonesetters (0.3%) use herbs in addition to their skills of physical manipulation of injured bones (Anokbonggo, 1992). Traditional medicine is more accessible than modern health facilities to most of the population in the developing world, and traditional medicine is also socio-culturally more accepted (Sofowara, 1993). Consequently, people trust traditional medicine and often consult practitioners at the same time they use biomedicine, where available. Even urban residents in Uganda return to their villages when they are sick because they have more confidence in the old ways of doing things (Adkisson, 1989).

However, the death of elderly custodians of certain traditional knowledge will mean loss of certain practices unless they are passed on to younger generations since folk knowledge among the Banyankore, like many traditional tribes, is orally transmitted. Modernization and rapid changes in people's lifestyles, especially with regard to education, customs and traditions, rural-urban migration and environmental degradation, militate against and disrupt the transmission folk knowledge. While nearly all people hold much of the knowledge about certain medicinal plants, some knowledge is closely kept as a secret, as in cases of the polio healer and bonesetters encountered during this study.

Due to the scarcity of HC in Nyabushozi County, medicinal plants have continued to play a significant role in primary health care delivery. The diseases treated are of common occurrence in the area. According to Nyafuona *et al.* (2000) *Hydnora abyssinica*

A.Braun is the most coveted since it is used to treat other diseases. The other ailments include paralysis, hiccoughs, diarrhoea, diabetes, fever, sleeplessness, cough, measles, and haemorrhoids (Nyafuona *et al.*, 2000) in addition to heart palpitation associated with hypertension recorded during this study. Hydnora is often mixed with other herbs and/or and honey during the preparation of decoctions/infusions. Nyafuono *et al.* (2000) recorded 14 species with which it is mixed with: *Justicia exigua* S.Moore, *J. betonica* L., *Dracaena steuneri* Engl., *Microglossa angolensis* Oliver & Hiern, *Vernonia amygdalina* Del., *Kigelia africana* (Lam.) Benth., *Wurburgia ugandensis* Sprague, *Kalanchoe pinnata* (Lam.) Pers., *Sapium ellipticum* Pax, *Bridelia micrantha* Baill., *Albizia coriaria* Welw., *Cissampelos mucronata* A.Rich., *Callistemon citrinus* Stapf and *Passiflora edulis* Sims. Other than use as medicine *Hydnora abyssinica* is used as food in some parts of Uganda.

5.1 Vulnerability to overexploitation

Cunningham (1996) noted that there is a relationship between the parts of the plant collected, or the collection method used, and the impact of harvesting on the plant. The widespread use of leaf material for herbal concoctions has been reported in similar studies (Cunningham, 1996, Kyoshabire, 1998, Kakudidi *et al.*, 2000). This method of collection is not damaging to the plants and therefore more easily sustainable, especially if they are not uprooted. The most vulnerable species are those whose root and bark are used. Trees are particularly endangered as this type of destructive collecting leads to death of the plant if the bark does not grow back, such as *Spathodea campanulata* (Kakudidi *et al.*, 2000). Sustainable use would be possible only if the harvesting methods ensured that the cambium remained, as is done for the bark of *Ficus* species in the process of making bark cloth in central Uganda. However, often this is not the case for many trees whose bark is exploited. Similarly, the use of whole plants and roots also poses threat to plants. Nyafuono *et al.* (2000) noted the increasing use of *Hydnora abyssinica* for medicinal and other purposes, which may imply more intense harvesting.

Kamugisha *et al.* (1997), who worked in Lake Mburo National Park, noted that trees and shrubs comprise an important resource for local people in the area in addition to being used for medicine. They provide fuel wood for 100% of the households in the area, as well as poles for construction of residential houses, and cattle enclosures. Notable among the trees is *Fagara chalybea* (Entare y'eirungu), which is also an important cure for most common diseases in the area (Kamugisha *et al.*, 1997).

6 Conclusion

Traditional medical practitioners (TMP) complement modern health providers in Nyabushozi County and should not be ignored by them. The World Health Organisation has underscored the contribution of traditional medicine to rural communities since much of the rural population still depends on herbal medicine even with the advent of Western medicine. Herbal remedies in Nyabushozi County remain the cheapest, most easily available and commonly used form of health care among the local communities and often are quite effective in the treatment of certain diseases; and Nyabushozi is not exceptional in this regard. Uganda has not yet integrated TMP and modern medicine. Unfortunately many herbs in Uganda are not validated to determine the efficacy and dosage for the diseases they treat. There are still gaps in our understanding of how traditional knowledge systems of health work, their limitations and prospects, which is an impediment to integration. Further research on traditional herbal medicine will help to ensure precious knowledge is not lost completely, and will also aid in the conservation of the flora through increased awareness of sustainable harvesting methods.

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ETHNOBOTANICAL STUDIES OF MEDICINAL PLANTS USED IN GENDER INFERTILITY TREATMENT IN WESTERN UGANDA

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Abstract

Infertility in Uganda is a big problem in family interactions. Solutions to infertility are yet to be found. The main purpose of this study was to document indigenous knowledge (IK) on the use of herbal remedies to solve problems of infertility. From this study, 73 medicinal plants were documented as being used in the treatment of infertility. Accordingly, most commonly and widely used medicinal plant species include *Warburgia ugandensis, Tetradenia riparia*, *Mondia whitei*, *Cola acuminata* and *Allium sativum.* Additionally, some of the medicinal plants used in infertility management are foodstuffs such as *Passiflora edulis* and *Hypericum peplidifolium.* Hence, the nutritional status of an individual plays a role in infertility management. Nonetheless, this indigenous knowledge in infertility treatment requires further scientific documentation and validation in Uganda and elsewhere in Africa.

Résumé

Etudes ethnobotaniques de plantes médicinales utilisées dans le traitement de l'infertilité féminine dans l'ouest de l'Ouganda. En Ouganda, l'infertilité pose un grave problème de relations familiales. Des solutions à l'infertilité n'ont pas encore été trouvées. L'objet de cette étude était de documenter la connaissance indigène (IK) à propos de l'usage de remèdes à base d'herbes destinés à résoudre les problèmes d'infertilité. A travers cette étude, 73 plantes médicinales possédant cette propriété ont été mises en évidence. Les espèces les plus communément et largement utilisées sont *Warburgia ugandensis*, *Tetradenia riparia*, *Mondia whitei*, *Cola acuminata* et *Allium sativum.* Par ailleurs, certaines plantes alimentaires comme *Passiflora edulis* et *Hypericum peplidifolium*, sont utilisées pour soigner l'infertilité. Le statut nutritionnel d'un individu joue un rôle dans le traitement de l'infertilité. Néanmoins, cette connaissance indigène du traitement de l'infertilité nécessite d'être mieux documentée d'un point de vue scientifique et requiert une validation tant en Ouganda qu'ailleurs en Afrique.

Key words: gender, herbal medicine, infertility, traditional knowledge, Uganda

1 Introduction

Infertility and childlessness is a long-standing problem worldwide. Although infertility can occur in both males and females, in most African cultures it is blamed on women. Infertility is defined as the inability of a couple to conceive after one year of sexual intercourse without using any type of contraception (Mishell *et al.*, 1991). Male sterility is defined as the inability of semen to fertilize a female ovule (Pamplona-Roger, 2000). Among males, infertility is associated with abnormalities in the male reproductive system due to oligoazoospermia, high viscosity of semen, low sperm mobility and low volume of semen (Mishell *et al.*, 1991) and it may be affected by diseases and low libido. Female sterility is defined as the inability of mature women to conceive. Female infertility is triggered by pressure to reproduce, poverty and ignorance, causing malnutrition and diseases. Young age at marriage, obstetrical problems associated with first conception and sexually transmitted diseases, especially gonorrhoea, contribute a great deal to infertility (Leke & Nasah, 1981). Salpingitis and pelvic inflammatory diseases are the most common complications of gonorrhoea that often result in tubal occlusion, which interferes with normal ovum transportation (Osoba, 1984). Investigations show the relationship between abnormalities in spermatozoa/semen parameters and the incidence of male factor mediated fertility problems in couples (Mishell *et al.*, 1991; Nduka *et al.*, 2001). In Gabon, more than 30% of couples are infertile at the end of their reproductive lives due to longstanding tubal occlusion in women and occlusion of the vas deferens and/ epididymis producing azoospermia in men (Okonofua, 2001).

Infertility rates among married couples in African countries range from 15% to 30%, whereas in developed countries it ranges from 5% to 10% (Okonofua, 2001). Generally, sub-Saharan Africa has one of the highest infertility rates in the world due to infections - mainly sexually transmitted diseases and HIV/AIDS that produce irreversible damage to the reproductive tract. Apart from the size of the problem, it is also now well known that infertility in African countries has severely negative consequences for women's reproductive health. Due to the high cultural premium placed on childbearing in many African countries, infertility often poses serious social problems for couples (Neema, 1999; Okonofua, 2001; Kamatenesi-Mugisha, 2004). However, women are more severely affected than men, even when the infertility is due to a male factor. This often leads to divorce, social ostracisation and sometimes physical abuse of women (Kamatenesi-Mugisha, 2004).

Despite the high prevalence of infertility in Africa, very few resources presently exist for the treatment of infertile couples. Conventional methods of infertility treatment are poorly developed in many African countries, with treatment effectiveness not exceeding 10% of infertile couples when these methods are applied. One of the reasons for poor effectiveness of conventional methods is that many cases of infertility must have gone beyond the scope of these methods before they are presented for orthodox treatment.

Recent research has shown that infertility or sterility may be associated with consumption of fungal-contaminated foodstuffs. Nduka *et al.* (2001) reported that infertility in men has been linked to the consumption of mycotoxins (e.g. aflatoxins) from microfungi. The most notorious and common genus is *Aspergillus*. Pitt (1996) observed that the consumption of mycotoxins through ingestion, inhalation and absorption through the skin causes lowered performance of the body, sickness or death in humans and animals. Exposure to mycotoxins can produce both acute and chronic toxicities varying from death to deleterious effects on the central nervous system, cardiovascular and pulmonary systems and on the alimentary canal (FAO, 2001). Mycotoxins are also carcinogenic, mutagenic, teratogenic and immunosuppressive (Sharma, 1998; FAO, 2001). In a Nigerian study (Nduka *et al.*, 2001) it was reported that men who were infertile had significantly higher concentrations of aflatoxin levels in the blood and semen than fertile men.

Although infertility is a big problem, its solution has not been well researched. In particular, most of the African indigenous knowledge (IK) in infertility management has not been well documented. Therefore, this study was conducted to document indigenous knowledge in medicinal plants used in infertility treatment or management in Uganda.

2 Study area description

The study was carried out in Bushenyi and Kasese districts in Western Uganda between January 2000 and March 2003. The sampling sites were mainly in the sub-counties of Kichwamba and Katerera, neighbouring the Queen Elizabeth Biosphere Reserve and the fishing villages (human settlements) within the biosphere reserve. These fishing villages included: Katwe, Mweya, Katunguru, Hamukungu, Kahendero and Kayanja. The neighbouring Parishes included Katolhu and Nyakatonzi in Kasese District and Kichwamba and Katerera sub-counties in Bushenyi District. Another distant village that was sampled was Kitagata Sub-county in Bushenyi district.

Queen Elizabeth Biosphere Reserve is found in western Uganda. It was established in April 1952 as Queen Elizabeth National (Rwenzori) Park and designated as a Biosphere Reserve by UNESCO in November 1979. It straddles the Equator, to the west of the rift valley and it includes Lakes Edward and George and several salt lakes like Lake Katwe. It lies astride Latitude: 00°15'S–00°10'N and Longitude: 29°45'–30°05'E. Lake George is a wetland, internationally recognised as a RAMSAR site. The biosphere reserve is about 2500 km^2. It is continuous with Kigezi Wildlife Reserve (330 km^2), Kyambura Wildlife Reserve (157 km^2) and Kibale Forest Corridor (339 km^2) which form its buffer in Uganda. It is also continuous with Virunga National Park (8,090 km^2) that is found in the Democratic Republic of Congo. Kasese, Bushenyi, Rukungiri and Kabarole Districts in Western Uganda share the biosphere reserve.

The ethnic groups in the area of study are mainly the Bakonjo, Banyankole, Batooro, Banyaruguru, Baziba, Basongora, Congolese, Baganda, Banyarwanda and the Bakiga (Kamatenesi-Mugisha, 2004). The composition of the migrants coming in for fishing, salt winning and various businesses and national park staff living in and around Queen Elizabeth Biosphere Reserve is variable.

The areas selected were based on the unavailability of health facilities in and around Queen Elizabeth Biosphere Reserve. These areas of study in the districts of Bushenyi and Kasese were selected because the distribution of modern health centres is limited to a few ill-equipped ones. Furthermore, the local communities are far from the existing health facilities. Young girls marry at an early age and the illiteracy rates are high.

3 Methods

Ethnobotanical data collection methods included visiting traditional healers that were identified by a local guide and local council leaders in each village to document the IK, in particular the medicinal plants used, and gender and socio-cultural aspects. Informal and formal conversations, discussions and interviews, market surveys, health surveys and field visits were conducted. The medicinal plants used were collected, identified and documented. Some of the medicinal plants that are harvested from distant places such as the Democratic Republic of Congo, other districts and unsafe areas within the reserve were not collected and are thus not included in this study.

Traditional healers, traditional birth attendants (midwives), young women and old people totaled about 170 main respondents in the study. The research methods used were mainly those that promoted free sharing of information between the researcher, the herbalists and other people. Therefore, informal conversations and semi-structured interviews and discussions were used to generate the ethnobotanical data (Martin, 1995). To connect with the traditional medical practitioners (TMPs) and traditional birth attendants (TBAs), the local authorities (Local Councils), herbalists associations in villages and chairpersons of Wildlife Clubs (CWCs) were consulted. When going to the forests, game reserve or other areas where they collect plant specimens, prior arrangements were made with the community leaders and park staff.

The informal conversations were held with the specialist resource users and other knowledgeable people on particular ailments with reference to infertility management. The meeting places were the gardens, women's group meetings, at their homes, and any other places convenient to them. Through conversations, the sources of knowledge of the healers on medicinal plants, the medicinal plants used and changes in the availability of medicinal plants were established. Those who were more knowledgeable were later followed and interviewed further especially the TBAs. Focused discussions were held with them later for formal recording. This was done to verify the information gathered and the spread of the indigenous knowledge (IK) in reproductive health care among the different reproductive groups.

The semi-structured interviews and discussions were held with the specialist resource users and other knowledgeable people on particular ailments by use of interview schedules for each respondent. Interviewed people were mainly the herbalists (both men and women) and TBAs. The time and place of interviews were arranged according to the schedules of the respondents. Meetings with them were, for example, at their places of work such as the farms where they treat the patients. Depending on where the interviews and discussions were held, recording was done immediately or afterwards, or appointments were made to get more details in a more convenient place arranged with the respondent. Key informants were identified and later interviewed separately and even followed for further details.

The field visits and excursions were arranged with the healers to places far from their homesteads or took place concurrently with the interviews and discussions. This was done with individuals or groups depending on where the herbs were collected. In the shared areas such as the fishing villages, or the multiple use areas, group excursions were conducted. The data collected was to supplement the information on plant names, parts used, collection of the herbarium specimens, and any other aspects of medicinal plants used for various ailments. The plants collected were given voucher numbers for later identification in the herbarium of the Botany Department, Makerere University.

The local market surveys were conducted within the areas of research to document the medicinal plants used in reproductive health care that are sold in local markets and about ten market vendors selling medicinal plants were interviewed. The local weekly markets and monthly markets were visited and these included Katerera, Kirugu and Ndekye in Bushenyi district.

The medicinal plants used were collected, identified and documented. The ethnic groups of the respondents were noted for purposes of getting the dialects of plant and the diseases naming by the various traditional healers interviewed and plants used. The medical ethnobotanical data collected has been analyzed, medicinal plants from the study areas have been listed and methods of administering the herbal drugs were also documented.

4 Results

Seventy-three species of medicinal plants were recorded as being used for treating infertility in both men and women (Table 1). The family Asteraceae (12) followed by Lamiaceae (10) has the largest number of species used as herbal remedies for treating infertility. Various plant parts are harvested and used in herbal medication, including the leaves, roots, stem bark, fruits, seeds, stem, fruit peelings, inflorescence, juice, flowers and gum. The most common plant parts harvested for medicine are the leaves: 38.9 % (28). The commonest growth forms harvested are the herbs (58.9%), followed by shrubs (21.9%) and trees (19.2%).

Wild medicinal plants collected account for 72.6% (53) of the total. The cultivated medicinal plants represent 13.7% (10), and the medicinal plants that are both harvested from natural ecosystems and partially cultivated account for 13.7% (10).

The most commonly and widely used medicinal plant species are *Cola acuminata, Warburgia ugandensis*, *Tetradenia riparia*, *Mondia whitei*, *Allium sativum*, *Cinnamomum verum*, *Erythrina abyssinica*, and *Hallea rubrostipulata.*

The most common methods of preparation of infertility herbal drugs were found to be boiling, pounding and squeezing. The herbal drugs from *Mondia whitei* and *Cola acuminata* can be roasted as well as boiled and pounded. The herbal medicines from the family Lamiaceae are mainly prepared by squeezing, boiling and steaming, and are then administered orally as well as by insertion in the birth canal. All the herbal medicines are orally administered.

4.1 Medicinal plants used in infertility treatment of commercial value

Twenty two medicinal plant species used for treating infertility were recorded as being sold in local markets (Table 2). Thirteen plants are also used as foodstuffs. These medicinal plants are distributed in fifteen families with Asteraceae and Rutaceae the most represented families with three medicinal plant species each used as herbal remedies for treating infertility. The most common plant parts harvested for medicine are the bark, followed by leaves, and roots. The commonest growth forms harvested are the trees (50 %), followed by herbs (36.4%) and shrubs (13.6%). Wild medicinal plants sold in markets for infertility treatment account for 54.5% (12) of the total and the cultivated plants represent 45.5% (10).

TABLE 1. Medicinal plants used in treatment of infertility.

Family	Scientific name	Parts used	Growth form	Origin of collected plants	Methods of preparation	Methods of administration
Alliaceae	*Allium cepa* L.	WP	H	C	boiling, pounding	oral
	Allium sativum L.	WP	H	C	boiling, pounding	oral
Aloaceae	*Aloe vera* (L.) Webb.	L	H	W	boiling, pounding	oral
Amaranthaceae	*Cyathula uncinulata* (Schrad.) Schinz	L	H	W	boiling, pounding	oral
	Aerva lanata (L.) Schult.	L	H	W	boiling, pounding	oral
Anacardiaceae	*Mangifera indica* Blume	L	T	C	boiling, pounding	oral
	Rhus vulgaris Meikle	B, R, L	S	W	boiling, pounding	oral
Apocynaceae	*Catharanthus roseus* (L.) G.Don	L	H	W/C	boiling, pounding	oral
Asclepiadiaceae	*Asclepias pedunculata* (Decne.) Dandy	FR, SE	H	W	boiling, pounding	oral
	Mondia whitei Skeels	R	H	W	boiling, roasting, pounding	oral
Asteraceae	*Ageratum conyzoides* L.	L	H	W	squeezing, boiling	oral
	Conyza persicifolia Oliver & Hiern	L	H	W	squeezing, boiling	oral
	Crassocephalum bojeri (DC.) Robyns	L	H	W	squeezing, pounding, boiling	oral
	Crassocephalum vitellinum (Benth.) S.Moore	L, ST	H	W	squeezing, boiling	oral
	Erlangea cordifolia (Oliv.) S.Moore	R, L	H	W	squeezing, boiling	oral
	Guizotia scabra Chiov.	L	H	W	squeezing, boiling	oral
	Launaea cornuta (Hochst.ex Oliv. & Hiern) C.Jeffrey	R	H	W	squeezing, boiling	oral
	Pluchea ovalis DC.	L	H	W	squeezing, boiling	oral
	Tagetes minuta L.	L	H	W	squeezing, boiling	oral
	Vernonia amygdalina Del.	L, R	S	W	squeezing, boiling	oral
	Vernonia cinerea (L.) Less.	L, R	S	W	squeezing, boiling	oral
	Vernonia lasiopus O.Hoffm.	L, R	H	W	squeezing, boiling	oral
Bromeliaceae	*Ananas comosus* (L.) Merr.	FR-PE	H	C	squeezing, boiling, peeling	oral
Caesalpiniaceae	*Cassia siamea* Lam.	L, R	S	W	boiling, pounding	oral
	Cassia spectabilis DC.	L,R	S	W	boiling, pounding	oral
	Senna occidentalis (L.) Link	L, R	H	W	boiling, pounding	oral
Canellaceae	*Warburgia ugandensis* Sprague	B, L, R	T	W	boiling, pounding	oral
Chenopodiaceae	*Chenopodium procerum* Moq.	L, SE	H	W/C	boiling, pounding, squeezing	oral

TABLE 1. continued

Family	Scientific name	Parts used	Growth form	Origin of collected plants	Methods of preparation	Methods of administration
Colchicaceae	*Gloriosa superba* L.	L	H	W	boiling, pounding	oral
Convolvulaceae	*Ipomoea cairica* (L.) Sweet	L, ST	H	W	boiling, pounding	oral
Cucurbitaceae	*Momordica foetida* Schum.	L, R	H	W	boiling, pounding	oral
	Zehneria scabra (L.f.) Sond.	L, ST	H	W	boiling, pounding	oral
Cupressaceae	*Cupressus lusitanica* Franco	L	T	C	boiling, pounding	oral
Euphorbiaceae	*Flueggea virosa* (Willd.) Voigt	L, R	S	W	boiling, pounding	oral
Hypericaceae	*Hypericum peplidifolium* A.Rich.	WP	H	W	boiling, pounding	oral
Lamiaceae	*Hoslundia opposita* Vahl.	L, R	S	W	steaming, boiling, squeezing	oral, inserted in birth canal
	Leonotis nepetifolia (L.) R.Br.	L	S	W	steaming, boiling, squeezing	oral, inserted in birth canal
	Leucas martinicensis (Jacq.) R.Br.	L	H	W	steaming, boiling, squeezing	oral, inserted in birth canal
	Ocimum kilimandscharicum Guerke	L, FR	H	W	steaming, boiling, squeezing	oral, inserted in birth canal
	Ocimum lamiifolium Benth.	L, FR	S	W	steaming, boiling, squeezing	oral, inserted in birth canal
	Solenostemon latifolius (Benth.) J.K.Morton	L	H	W	steaming, boiling, squeezing	oral, inserted in birth canal
	Becium affine (Hochst.) Chiov.	L	H	W/C	steaming, boiling, squeezing	oral, inserted in birth canal
	Ocimum gratissimum L.	L	H	W/C	steaming, boiling, squeezing	oral, inserted in birth canal
	Plectranthus prostratus Guerke	L	H	W/C	steaming, boiling, squeezing	oral, inserted in birth canal
	Tetradenia riparia (Hochst.) Codd	L	S	W/C	squeezing, boiling	oral
Lauraceae	*Cinnamomum verum* J.Perls.	B, L	T	C	boiling, pounding	oral
Malvaceae	*Hibiscus fuscus* Garcke	L, R, B	S	W/C	boiling, pounding	oral
Meliaceae	*Melia azedarach* L.	R, L	T	C	boiling, pounding	oral
Mimosaceae	*Albizia coriaria* Oliv.	L, B	T	W	boiling, pounding	oral

TABLE 1. continued

Family	Scientific name	Parts used	Growth form	Origin of collected plants	Methods of preparation	Methods of administration
Musaceae	*Musa acuminata* Colla	INFLO, JU	S	C	boiling, pounding	oral
	Musa sapientum L.	INFLO, JU	S	C	boiling, pounding	oral
Myrsinaceae	*Maesa lanceolata* Forssk.	L, B	T	W	boiling, pounding	oral
Myrtaceae	*Psidium guajava* L.	R, L	T	C	boiling, pounding	oral
	Eucalyptus citriodora Hook.	L, FR, GUM	T	W/C	boiling, pounding	oral
	Eucalyptus grandis Maiden	L	T	W/C	boiling, pounding	oral
Papilionaceae	*Canavalia africana* Dunn ex Hutchinson	L	H	W	boiling, pounding	oral
	Erythrina abyssinica DC.	L,B,FL	T	W	boiling, pounding	oral
	Indigofera arrecta Hochst. ex A.Rich.	L, R	H	W	boiling, pounding, squeezing	oral
	Indigofera spicata Forssk.	L	H	W	boiling, pounding, squeezing	oral
Passifloraceae	*Passiflora edulis* Sims	L	H	W/C	boiling, pounding, squeezing	oral
Polygonaceae	*Rumex abyssinicus* Jacq.	L, ST	H	W	boiling, pounding, squeezing	oral
Ranunculaceae	*Clematis brachiata* Thunb.	L	H	W	boiling, pounding, squeezing	oral
Rosaceae	*Rubus apetalus* Poir.	L	S	W	boiling, pounding, squeezing	oral
Rubiaceae	*Hallea rubrostipulata* (K.Schum.) Leroy	B, R	T	W	boiling, pounding,	oral
	Rubia cordifolia L.	L, FR	H	W	boiling, pounding, squeezing	oral
Rutaceae	*Zanthoxylum gilletii* (De Wild.) Waterm.	B, R	T	W	boiling, pounding	oral
Solanaceae	*Physalis minima* Link.	L	H	W	boiling, pounding, squeezing	oral
Sterculiaceae	*Cola acuminata* Schott & Endl.	FR	T	W	boiling, roasting, pounding	oral
Tiliaceae	*Triumfetta longicornuta* Hutch. & Moss	L, R	H	W	boiling, pounding, squeezing	oral
	Triumfetta rhomboidea Jacq.	L, R	H	W	boiling, pounding, squeezing	oral
Verbenaceae	*Lantana camara* L.	R, L	S	W	boiling, pounding, squeezing	oral
	Lantana trifolia L.	R, L , SE	S	W	boiling, pounding, squeezing	oral
Vitaceae	*Cissus oliveri* Gilg ex Engl.	L	H	W	boiling, pounding, squeezing	oral

Key: WP (whole plant); L (leaves); R (roots); B (bark); SE (seeds); FR (fruits); ST (Stem); FL (flowers); INFLO (inflorescence); GUM (gum); T (tree); S (shrub); H (herb); W (wild); C (cultivated)

TABLE 2. Medicinal plants used in infertility treatment of commercial value sold in local markets.

Scientific name	**Parts used**	**Growth form**	**Origin**
Albizia coriaria Oliv. (Mimosaceae)	L, B	T	W
Allium cepa L. (Alliaceae)*	WP	H	C
Allium sativum L. (Alliaceae)*	BU	H	C
Aloe vera (L.) Webb. (Aloaceae)	L	H	W
Ananas comosus (L.) Merr. (Bromeliaceae)*	FR-PE	H	C
Capsicum frutescens L. (Solanaceae)*	FR, SE	H	C
Cinnamomum verum J.Perls. (Lauraceae)*	B, L	T	C
Citropsis articulata Swingle & Kellerman (Rutaceae)	B, R	T	W
Citrus limon (L.) Burm.f. (Rutaceae)*	FR, SE	T	C
Cola acuminata Schott & Endl. (Sterculiaceae)*	B, SE	T	W
Erlangea cordifolia (Oliv) S.Moore (Asteraceae)*	R	H	W
Erythrina abyssinica DC. (Papilionaceae)	B	T	W
Mangifera indica Blume (Anacardiaceae)*	L	T	C
Melia azedarach L. (Meliaceae)	R, L	T	C
Mondia whiteii Skeels (Asclepiadiaceae)*	R	H	W
Psidium guajava L. (Myrtaceae)*	R	T	C
Rhus vulgaris Meikle (Anacardiaceae)*	B	S	W
Vernonia amygdalina Del. (Asteraceae)	L, R	S	W
Vernonia lasiopus O.Hoffm. (Asteraceae)	L	S	W
Warburgia ugandensis Sprague (Canellaceae)	B	T	W
Zanthoxylum gilletii (De Wild.) Waterm. (Rutaceae)	B	T	W
Zingiber officinale Roscoe (Zingiberaceae)*	RH	H	C

Key: WP (whole plant); L (leaves); R (roots); B (barks); SE (seeds); FR (fruits); RH (rhizome); FR-PE (fruit-peelings); W (wild); C (cultivated); T (tree); S (shrub); H (herb)
* Foodstuffs as well as medicinal plants used in infertility treatment sold in the local markets

5 Discussion

Vital medicinal plants used widely in communities to treat infertility were on sale in the local markets (Fig. 1). Rare medicinal plants of therapeutic value to the communities but from distant lands were also on sale; for example, *Cola acuminata* (cola nut) is harvested from forests in the Democratic Republic of Congo. Medicinal herbs from natural ecosystems that were of importance to the community were sold in the local markets at expensive prices. Some medicinal plant species are difficult to find in the markets because of their very limited ecological distribution. *Cola acuminata* and *Warburgia ugandensis* are examples of scarce medicinal plants that were sold expensively possibly due to high demand and/or the fact that they are not easily accessed nearby. For instance the fruit of *Cola acuminata* costs over 2000 Uganda Shillings (over $1 USD) and a piece of *Warburgia ugandensis* bark of 2 × 2 cm may cost over 500 Uganda Shillings (about $0.4 USD).

Citropsis articulata and *Warburgia ugandensis* were harvested from the protected areas in Uganda and sold in markets. The sale of plants from wild ecosystems points to the need to conserve the wild plant populations and the need for *ex situ* conservation to meet the potential market demands for the future. The dilemma lies in the eroded indigenous knowledge by commercialization of useful plant products, thus e*x situ*

FIG. 1. Market survey of medicinal plants and herbal medicine vendors with various herbal drug mixtures (A) and (B) on sale in Ndekye local market in Bushenyi District, Western Uganda.

conservation is urgently required in Uganda to protect our valuable biodiversity and improve the health and livelihoods of the people relying on biodiversity. The challenges of conservation, commercialization and sustainable utilization of plant genetic resources need to be interwoven with intellectual property rights (Williams *et al.*, 2003). Thus, the local communities who are the custodians of indigenous knowledge require equitable access and benefit sharing accruing from the use of genetic resources (Glowka *et al.*, 1994; Williams *et al.*, 2003).

Interestingly, cultivated medicinal plants such as *Zingiber officinale, Psidium guajava, Capsicum frutescens, Passiflora edulis*, *Ananas comosus, Hypericum peplidifolium, Mangifera indica* and *Allium sativa* were mainly foodstuffs. Although some of these plants listed as foods might have therapeutic value, the nutritional status of the couple may also play a big role in infertility treatment.

Most of these plants used for infertility treatment are boiled, pounded, squeezed and given mainly orally in form of herbal teas or decoctions. Furthermore, the pounding and boiling of the plant parts possibly improves the extraction of the potent compounds.

The men and women who have failed to have children are given some herbal concoctions to treat infertility. These medicinal plants such as *Lantana camara, Rubia cordifolia, Vernonia amygdalina, Crassocephalum vitellinum, Ocimum gratissimum* and many more medicinal plants are also used locally in the treatment of antifungal and antibacterial infections. Infertility triggered by the presence of infections (Leke & Nasah, 1981; Osoba, 1984; Pamplona-Roger, 2000) may be treated by use of medicinal plants with antimicrobial activities.

Infertility has inherent negative consequences for the health of individuals. For example, infertility is viewed as one of the many causes of poverty and HIV/AIDS spread in some patriarchal communities in Uganda. Many infertile spouses end up in polygamy in quest for children. Most African cultures blame barrenness on women while men are given the upper hand to look for children from other women. Thus, men become polygamous and in the process few resources are shared among many wives, which escalates the poverty levels in some homes and can introduce diseases like HIV/AIDS.

In attempts to manage infertility, medicinal plants are used and most of these medicinal remedies are harvested from wild plant populations. Examples of the medicinal plants harvested from wild places include *Warburgia ugandensis* and *Cola acuminata.* Some of these plants are regarded as aphrodisiacs, or just thought to have the ability to increase sexual desire and a revitalizing action on the body. Some of these plants, besides being therapeutic, are also used as foodstuffs. The common examples include *Passiflora edulis* and *Hypericum peplidifolium*, and several others.

This study suggests that the useful medicinal plants used in the treatment of infertility are worth further investigation since some plants may have curative properties. In addition, this indigenous knowledge in infertility treatment requires further scientific documentation and validation in an attempt to find remedies for infertile couples in Uganda and Africa. The commonly used medicinal plants with commercial value such as *Warburgia ugandensis*, *Cola acuminata*, *Erythrina abyssinica* and *Zanthoxylum gilletii* need to be domesticated since 72.6% of all the documented medicinal plants are harvested from the wild ecosystems.

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THE ACHIEVEMENTS OF THE SOUTHERN AFRICAN BOTANICAL DIVERSITY NETWORK (SABONET) – A SOUTHERN AFRICAN BOTANICAL CAPACITY BUILDING PROJECT

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Abstract

The Southern African Botanical Diversity Network (SABONET) is a donor-funded capacity-building project involving southern African botanists. Incorporating the ten southern African countries, the Project has involved 17 herbaria and 22 botanical gardens. Some of its major activities include the preparation of botanical inventories, national plant checklists, national and regional plant collecting expeditions, computerisation of herbaria, postgraduate support for herbarium staff, national and regional training courses, internships for in-service training, production of plant Red Data Lists, Threatened Plants Programmes in botanical gardens, and workshops for the end-users of taxonomic information. SABONET has made a significant contribution towards the networking and capacity development of botanists in southern Africa to provide a strong core of capable and equipped institutions. This paper provides an update (December 2003) on the regional botanical expertise built with SABONET assistance and shows the increased level of capacity in herbaria and botanical gardens.

Résumé

Les réalisations du 'Southern African Botanical Diversity Network' (SABONET) – Un projet de mise en place d'expertise en matière botanique en Afrique australe. Le réseau 'Southern African Botanical Diversity Network' (SABONET) est un projet financé par des donations et qui consiste en la mise en place d'expertise impliquant des botanistes d'Afrique australe. Il intègre les dix pays d'Afrique australe et concerne 17 herbiers et 22 jardins botaniques. Quelques-unes de ses activités principales sont la préparation d'inventaires botaniques, de check-lists botaniques nationales, d'expéditions nationales et régionales de récoltes de plantes, d'informatisation des herbiers, d'appui en matière de formation au personnel des herbiers, d'organisation de cours de formation au niveau national et régional, de sessions internes de formation, de production de listes rouges, de programmes sur les plantes protégées dans les jardins botaniques et de séminaires pour les utilisateurs de l'information taxonomique. SABONET a contribué d'une manière significative à la mise en réseau et à l'amélioration de l'expertise de botanistes d'Afrique australe et créé un noyau robuste d'institutions compétentes et équipées. Cet article constitue une mise à jour (décembre 2003) des informations sur l'expertise botanique régionale bâtie grâce à l'assistance de SABONET et montre le niveau de compétence acquis dans les herbiers et les jardins botaniques.

Key words: biodiversity, botanical gardens, capacity building, conservation, herbaria

1 Introduction

Southern Africa (Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland, Zambia and Zimbabwe) is one of the richest botanical regions on earth (Groombridge & Jenkins, 2002) and with well over 30,000 vascular plant species has the richest flora of any region of comparable size in the world, with more than 10% of the world's vascular plant species concentrated on less than 2% of the earth's land-surface (Huntley, 1989). Higher order taxonomic diversity and endemism is also exceptionally high and comprises two of the world's six floristic regions, namely the Palaeotropical and Cape Floristic Kingdoms (Takhtajan, 1986). Of the over 200 centres of plant endemism and diversity recognised worldwide, 14 are in southern Africa (Beentje *et al.*, 1994). In addition, several smaller centres of plant endemism and diversity are also located in southern Africa (Van Wyk & Smith, 2001).

Rapid economic development and human population growth during the latter parts of the twentieth century showed the importance for a southern African body to be established that could address regional degradation and loss of natural ecosystems. Subsequent efforts by regional botanical experts to facilitate conservation of southern Africa's botanical diversity were hampered by inadequate information on the vast majority of the subcontinent's plants. During the early 1990's when a regional effort was conceived to take responsibility for meeting the obligations of the Convention of Biological Diversity, the botanical institutions across southern Africa came together to establish a regional network of botanical expertise that could recognise, label and interpret the botanical diversity of southern Africa (Huntley, 1994). However, it was soon realised that efforts to facilitate this process were held back by lack of expertise and funds in participating institutions.

Post-colonial African herbaria and botanical gardens had suffered a steady decline over the past 40 years – most specimens of African plants have been deposited in Northern herbaria. In addition, botanical institutions suffered from a lack of local expertise that has been drawn away from Africa for studies and work abroad, or opportunities in the private sector. The Southern African Botanical Diversity Network's (SABONET) local capacity and institution building programme was aimed at changing this situation. To obtain the necessary funds, the international community had to be convinced of the need of such a capacity building initiative.

Regional collaboration and extensive international lobbying led to funds being secured by the National Botanical Institute (NBI) of South Africa. In 1995, SABONET was established (Willis & Huntley, 2001), aiming at strengthening the level of botanical expertise, expanding and improving herbarium and botanical garden collections, and fostering closer collaborative links among botanists in the southern African subcontinent. SABONET received core grants from the Global Environment Facility (GEF)/United Nations Development Programme (UNDP) and was co-funded by the United States Agency for International Development (USAID)/World Conservation Union–Regional Office for southern Africa (IUCN-ROSA).

After five years, SABONET has met the project's main objective to develop a strong core of professional botanists, taxonomists, horticulturists, and plant diversity specialists within the ten countries of southern Africa, competent to inventory, monitor, evaluate, and conserve the botanical diversity of the region in the face of specific development challenges, and to respond to the technical and scientific needs of the Convention on Biological Diversity (Mittermeier & Bowles, 1993; Huntley, 2003).

However, capacity is an abstract entity and very difficult to measure. In SABONET, assessments were conducted internally, for instance by describing the financial and human resource input provided to build capacity (Siebert *et al.*, 2001; Willis & Huntley 2001; Huntley *et al.*, 2002) and documenting the many lessons learned and needs established whilst establishing the project as a regional capacity building initiative (Steenkamp & Smith, 2003; Siebert & Smith, 2004). In addition, the Project has been evaluated externally by the donor organisations, for instance the UNDP Midterm Review (Timberlake & Paton, 2001) and the Second Study of GEF's Overall Performance (GEF, 2002). Measured against SABONET's requirements and achievements, these evaluations rated the project as satisfactory.

In this paper we will evaluate the achievements of SABONET, specifically in terms of its history as a ten country, donor funded, African botanical diversity network. We will address it in a way that illustrates SABONET's contribution towards regional and international recommendations to overcome obstacles in systematic and conservation science in Africa (as proposed by Smith *et al.* (1996) and Western (2003)) through capacity building.

2 Methods

Data presented in this paper were extracted from various unpublished internal sources, which include the Minutes of the 9th to 14th SABONET Steering Committee Meetings, four sets of Tripartite Review recommendations, six Project Implementation Review reports submitted to UNDP (1998–2003), five Annual Project Reports submitted to the NBI (1998–2002), one Midterm Review Report (2001) and 25 Quarterly Reports per participating country (1998–2003). All documentation consulted for this paper is available from the SABONET Regional Office and tables with statistics are posted on the SABONET website (www.sabonet.org).

3 Results and discussion

Smith *et al.* (1996) recommended that in order to become pro-active in meeting the needs of end-users of taxonomic information and herbaria, certain priorities are pivotal to assure that when herbaria are called upon to partake in, for instance, informed decision-making in plant conservation, the necessary activities and processes are in place to produce the required information. They listed nine priorities that should be addressed before southern Africa could become re-established as an important role-player in regional and international affairs. Recently Western (2003) indicated the need for the international community to play an important role in speeding up Africa's capacity to conserve its biodiversity and recommended that to stimulate conservation science in Africa, international collaboration through a constructive partnership is vital. He proposed fourteen pointers on how to identify priorities that could address the obstacles hampering the progress of African conservation science. During the life of SABONET, the Project has regularly addressed issues raised by Smith *et al.* (1996) and Western (2003). Below we combine their recommendations into eleven points of importance against which SABONET's achievements are discussed.

3.1 Establishing an intra-continental information network between herbaria and botanical gardens

SABONET was initially conceived in 1995 and comprises herbaria and botanical gardens (Table 1) that serve as focal points for its activities. These institutions have benefited in many ways as members of a strong and functional regional botanical network. Contributions of resources and support provided by SABONET to these institutions have been documented on several occasions (Willis & Huntley, 2001; Huntley *et al.*, 2002; Huntley, 2003; Siebert *et al.*, 2001).

SABONET News, the project newsletter, is the 'voice' of the project and announces activities and project decisions, discusses relevant topics, and documents project outputs. Eight volumes (22 issues) of the newsletter have been published, and distributed to 77 countries comprising over 1000 environmentalists in southern Africa and approximately another 1000 in the rest of the world.

A dedicated project website was also established (www.sabonet.org), which features relevant information about the project and the Southern African Plant Red Data Lists. Most SABONET publications are available at this site in a PDF format. After the publication of all planned SABONET Reports, the website will be updated to include all SABONET publications in PDF format. In addition, an updated and comprehensive list of e-mail addresses for southern African botanists is hosted, as well as a Red Data List discussion group and database.

Many southern African botanists attend the triennial AETFAT congress with support from SABONET (Meise, Belgium and Addis Ababa, Ethiopia). Recently the first African Botanic Gardens Congress was held in South Africa and was attended by more than 30 horticulturists from southern Africa with sponsorship from SABONET. However, southern Africa still lacks a specifically regional congress that could draw together all botanical disciplines to an event that could alternate between the ten countries.

3.2 Creating demand for existing African expertise by promoting and marketing plant systematics

During the establishment of the project, it was soon realised that the solutions to most problems lie in a south-south approach. To enable participating institutions to maintain routine services and duties, and at the same time address SABONET activities, the Project sponsored the employment of over 72 southern Africans as contract staff (Huntley *et al.*, 2002), namely research officers, technical assistants, data entry clerks, horticulturists and information technology specialists.

Of the contract workers, over thirty people filled positions as practising botanists. They were trained during short courses and exposed to research activities to enhance their experience and to build a strong core of capable, available staff that could be absorbed into southern African institutions.

Regional collaboration between plant systematists in southern Africa has been highlighted (Huntley *et al.*, 2002; Smith & Willis, 1999a; Smith *et al.*, 2003) and has served to market the Project internationally. Plant diversity specialists have through SABONET also attended workshops of the Global Taxonomy Initiative and contributed towards recommendations for demand-driven plant systematics (Klopper *et al.*, 2001).

SABONET comes to an end in December 2004. To strengthen participating institutions during its exit strategy, it had to prioritise activities that would be useful to stakeholders. At the same time it had to show the value of the capacity built over the years. The preparation, production and publication of national checklists were seen as a good way of doing this and were adopted as a major output. So far, nine checklists of national floras or selected groups have been published (Craven, 1999; Roux, 2001,

TABLE 1. Herbaria and botanical gardens benefiting directly from the SABONET Project.

Country	**Institutions**
Angola	Luanda Herbarium (LUAI)
Botswana	National Herbarium (GAB)
	Peter Smith Herbarium (PSUB)
	University of Botswana Herbarium (UCBG)
	National Botanical Garden
Lesotho	Maseru Herbarium (MASE)
	National University of Lesotho Herbarium (ROML)
	Sehlabathebe National Park Herbarium (SNPH)
	Katse Dam Botanical Garden
Malawi	National Herbarium (MAL)
	Lilongwe Botanic Garden
	Mzuzu Botanic Garden
	National Botanic Garden
Mozambique	Eduardo Mondlane University Herbarium (LMU)
	INIA Herbarium (LMA)
	EMU Botanical Garden
	INIA Botanical Garden
	Tunduru Botanical Garden
Namibia	National Herbarium (WIND)
	National Botanic Garden
South Africa	Compton Herbarium (NBG)
	Natal Herbarium (NH)
	National Herbarium (PRE)
	Durban Botanic Gardens
	Free State National Botanical Garden
	Harold Porter National Botanical Garden
	Karoo Desert National Botanical Garden
	Kirstenbosch National Botanical Garden
	Lowveld National Botanical Garden
	Natal National Botanical Garden
	Pretoria National Botanical Garden
	Witwatersrand National Botanical Garden
Swaziland	National Herbarium (SDNH)
Zambia	University of Zambia Herbarium (UZL)
	University of Zambia Botanical Garden
Zimbabwe	National Herbarium (SRGH)
	Ewanrigg Botanical Garden
	National Botanic Garden
	Vumba Botanical Garden
10 countries	17 herbaria & 22 botanical gardens

2003; Chapano, 2002; Craven, 2003; Kobisi & Kose, 2003; Setshogo & Venter, 2003; Kabelo & Mafokate, 2004; Manyanga & Perold, 2004). It is hoped to publish at least one checklist for each participating country.

3.3 Developing communication tools and training for capacity-building in plant systematics

As part of the Project's capacity building initiatives over the last five years, participating institutions were donated over 50 computers and accessories, and internet connections have been installed at most participating herbaria (Siebert *et al.*, 2001). Computer based research was part of a major drive to provide online assistance and interchange between plant diversity specialists. In addition to the provision of hard- and software, national and regional computer training courses were held to train staff in using these systems. National courses were initiated in-country and were based on the development of basic skills. Regional courses were structured to address more advanced basic skills and the management of databases, and include four Botanical Garden Management courses (96 participants), five Herbarium Management courses (60), seven Plant Identification courses (95), eight Database Management courses (100), two Threatened Plants courses (41), one Botanical Art Drawing course (3), one Environmental Impact Assessment course (11), and one Cycad Conservation course (4).

Herbaria are regularly requested to make their information more accessible and available to stakeholders. To make herbaria more relevant to these needs, SABONET has supported the computerisation of herbarium specimens by supporting the development of software, and training staff on PRECIS (Pretoria National Herbarium Computerised Information System), which was specifically developed for southern Africa (Prentice & Arnold, 1998). Using PRECIS the participating institutions have captured the label information of over 500,000 specimens housed in the 17 participating southern African herbaria (Table 2). Staff can now provide stakeholders with distribution maps of species and run queries to provide specific information addressing a range of botanical needs.

3.4 Strengthening existing centres of expertise

Most of the major herbaria and botanical gardens in southern Africa were poorly equipped to conduct research at a higher level or to deliver relevant products. To address this, SABONET provided countries with funds to purchase capital equipment according to the needs determined during regional surveys (Smith *et al.*, 1999; Botha *et al.*, 2000). For research purposes and general upkeep, participating institutions have received a wide range of capital equipment based on individual needs, including digital and film cameras, camping equipment, deep freezers, drying ovens, computers and peripherals, fax machines, GPS's, guillotines, herbarium cabinets, light and stereo-microscopes, microwave ovens, off-road vehicles, overhead projectors, slide projectors and photocopiers.

Participating botanical institutions have not had the opportunity to stay updated with the latest literature and efforts have been made to stimulate a steady inflow of literature, such as journals, to libraries. Copies of the Flora of Southern Africa (FSA) and Flora Zambesiaca (FZ) have been regularly donated to SABONET countries by the producers, namely the National Botanical Institute, Pretoria and Royal Botanic Gardens, Kew respectively. During the past two years numerous books on horticulture have been purchased and sent to poorly resourced botanical gardens.

TABLE 2. Number and percentage of herbarium specimens computerised by each of the participating herbaria since 1998.

Country	Poaceae specimens in participating herbaria	Number computerised	Percentage of total	Total specimens in participating herbaria	Number computerised	Percentage of total
Angola	7,796	2,864	37%	36,000	11,007	31%
Botswana	3,658	2,421	66%	31,000	14,342	46%
Lesotho	3,860	3,657	95%	39,690	31,377	79%
Malawi	3,334	3,334	100%	100 000	45,400	45%
Mozambique	9,206	9,026	98%	122,000	27,400	22%
Namibia	11,414	11,414	100%	81,311	81,211	100%
South Africa	116,464	116,464	100%	1,800,000	923,702*	51%
Swaziland	727	617	85%	8,103	7,553	93%
Zambia	2,281	2,281	100%	25,000	16,850	67%
Zimbabwe	18,629	18,629	100%	500,000	105,983	21%
Total	177,369	170,707	96%	2,743 104	1,264,925*	46%

*760,000 were computerized by PRE before SABONET started

TABLE 3. Number of students supported by SABONET to study towards postgraduate degrees in systematics (1998–2003).

Country	BSc Hons	MSc	Total degrees/country	Male/female ratio
Angola	1*	1#	1	0:1
Botswana	2*	1	2	2:0
Lesotho	3	3	6	2:4
Malawi	3	3	6	4:2
Mozambique	0	1	1	0:1
Namibia	2**	2#	4	0:4
South Africa	1	3	4	4:0
Swaziland	1	1	2	2:0
Zambia	3	3	6	4:2
Zimbabwe	0	4	4	3:1
Total	14	21	36	21:15

* One person each from Angola and Botswana did not complete their degrees.

** One person from Namibia completed a BTech degree in conservation.

\# One person each from Angola and Namibia will only be completing their degrees in 2004.

3.5 Training personnel in applied science, species-level diversity and phylogenetics

SABONET has organised and presented 29 regional courses and afforded 200 southern African botanists an opportunity to learn more. Topics addressed included plant identification, databasing, herbarium and botanical garden management, and plant conservation. In addition, the project has supported 26 (13 male and 13 female) young botanists to obtain 14 B.Sc. Hons., one B.Tech. and 21 M.Sc. degrees in systematics (Table 3). The drive behind this training programme was to expand the strong core of plant diversity specialists of southern Africa, and to then equip them to meet the challenges posed by the Convention on Biological Diversity (Huntley, 2003). The postgraduate research results of phylogenetic and species-level diversity have been presented at various international and national conferences.

3.6 Staff exchanges to build skills and international liaison

SABONET countries were afforded the opportunity to make use of the Project's internship programme, whereby staff members involved in priority outputs could travel to other institutions in the region to work with experts (Siebert, 2003). So far there have been 52 herbarium and 23 botanical garden internships to collaborate with institutions and colleagues in the region to produce outputs such as national plant checklists and threatened plant programmes.

Participants from Angola and Mozambique were assisted by the project to secure NETCAB fellowships from IUCN to travel to Lisbon, Portugal, to work on the floras of lusophone countries (Izidine & Duarte, 2003). SABONET also initiated support for taxonomists from the National Herbarium of Zimbabwe to partake in training on Environmental Impact Assessment funded by USAID.

3.7 Drawing a roster of regional taxonomic expertise, directories of botanical information and checklists

Some of the first activities of the SABONET Project were to prepare and publish rosters of the plant taxonomic projects (Arnold & Mössmer, 1998), expertise (Mössmer & Willis, 2000), herbaria (Smith & Willis, 1999) and botanical gardens (Botha *et al.*, 2000) of the southern African region.

3.8 Thematic workshops to address priority topics

One of the major success stories of the SABONET Project was the holding of 14 national Red List workshops culminating in the publication of *Southern African Plant Red Data Lists* (Golding, 2002). During these workshops, specialists from the region conducted a preliminary investigation into the threat status of rare plants in southern Africa.

The Red Lists contributed significantly towards the implementation of the *Action Plan for Southern African Botanical Gardens* (Willis & Turner, 2001) which was developed at a regional workshop for botanical gardens. This formed the basis for the activities of the SABONET Southern African Botanical Garden Network. The vision of the newly formed network was that each garden would have an indigenous Threatened Plants Programme in place by 2004.

End-user workshops to determine the needs of the users of botanical information have become a major drive in the SABONET Project (Steenkamp & Smith, 2002). Herbarium staff and users of taxonomic information have attended end-user workshops in all ten countries, and numerous outcomes and decisions regarding the most important services and stakeholder needs emanated from the various proceedings (Smith *et al.*, 2004).

3.9 Exchanging skills with developed countries

A consortium to compile an African Plant Checklist was put together by the National Botanical Institute of South Africa and the Conservatoire et Jardin botaniques de la Ville de Genève of Switzerland. SABONET has sponsored and supported the participation of the southern African delegation in this initiative and will publish the checklist as part of its report series. The Project is striving to complement the skills of the developed world in achieving an output that could be put to good use in Africa.

Over the past five years a task group has intensively studied herbarium practices and will be publishing a herbarium handbook for southern Africa. This book will not only be of use to African taxonomists, but could prove useful to herbarium technicians and students elsewhere. It is based and builds extensively on the handbook of the National Botanical Institute (Fish, 1999).

SABONET initiated its work with botanical gardens through a publication on the interpretation of living collections (Honig, 2000). This was well received internationally (specifically by BGCI) and formed the basis for activities to build capacity in southern African botanical gardens. As a follow-on initiative, information on the cultivation of rare and threatened southern African species with horticultural potential will be published. Botanical gardens elsewhere will benefit, as many rare southern African plant species are cultivated worldwide.

3.10 Complementing conservation initiatives through plant collecting programmes in under-collected areas

SABONET's core business is to build the institutional capacity of regional centres of expertise to equip them to discover, describe and document the flora of southern Africa. It was therefore important to conduct as many targeted field trips as possible to collect information about plants and their geographical distributions. Each of the participating countries received a four-wheel drive vehicle, and have together embarked on 101 national plant collecting expeditions and collected almost 20,000 specimens (both general and targeted plant research).

The project also carried out two large, regional expeditions to under-collected centres of diversity. Expedition members of the 2000 Nyika Plateau expedition in northern Malawi (Willis *et al.*, 2001), and the 2001 Maputaland expedition in southern Mozambique (Izidine *et al.*, 2003), contributed significantly towards the botanical knowledge of these centres by collecting more than 5,000 plant specimens.

3.11 Indicating the conservation status of threatened species

As part of the Red List initiative of the SABONET Project, Golding & Timberlake (2003) have stressed the importance of indicating conservation status and rarity on herbarium specimens and subsequently in monographs and Floras. Participating institutions from southern Africa and international institutions working on the southern African flora are now provided with a set of recommendations that could be followed.

This process of providing additional conservation information on herbarium specimens is closely linked to the standard use of data on plant species distribution. Plant distribution patterns are important when identifying threatened species and areas of high endemism and diversity. The benefits of providing accurate locality data and capturing such information forms the basis of the production of maps (Fish, 1999) which can be used to answer conservation questions.

As part of the SABONET Exit Strategy, a regional Important Plant Areas (IPA) workshop was conducted, with the objective of adapting the European IPA selection criteria for southern African conditions. This workshop was attended by 28 participants from the region, as well as by stakeholders from Europe and East Africa. The workshop will be followed by national IPA workshops in some of the countries with the aim of selecting IPA sites in those countries.

4 Conclusions

During its eight years of existence, SABONET, as an established and functional botanical network, has achieved significant impact in southern Africa by building the botanical capacity of the participating countries both in terms of infrastructure and human resources (expertise). This achievement meets most of the recommendations made by Smith *et al.*, (1996) and Western (2003). However, political realities and economic constraints in some southern African countries still hamper the rapid development of plant conservation activities at a national level.

In many ways the expertise and capacity built under the SABONET Project has yet to make an impact on the ground. Yet, thanks to SABONET, we now do have a strong group of botanists in the region; we now do know more about the region's flora; national institutions now do have a better ability (both expertise-wise and infrastructure-wise) to implement their national mandates, which often include the conservation of the region's flora. However, the focus within SABONET was very much on capacity building and not so much on implementation of the built capacity. It is now up to the institutions that benefited from the SABONET Project to really use their newly acquired capacity and to implement it in such a way that it makes a difference on the ground. Although there is no SABONET II planned, future projects in the region should focus on implementation of the capacity built under SABONET.

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SPECIES AND GENERIC DELIMITATION IN *BIKINIA* AND *TETRABERLINIA* (LEGUMINOSAE–CAESALPINIOIDEAE) USING ITS AND AFLP

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Abstract

We have assessed the monophyly and internal topology of *Bikinia* and *Tetraberlinia* along with some other systematic and methodological questions using AFLP analyses. In addition to AFLP analyses we tried to determine the sister group of these two genera by adding additional sequences to an existing ITS data set. Our analyses suggest *Julbernardia* is the closest related genus, but *Icuria* is also a candidate since the position of this genus remains unclear. Although ITS provides us with some good resolution at the generic level, we have to conclude ITS is not a good marker in this group due to the presence of several non-homologous copies. Evidence for a monophyletic *Bikinia* is quite strong. However, more evidence is needed to test the monophyly of *Tetraberlinia*. Within *Bikinia*, only a clade consisting of *B. aciculifera* and *B. durandii* was supported by a jackknife analysis. We show that *B. le-testui* and *B. pellegrinii* are separate species. Aberrant *Bikinia* material from the Crystal Mountains in Gabon proved to be a new species. A sapling collected under a tree of *B. le-testui* could be identified as a hybrid between this species and *B. media*. Another new species, *T. apiphila*, is clearly related to *Tetraberlinia*, although it also shares some morphological characters with *Bikinia*. We demonstrated that AFLP results can be reproduced and that the errors of such replications fall within the variation present at the population level. AFLP can discriminate between different populations of a single species, even with high jackknife support. In the sample of genera studied here the AFLP technique provides high resolution at generic level and we even expect it to work between several closely related genera. Finally, we describe how the AFLP technique can be used to identify hybrids.

Résumé

Délimitation spécifique et générique chez *Bikinia* et *Tetraberlinia* (Leguminosae, Caesalpinioideae) grâce à l'utilisation d'ITS et d'AFLP. Nous avons évalué la monophylie et la topologie interne de *Bikinia* et *Tetraberlinia* ainsi que d'autres aspects systématiques et méthodologiques, en utilisant des analyses AFLP. Par ailleurs, nous avons essayé de déterminer le groupe-sœur de ces deux genres en complétant les données ITS existantes par des séquences additionnelles. Nos analyses suggèrent que *Julbernardia* est le genre le plus proche mais également que le genre *Icuria* est un candidat car sa position reste incertaine. Bien que l'ITS permette une bonne résolution au niveau générique, nous devons conclure que l'ITS n'est pas un bon marqueur dans ce groupe du fait de la présence de nombreuses copies non-homologues. Les preuves de la monophylie de *Bikinia* sont assez évidentes. Par contre, d'autres preuves sont nécessaires pour tester la monophylie de *Tetraberlinia*. Au sein de *Bikinia*, un seul clade constitué de *B. aciculifera* et *B. durandii* a été supporté par une analyse jackknife. Nous montrons que *B. le-testui* et *B. pellegrinii* sont des espèces distinctes. Le matériel aberrant de *Bikinia* provenant des Monts de Cristal au Gabon s'est révélé être une nouvelle espèce. Une plantule collectée sous un arbre de *B. le-testui* pourrait être un hybride entre cette espèce et *B. media*. Une autre nouvelle espèce, *T. apiphila*, est clairement apparentée à *Tetraberlinia*, quoiqu'elle partage aussi certains caractères morphologiques avec *Bikinia*. Nous avons démontré que les résultats AFLP pouvaient être reproduits et que les erreurs de telles réplications étaient expliquées par la variation inter-population. L'AFLP peut différencier des populations d'une même espèce, même avec l'aide d'une analyse jackknife. Au sein de l'échantillon de genres étudié, la technique de l'AFLP fournit une haute résolution au niveau générique et nous pouvons même nous attendre à ce qu'elle fonctionne entre différents genres très proches. Finalement, nous décrivons comment la technique AFLP peut être utilisée pour identifier des hybrides.

Key words: AFLP, *Bikinia*, hybrid, phylogeny, *Tetraberlinia*

1 Introduction

The genera *Bikinia* Wieringa and *Tetraberlinia* (Harms) Hauman comprise at present 17 species, which occur in rain forests in West and Central Africa. They are medium-sized to large trees, which may constitute co-dominant or even monodominant forest (Wieringa, 1999). *Bikinia* and *Tetraberlinia* are related to the genera *Aphanocalyx* Oliv., *Brachystegia* Benth., *Icuria* Wieringa, *Julbernardia* Pellegr., and possibly *Michelsonia* Haumann (Gervais & Bruneau, 2002; Wieringa & Gervais, 2003: Bambijt-clade). Although this group of genera has high support in phylogenetic analyses, the relationships within this clade remain unclear. In most analyses these genera come out as monophyletic, but relationships between the genera and between species within each genus are poorly resolved or without support.

Recent collections from Gabon and Cameroon provided material of a new species of *Tetraberlinia*. This new species, *Tetraberlinia apiphila* Wieringa ined., recognised on floral characters, clearly fits within *Tetraberlinia*, but because it also shares a few morphological characters with *Bikinia*, cladistic analyses based on morphological data that include this species result in a paraphyletic *Tetraberlinia*, though without support (Wieringa & Gervais, 2003).

Other new (sterile) collections of a *Bikinia* from the Crystal Mountains in Gabon fall in between *Bikinia le-testui* (Pellegr.) Wieringa and *B. pellegrinii* (A. Chev.) Wieringa. In the notes of both species Wieringa (1999: 227 & 239) mentions such intermediate material, which may either constitute a separate species, be of hybrid origin or challenges the delimitation of both species.

A pilot AFLP study that included only eight samples of *Aphanocalyx*, *Bikinia*, *Julbernardia* and *Tetraberlinia* provided some proof that AFLPs may resolve some nodes where other phylogenetic methods using morphology or sequencing fail, and that in this clade the technique may be applied around and above the generic level (Wieringa & Zevenbergen, 1999). However, AFLP studies focussing on more than one genus or on tropical groups like Caesalpinioideae are rare, and hence little data exists on the applicability of this method for different systematic questions.

This study aims to test whether AFLP results can be reproduced, at which level AFLPs can find differences among samples, whether AFLPs can be used to assess relationships between related genera and whether AFLPs can help identify hybrids. Next to these methodological questions, we would like to solve a range of systematic questions: What is the sister group to the *Bikinia–Tetraberlinia* clade? What is the phylogenetic position of *Icuria*? What is the internal topology of *Bikinia* and *Tetraberlinia* and are these two genera monophyletic? Are *Bikinia pellegrinii* and *B. le-testui* separate species and does the aberrant material from the Crystal Mountains belong to a separate species or is it a hybrid between these two? Where does the new species *Tetraberlinia apiphila* fit and can AFLPs prove whether or not a seedling belongs to this (in sterile state) cryptic species? To address the questions above the generic level we will use sequences of the rDNA internal transcribed spacer (ITS), while we expect the questions on and below the generic level to be most powerfully resolved with AFLP.

2 Material and methods

2.1 ITS-sequences

To identify which genus should be considered sister to the *Bikinia–Tetraberlinia* clade and to gain a better understanding of the position of *Icuria*, we have sequenced ITS of 9 additional samples of *Aphanocalyx*, *Bikinia*, *Julbernardia* and *Tetraberlinia* (Table 1). DNA isolation and ITS sequencing follows the protocol of Bakker *et al.* (1998) using only fluorescent labelling. These sequences have been included in the data set as used by Gervais & Bruneau (2002) and Wieringa & Gervais (2003). Alignment was performed manually using Megalign. The data set was analysed using both parsimony and Bayesian inference. A second parsimony analysis was conducted that excluded *Icuria*.

2.2 AFLPs

AFLPs were performed on 26 samples of *Bikinia*, *Julbernardia* and *Tetraberlinia* (Table 1). To test reproducibility of the results, three samples were used twice. AFLPs were performed according to the ABI PRISM 377 protocol of Perkin-Elmer. As restriction enzymes we used EcoRI and MseI. For amplification we used Goldstar Taq polymerase. The first pre-amplification PCR was run using pre-selective primers E01 (Eco+A) and M02 (Mse+C). The selective amplification PCR was run using three different primer combinations: M48E35 (Mse+CAC, Eco+ACA), M59E35 (Mse+CTA, Eco+ACA) and M61E36 (Mse+CTG, Eco+ACC). We used fluorescent labelling; E35 is a 6-FAM (blue) fluorescent primer, E36 a JOE (green) fluorescent primer. The PCR products and an added internal size standard (ROX 500) were analysed on a 5% polyacrylamide Long Ranger (BMA) gel using an ABI PRISM 377 automated sequencer. Resulting trace-files were analysed using Genographer 1.6.0 (Benham, 2001). Bands were scored as either present or absent, in a few cases as unknown (?). The resulting data matrix was checked manually and subjected to a parsimony analysis.

2.3 Data analyses

The parsimony analyses were performed using PAUP* 4.0b8a (Swofford 2002) on a PowerMac G4. Heuristic searches were performed with 100 random addition sequence replicates and tree bisection-reconnection branch swapping. Branches of zero length were collapsed. Robustness of the results was tested by jackknife analyses (36% deletion, fast stepwise addition) with 10000 replicates. The outgroup in all analyses was

TABLE 1. Species and voucher specimens (first collector + number) of the samples used for the AFLP analysis and/or for additional ITS sequencing.

A	**S**	**Species**	**Voucher**	**Provenance**
	AY615899	*Aphanocalyx djumaensis*	Wieringa 4149	Gabon, Lopé
	AY615893	*Bikinia aciculifera*	Wieringa 4503 (tree)	Gabon, Chaillu Massif, Ikobey
*		*Bikinia aciculifera*	Wieringa 4503 (sapl.1)	Gabon, Chaillu Massif, Ikobey
*		*Bikinia aciculifera*	Wieringa 4503 (sapl.2)	Gabon, Chaillu Massif, Ikobey
*		*Bikinia aciculifera*	Wieringa 4533	Gabon, Chaillu Massif, Ikobey
*		*Bikinia durandii*	Wieringa 4515	Gabon, Chaillu Massif, Ikobey
*		*Bikinia durandii*	Wieringa 4479	Gabon, Chaillu Massif, Ikobey
*	AY615894	*Bikinia le-testui* ssp. *le-testui*	Wieringa 3795	Gabon, Mékambo
*		*Bikinia le-testui* ssp. *le-testui*	Wieringa 3927	Gabon, Mt. Sassamongo
**		*Bikinia le-testui* ssp. *le-testui*	Wieringa 4606	Gabon, Chaillu Massif, Mbigou
*		*Bikinia le-testui* ssp. *le-testui*	Wieringa 4681 (sapl.2)	Gabon, Chaillu Massif, Bongolo
*	+	*Bikinia le-testui* ssp. *mayumbensis*	J.J.F.E. de Wilde 11088	Congo (Brazzaville)
*		*Bikinia le-testui* × *B. media*	Wieringa 4681a (sapl.1)	Gabon, Chaillu Massif, Bongolo
	AY615891	*Bikinia media*	Wieringa 4543 (tree)	Gabon, Chaillu Massif, Mouila
**		*Bikinia media*	Wieringa 4543 (sapl.1)	Gabon, Chaillu Massif, Mouila
*		*Bikinia media*	Wieringa 4543 (sapl.2)	Gabon, Chaillu Massif, Mouila
*	AY615892	*Bikinia media*	Wieringa 4633	Gabon, Chaillu Massif, Mbigou
*	AY615896	*Bikinia pellegrinii*	Wieringa 3757	Gabon, Mékambo
*	AY615895	*Bikinia pellegrinii*	Wieringa 3944	Gabon, Mt. Sassamongo

TABLE 1. continued

A	S	Species	Voucher	Provenance
*		*Bikinia* sp. nov.	Wieringa 4695 (sapl.2)	Gabon, Crystal Mountains
*		*Bikinia* sp. nov.	Wieringa 4695 (sapl.4)	Gabon, Crystal Mountains
*		*Bikinia* sp. nov.	Wieringa 4695 (sapl.5)	Gabon, Crystal Mountains
*		*Bikinia* sp. nov.	Wieringa 4711 (tree)	Gabon, Crystal Mountains
*		*Julbernardia brieyi*	Wieringa 4678	Gabon, Lebamba
	AY615898	*Julbernardia pellegriniana*	Wieringa 4078	Gabon, Forêt des Abeilles
*		*Julbernardia* sp.[1)]	Wieringa 4037	Gabon, Mt. Sassamongo
**		*Tetraberlinia apiphila*	Wieringa 4129	Gabon, Forêt des Abeilles
*		*Tetraberlinia apiphila*	Wieringa 4148	Gabon, Forêt des Abeilles
*		*Tetraberlinia "bifoliolata"*	Wieringa 4518	Gabon, Ikobey
	AY615897	*Tetraberlinia korupensis*	Burgt 548	Cameroon, Korup
*	+	*Tetraberlinia polyphylla*	Wieringa 3123	Gabon, Chaillu Massif, Lebamba

Column A = used for the AFLP analysis; ** = used twice (replicate); S = used for ITS sequencing, the GenBank accession number is listed; + = already sequenced by Gervais & Bruneau (2002); sapl. = sapling; [1)] *J. seretii* or *J. hochreutineri*.

Microberlinia brazzavillensis A.Chev. A Bayesian Inference analysis was performed using MrBayes 2.01 (Huelsenbeck & Ronquist, 2001). The maximum likelihood model employed 6 substitution types, with base frequencies set to the empirically observed values. Rate variation across sites was modelled using a gamma distribution. The Markov chain Monte Carlo search was run with 4 chains for 1,000,000 generations, with trees sampled every 100 generations, while the first 1000 sampled trees were discarded to allow for the 'burn-in' process.

3 Results

3.1 ITS

The parsimony analysis of the ITS sequences resulted in a small set of trees (Fig. 1) which all show a monophyletic *Julbernardia* and a monophyletic *Tetraberlinia* which is sister to a clade containing both *Bikinia* and *Icuria*. Jackknife (jac) support for *Julbernardia* is fairly high (79%). Four of the included *Tetraberlinia* species receive high support (82% jac) as a clade, but the inclusion in this genus of the single sequence of the fifth species *T. bifoliolata* (Harms) Hauman (which has a long terminal branch) is not supported. The combined clade of *Bikinia* and *Icuria* hardly receives any support (55% jac). The clade containing all *Bikinia*, *Icuria*, *Julbernardia* and *Tetraberlinia* (BIJT-clade) is highly supported with 91% jac, which is a result not obtained previously, and may well be the result of the inclusion of a second sequence of *Julbernardia pellegriniana* Troupin which broke up the previously found long branch leading to this species (see Wieringa & Gervais, 2003). The Bayesian analysis results are similar to the parsimony analysis, except that *Bikinia* is now highly (100% posterior probability: pp) supported as monophyletic with *Icuria* as its sister, while *T. bifoliolata* has moved from within *Tetraberlinia* to being sister to all other *Tetraberlinia*, *Icuria* and *Bikinia*, with high support (98% pp for the clade containing *Icuria*, *Bikinia* and all other *Tetraberlinia*). *Julbernardia* receives high support (100% pp) for being monophyletic, so does the BIJT-clade (also 100% pp). The shift in position of *Icuria* may well be attributed to long branch attraction as discussed by Wieringa & Gervais (2003). In the parsimony analysis where *Icuria* was excluded the *Bikinia* clade is supported by 83% jac, suggesting that the previous lack of support was caused by *Icuria*. Also the *Julbernardia* clade receives a higher support (now 94% jac), while some support emerges for a clade containing both *Tetraberlinia* and *Bikinia* (58% jac). In all ITS analyses some internal structure is present in *Tetraberlinia*. However, in *Bikinia* different sequences of the same species end up in quite different parts of the genus. Gervais & Bruneau (2002) already noted similar discrepancies, but thought they might be due to misidentifications. The inclusion of more *Bikinia* sequences now reveals this is more a structural character of ITS sequences within *Bikinia*, probably due to the presence of different ITS copies as has already been observed in *Aphanocalyx* (Gervais & Bruneau, 2002; Wieringa & Gervais, 2003). Several additional ITS sequences we tried to include were uninterpretable because we did not clone the ITS DNA previous to sequencing. This happened both in *Bikinia* and *Tetraberlinia*.

3.2 AFLPs

The AFLP analysis resulted in 220 bands of which 218 were polymorphic. The parsimony analysis of these AFLP data reveals a highly resolved cladogram (Fig. 2), where the branches to all three incorporated genera (*Bikinia*, *Julbernardia* and *Tetraberlinia*) receive 100% jackknife support. The internal branches of *Tetraberlinia* receive support as well, but several of those within *Bikinia* are not or only moderately supported.

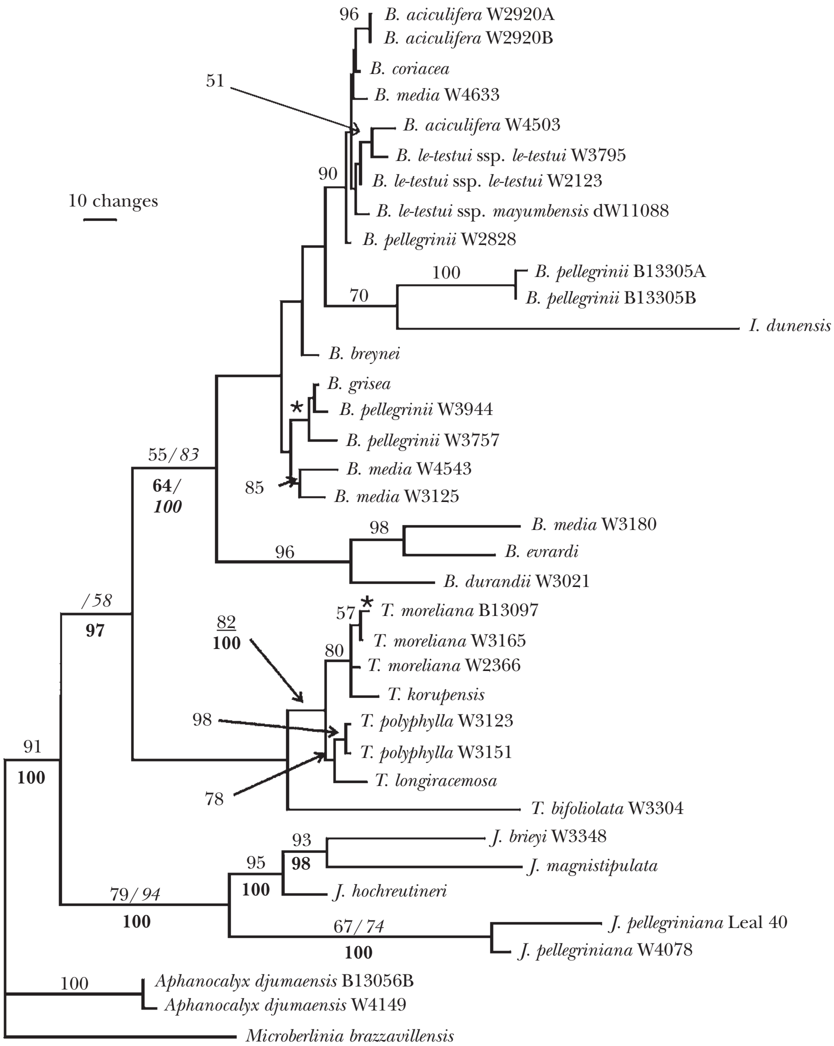

FIG. 1. One of the shortest trees resulting from the parsimony analysis of the ITS data set. For species with more than one sample present the voucher specimens are indicated, where B = Breteler, dW = J.J.F.E. de Wilde, W = Wieringa. When a single collection supplied more than one ITS clone these are referred to as A and B after the collection number. Abbreviated genera are B = *Bikinia*, I = *Icuria*, J = *Julbernardia* and T = *Tetraberlinia*. Jackknife values higher than 50% are given above the branches, branches that collapse in the consensus tree are marked with *. In case jackknife values for a clade (with *Icuria* pruned) differ substantially when *Icuria* is left out of the analysis these are given in italics after a slash. Bayesian posterior probabilities are given in bold below a branch, since the Bayesian analysis puts *Icuria* as sister to *Bikinia*, the Bayesian support for a monophyletic *Bikinia* is given in italics again.

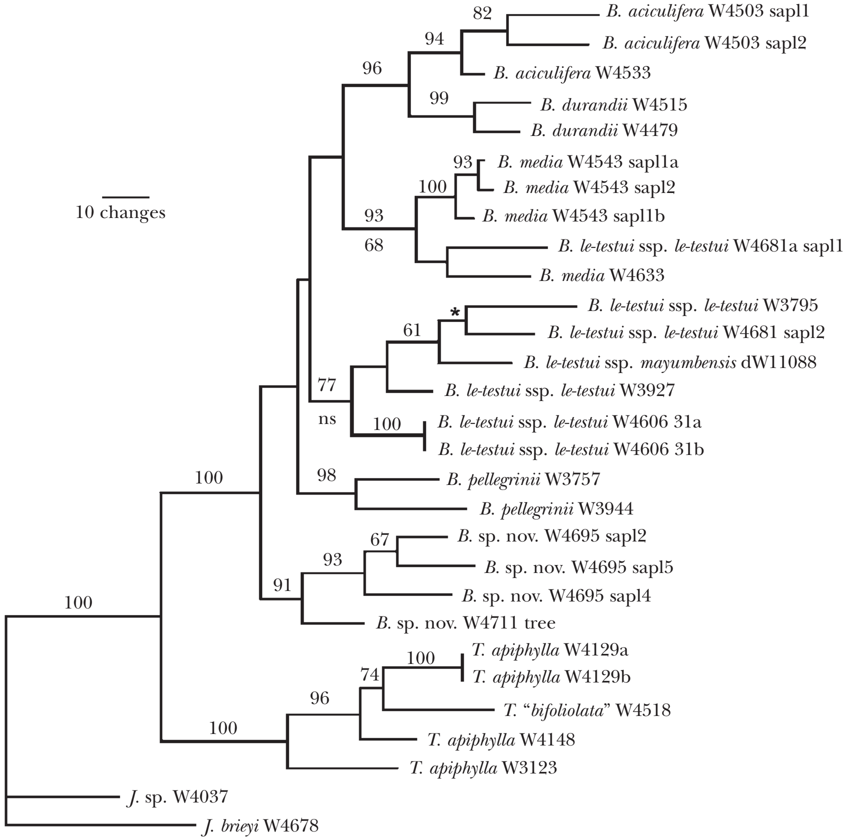

FIG. 2. One of the shortest trees resulting from the parsimony analysis of the AFLP data set. For abbreviations of genera and collectors of voucher specimens see Fig. 1. Samples that were used twice are marked as a and b. Jackknife values higher than 50% resulting from the analysis excluding the hybrid sample W4681 sapl1 are given above the branches, branches that collapse in the consensus tree are marked with *. Jackknife values that differ substantially (>2%) when the hybrid is included are given below the branch.

Of the three replicates that were incorporated in this analysis, one (W4606) came out as completely identical, one (W4129) was slightly different, but still similar enough to be included as sisters in the cladogram, while the third (W4543 sapling 1) was so different that the other included sapling of the same population (W4543 sapling 2, probably a sibling plant) was placed closer to one of the two replicates. Re-examination of the band scoring shows that one of the two samples produced weaker bands, resulting in some bands being scored negative, while the other replicate was scored positive. The sample with the stronger bands was linked to the sibling plant in the analysis, probably based on several shared bands that were missed in the second replicate. The three samples together still formed a 100% jackknife supported clade.

Samples originating from the same population that can probably be considered as siblings (saplings from under the same group of trees) were well supported (82–100% jac) clades in the cladogram (except one, see below), while for all these cases another specimen of the same species was included as well. This shows AFLPs can distinguish populations or groups of siblings of the same species from one another.

There was one striking exception to the grouping of siblings: *Wieringa et al.* 4681 sapling 1 was grouped within *Bikinia media* Wieringa while its sibling, sapling 2, ended up between samples of *B. le-testui* ssp. *le-testui*, only the latter being as expected from the initial identification. Re-examination of the scored bands for sapling 1 showed that it shared some, otherwise species specific bands, with both *B. media* and *B. le-testui* (Fig. 3). If sapling 1 is a hybrid between these two species, we would expect it to: 1) have more bands than other samples, 2) share specific bands with both parent species, 3) cause a strong decrease in jackknife support for both parent species (because of the ambiguous signal that will cause placement in both parent species in different jackknife replicates) and 4) the actual plant to be morphologically intermediate between both parents. We have tested these 4 indications of a hybrid origin of sapling 1. Sapling 1 proved to show the highest number of bands of all samples included: 88, being 22% more than the average number of bands. As already reported it did share several specific bands with both parent species. To test the decrease in jackknife support caused by this sample we re-analysed the AFLP data but excluded sapling 1. This resulted in nearly the same cladogram with the same jackknife support values, except those of the two putative parents: the support for *Bikinia media* increased from 68 to 93%, while that for *B. le-testui* went from no jackknife support to 77% (see Fig. 2). Finally we examined the herbarium specimen of sapling 1. We discovered that this single sapling had unusual broad leaflets for *B. le-testui* and that it was not identifiable using the key of Wieringa (1999: 189–191). At the point in this key where *B. media* and *B. le-testui* split (point 3), all values of this sapling fall in the overlap range, while in other specimens some leaves or leaflets always fall in one of the two ranges. A difference between these two species not used at this

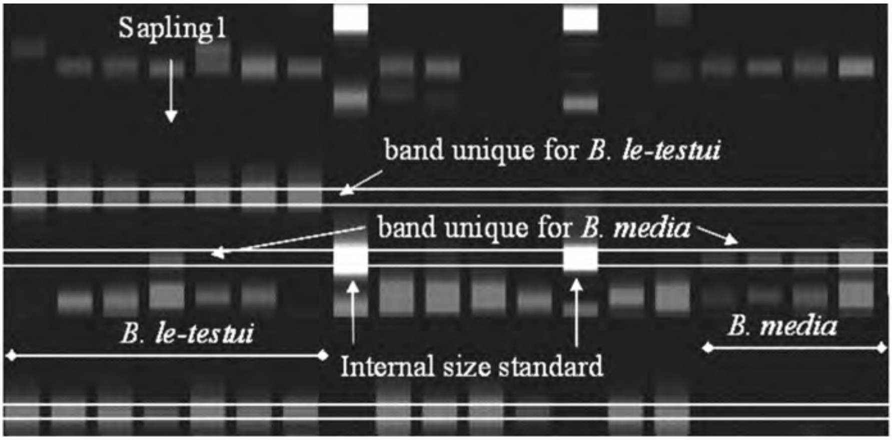

FIG. 3. Part of a composed gel image showing two bands that are unique for either *Bikinia le-testui* or *B. media*, but are both present in the hybrid sapling 1 of *Wieringa et al.* 4681a. The seven lanes on the left represent samples of *B. le-testui*, where the one in the middle (lane 4) is the hybrid sapling. The four lanes on the right represent *B. media*. Of the eight lanes in the middle, six belong to two other *Bikinia* specimens and two represent the internal size standard.

point in the key is that the leaf rachis of *B. le-testui* is glabrous above, while it is hairy in *B. media*. In sapling 1 it is sparsely hairy. The other saplings collected under *Wieringa et al.* 4681 all key out nicely as *B. le-testui*, as did the two trees under which the saplings were collected. All four tests of sapling 1 being a hybrid proved positive, which leads us to the conclusion that this sapling is of hybrid origin; the herbarium specimen is now labelled *Wieringa et al.* 4681a. For assessing the phylogeny of *Bikinia* this sample should be excluded from further analyses.

The aberrant *Bikinia* material from the Crystal Mountains, morphologically resembling *B. le-testui* and *B. pellegrinii*, clearly concerns a third, yet undescribed, species (Fig. 2, *B.* sp. nov.). This new species is not of hybrid origin, since it has a number of unique bands, while some bands occurring in both *B. pellegrinii* and *B. le-testui* are absent. Although without jackknife support, the position of this new species within *Bikinia* seems to be basal.

Even if we exclude the hybrid sapling from the analyses, the internal topology of *Bikinia* is still not very well resolved. All species now are recognised as clades with between 77 and 99% jackknife support, but only the grouping of *B. durandii* (F.Hallé & Normand) Wieringa and *B. aciculifera* Wieringa in a clade has jackknife support (96%). Branch length between the species-bearing nodes is usually short. These results seem to indicate that the diversification of the genus *Bikinia* happened during a relatively short period.

Most species that have more than one sample in the analysis come out as monophyletic. The only exception appears to be *Tetraberlinia apiphila*. Sterile specimens of this species are indistinguishable from *T. bifoliolata*. The saplings of *Wieringa et al.* 4129 were collected under a flowering tree (*Wieringa et al.* 4125) and were assumed to belong to the same species. By including them in this AFLP analysis we hoped to provide proof for this identity. However, these saplings link up with the single specimen of *T. bifoliolata* (*Wieringa et al.* 4518) that was included in this study. Our first interpretation of this result was that the seedlings, although collected under a definite specimen of *T. apiphila*, were actually seedlings of *T. bifoliolata*. However, doubt was cast on this conclusion when we realised that the voucher for *Wieringa et al.* 4518 is also a sterile sapling. It may well be that this specimen, although from an area where so far no unambiguous material of *T. apiphila* has been found, also belongs to this new species. Preliminary results of a larger AFLP analysis that includes several definite samples of *T. bifoliolata* indeed indicate that all four samples included in the present study belong to *T. apiphila* (Wieringa unpublished data).

4 Discussion

With this study we aimed to test several methodological questions. The first was whether AFLP results could be reproduced. The answer is that replicates may differ slightly, but that the differences as found in our study are only large enough to bring confusion within sibling or population level. For higher taxonomic level questions these differences are irrelevant and results can be reproduced.

The second question concerned the level where AFLPs are able to provide resolution. Given the origin of the method – fingerprinting – it is not a surprise it detects differences between individuals. However, it is good to demonstrate that in all cases (excepting the hybrid) all samples of a single species from a single locality not only are grouped together, but also receive a jackknife support of between 81 and 100%, indicating that AFLPs can discriminate between such populations.

A third methodological question concerned the applicability of AFLPs at the level of related genera. Our results at least show that up to the generic level AFLPs remain very powerful (all three genera receive 100% jackknife support). To be able to test applicability for phylogenetic relationships between genera and to see if it can still generate jackknife or bootstrap support we need to include at least a fourth genus. In the present data set already several bands are present that are shared by all three genera, indicating that at least some signal will be present for a clade containing these three genera as soon as other genera are included.

Our last methodological question concerned the use of AFLPs to trace hybrids. As was demonstrated by the unexpected tracing of the hybrid sapling, AFLPs can indeed be used to trace such F1 hybrids. If this sapling had not been placed among samples of its other, less obvious, parent, it would have been more difficult to identify hybridisation. However, now we have identified hybridisation, we can define some criteria how such hybrids can be located, and these criteria could be used on any AFLP data set to look for such hybrids. The easiest criterion to check is whether any sample has a relatively high number of bands. However, this difference is not very high (20% in our case). A far more powerful tool could be developed from the decrease in jackknife support that is caused by these hybrids. One should develop an automated tool in phylogenetic reconstruction programs that after an initial analysis leaves out single accessions and sets of such accessions. Jackknife or bootstrap supports for resulting clades should be compared to the initial support values for these clades (with the left-out samples pruned). As soon as any positive support shift reaches a threshold value (say 10%) the concerning left-out accessions that caused the shift should be reported as suspect, where the clades that received a higher support can be regarded as a potential parent. A confirmation of a suspected hybrid would be that not one but two species receive significantly higher support values. However, a single increase of support could be caused by the absence of one of the parents in the analysis, in which case a smaller increase may be present only in a clade of species related to the other parent. Our third criterion to identify hybrids, looking for the sharing of species specific bands with more than one species, is very time consuming and can only be performed on samples that are already suspected of being a hybrid or after a run of the above mentioned taxon resampling procedure. We demonstrated AFLPs can easily trace these F1 hybrids. However, it is not sure AFLPs can as easily trace other types of hybrids. Backcrosses to one of the parent species will become less and less obvious. Allotetraploid species on the other hand should be recognisable, as is the case with F1 hybrids, although slowly the number of additional bands may shrink, as will the distortion in support values of both parent species. Still, such hybrid species should remain detectable for quite some time.

An additional methodological result from this analysis is that AFLPs prove to be a good method to delimit species, as has been shown previously by i.e. Zhang *et al.* (2001) and Richardson *et al.* (2003). All conspecific samples (except for the two cases already discussed above) are being grouped together with 77 to 99% jackknife support. Especially in the case of sympatrically occurring species AFLPs may help clarify specific circumscription. For tropical taxa this may be a very welcome tool, since populations of such species can usually not be followed over time or subjected to crossing experiments. However, it is easy enough to take silica gel dried leaf samples of two co-occurring specimens, or even seedlings as in our case, to be analysed later.

Several of the systematic questions we have addressed with this project could be (partly) answered: based on ITS *Icuria* is either sister to *Bikinia,* or to both *Bikinia* and *Tetraberlinia* when we consider the relatively low Bayesian support for the branch leading to *Icuria* & *Bikinia*. However, analyses (partly) based on other genes (Gervais & Bruneau, 2002; Wieringa & Gervais, 2003; Herendeen *et al.,* 2003) place *Icuria* somewhat further away from *Tetraberlinia* and *Bikinia.* To investigate this incongruence, other methods should be sought such as sequencing another region or inclusion of *Icuria* in the AFLP data set. A definite result from our ITS analysis is the support for the BIJT-clade, indicating *Julbernardia* as the closest relative to *Bikinia* and *Tetraberlinia* (apart from *Icuria*). Since *Brachystegia* and *Michelsonia,* two other close relatives of the BAMBIJT-clade were missing from this analysis, the results should be treated with caution. What the support does tell us though is that the BAMBIJT-clade contains a subclade containing at least *Bikinia*, *Julbernardia*, *Tetraberlinia* and possibly *Icuria* but which does **not** contain *Aphanocalyx*, and that is something previous analyses were not able to establish. This result is corroborated by an analysis of the chemical content of these genera (Kite & Wieringa, 2003), where *Julbernardia* species contained hydroxypipecolic acids and/or hydroxyprolines which were also present in most species of *Bikinia* and *Tetraberlinia*, while these compounds were missing in *Aphanocalyx*, *Brachystegia*, *Icuria* and *Michelsonia*. *Michelsonia* did contain one hydroxypipecolic acid (ovalin), but this compound was not shared with any other species of this group, so no phylogenetic relationships could be established from it. The absence of any of these compounds in *Icuria* could be another indication that the ITS data put it too close to *Bikinia*, *Julbernardia* and *Tetraberlinia*. In three species of *Bikinia* these compounds are absent as well, but this is interpreted by Kite & Wieringa (2003) as a secondary loss, since these species already formed a clade within *Bikinia* in the morphological analysis (Wieringa, 1999) as the two included here are doing in the present AFLP analysis (see below).

Our questions on the *Bikinia le-testui* & *B. pellegrinii* complex have been answered quite well. The two samples of *Bikinia pellegrinii* and those of the five included populations of *B. le-testui* are grouped according to initial identification, and not according to provenance, even while for both sampled populations of *B. pellegrinii*, a sample of *B. le-testui* growing next to it was included. This means that they do represent two different species, although sometimes hard to tell apart. Further material of *B. pellegrinii*, especially from the Chaillu Massif area and from Estuaire province in Gabon, should be added to test if this species is a single species or is composed of an aggregate of sibling species as outlined by Wieringa (1999).

Another definite result from this analysis was that we were able to establish the identity of the aberrant *Bikinia* material from the Crystal Mountains. Both the presence (and absence) of unique specific bands and the phylogenetic analysis of the entire AFLP dataset clearly indicate it constitutes a separate species. So far no flowering material of this species has been collected, the only fertile collection that probably belongs to it is one with young pods (*Breteler, Wieringa & Nzabi* 12857). More material and further morphological research is needed to properly delimit this species. AFLPs may be used to test whether certain samples belong to it as well.

The internal topology of *Bikinia* and *Tetraberlinia* remains poorly resolved. Although we thought we started with three different species of *Tetraberlinia*, we now have to conclude we were probably dealing with only two species. In *Bikinia* we are dealing with a different situation. Since the aberrant material from the Crystal Mountains proved to be a new species, we have 6 different species of *Bikinia* in our analysis. Although the internal topology is entirely resolved, only a single clade has jackknife support within *Bikinia*. It is that of *Bikinia aciculifera* and *B. durandii* with 96% jackknife support. *B. aciculifera* is very closely related to *B. coriacea* (J.Morel ex Aubrév.) Wieringa, which was not included in this AFLP analysis. These three species already formed a clade in the morphological phylogenetic analysis of Wieringa (1999), but without support. These species also do not have hydroxypipecolic acids nor hydroxyprolines. Kite & Wieringa (2003) interpreted this as a secondary loss, which is now corroborated by the support we found for them forming a clade within *Bikinia*. The phylogenetic analysis based only on chloroplast sequences of Gervais & Bruneau (2002) also recognised a weakly supported clade of *B. aciculifera* and *B. durandii*, while *B. coriacea* was considered as one of the possible sisters to it. Their analysis including also ITS sequences, as well as our present one based solely on ITS sequences, shows *B. durandii* and *B. aciculifera* fairly far apart. The majority of the characters of this Gervais & Bruneau (2002) analysis consists of ITS sequences, rendering it feasible that the different position in these two analyses is caused by the sequencing of non-homologous ITS copies.

Tetraberlinia apiphila (still to be described) shows yellow petals and free stipules, which are typical characters of *Tetraberlinia*. However, it has a few odd characters for this genus like the hairy pods (at least when young), the pink-purple anthers and more or less free adaxial sepals that would better fit in *Bikinia*. It is reassuring that the AFLP analysis indeed puts this species solidly next to *Tetraberlinia polyphylla* (Harms) J.Léonard ex Voorh., with 100% jackknife support. Whether or not the tested seedling belongs to this new species as well, will only become clear when the analysis of the larger data set that is being prepared at present becomes available, but the result will probably be that both the seedling and the alleged sapling of *T. bifoliolata* collected 120 km away from it, belong to the new species.

Concerning the monophyly of *Bikinia* and *Tetraberlinia* we have found good evidence that *Bikinia* is monophyletic. Probably only two species of *Tetraberlinia* were included in our AFLP study and the ITS analysis is not able to support the inclusion of the type of the genus, *T. bifoliolata*, in the clade including the other *Tetraberlinia* species, hence we cannot yet conclude *Tetraberlinia* is monophyletic. However, we were able to establish that the new species *T. apiphila* belongs to the main *Tetraberlinia* clade, even though it shares some morphological characters with *Bikinia*, thus eliminating at least one of the question marks around the monophyly of *Tetraberlinia*.

Wieringa & Gervais (2003) discussed the occurrence of several long terminal branches in the ITS data, and proposed that adding more samples that could break up these long branches might solve part of this problem. Although they did not presume this method to work for the case of *Julbernardia pellegriniana*, apparently it did, because not only support for the position of *J. pellegriniana* as being part of *Julbernardia* increased, but even the support for the BIJT clade was now established for the first time. The new sequence of *J. pellegriniana* differs considerably from the first one, pointing to either a high substitution rate in this taxon, or to the presence of different ITS copies, as are occurring in *Aphanocalyx*, *Bikinia* and *Tetraberlinia*.

4.1 ITS sequencing

As is quite evident from the results of the ITS sequencing, these data do give a signal appropriate for the level we are interested in. However, as also shown and discussed above, the sequencing itself is already problematic and only feasible after cloning. Although more elaborate, this would not be a definite set-back for future sequencing. However, the presence of different ITS copies in the same sample gives us far larger problems for the phylogenetic analysis. Even analyses based on cloned ITS will result in gene trees not species trees, as demonstrated by the three different positions at which both *B. media* and *B. pellegrinii* can be found in the present ITS analysis, and the above discussed erroneous placement of a sequence of *B. durandii* relative to *B. aciculifera*. These problems for the analysis might be solved by using the coding method proposed by Wieringa & Gervais (2003), but only if each sequence can be assigned to a set of truly homologous copies. From the present ITS tree one gets the impression there are at least 4 different non-homologous ITS copies present within *Bikinia*, which would mean an enormous amount of cloning and sequencing to get each copy out of each species. In this case it seems better to start sequencing another marker. Regrettably, chloroplast markers so far proved to have too little variation between these closely related genera, but a combination of several such markers may work. Next to that, AFLPs may still have enough resolution at and above the generic level to bridge the gap between the higher and the lower phylogenetic levels.

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PHYLOGENETICS OF THE GENUS *KNIPHOFIA* MOENCH (ASPHODELACEAE)

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Abstract

The genus *Kniphofia* contains approximately 70 species with an African-Malagasy distribution, including one species from Yemen. The centre of diversity is the Drakensberg Mountain Range and the genus is generally found in most areas of the Afromontane Region. Species relationships and complexes are poorly understood due to morphological homogeneity. This study is part of a multidisciplinary effort to resolve the systematics of the entire genus. Here we report on preliminary studies of the phylogenetic relationships of South African representatives of *Kniphofia* using DNA sequence data from the *trnT-trnL* region of the chloroplast genome and leaf surface anatomical data. Preliminary DNA sequence data results suggest that there are three sub-generic groups, characterised by insertions/deletions. The molecular data does not support previous sub-generic classifications or the segregate genus *Notosceptrum*. Anatomical data, although variable, also failed to resolve species relationships. Furthermore, it could not be correlated with existing morphological groupings and/or the chloroplast DNA phylogeny. Increased sampling and morphological support for these groups, as well as a parallel nuclear phylogeny is needed to further resolve the phylogeny of this problematic genus.

Résumé

Phylogénie du genre *Kniphofia* Moench (Asphodelaceae). Le genre *Kniphofia* contient approximativement 70 espèces à distribution afro-malgache, et notamment une espèce au Yemen. Le centre de diversité du genre est la chaîne de montagnes du Drakensberg et il est généralement présent dans la plupart des zones de la région afromontagnarde. Les relations inter-spécifiques et les complexes sont mal compris à cause de l'homogénéité morphologique. Cette étude entre dans le cadre d'un effort pluridisciplinaire destiné à résoudre la systématique du genre dans son ensemble. Nous faisons ici le rapport des études préliminaires des relations phylogénétiques des représentants sud-africains de *Kniphofia* à l'aide de données de séquençage d'ADN de la région *trnT-trnL* du génome chloroplastique et de données d'anatomie de la surface foliaire. Les données préliminaires de séquençage d'ADN suggèrent qu'il y a trois groupes sub-génériques caractérisés par des insertions/délétions. Les données moléculaires ne corroborent pas les classifications sub-génériques antérieures ni la ségrégation du genre *Notosceptrum*. Les données anatomiques, bien que variables, n'ont pas permis non plus de résoudre les relations spécifiques. Par ailleurs, elles pourraient ne pas être corrélées avec les groupements morphologiques existants et/ou avec la phylogénie du DNA chloroplastique. Un échantillonnage plus important, un appui des données morphologiques pour ces groupes ainsi qu'une phylogénie nucléaire parallèle sont nécessaires pour résoudre la phylogénie de ce genre problématique.

Key Words: anatomy, Asphodelaceae, chloroplast DNA, *Kniphofia*, phylogenetics, *trnT-trnL*

1 Introduction

The genus *Kniphofia* Moench (Asphodelaceae), commonly known as the 'red hot pokers', consists at present of approximately 70 species. The genus is almost entirely African with two species from Madagascar and one from Yemen. *Kniphofia* is chiefly distributed in southern and eastern Africa, preferring mountainous grassland and moist habitats. In South Africa there are 48 species (Reid & Glen, 1993). The centre of diversity is the Drakensberg region of the KwaZulu-Natal and Eastern Cape provinces of South Africa. The genus has huge horticultural appeal because of the conspicuous inflorescences of some members.

Berger (1908) monographed the entire genus, recognising 67 species with 13 varieties. He upheld *Notosceptrum* Benth. as a separate genus with five species, which was segregated from *Kniphofia* by Bentham & Hooker (1883). Berger divided *Kniphofia* into 14 sections with formal rank. Codd (1968) revised the South African species of the genus, and recognised 45 species with eight subspecies. Codd (1968) found numerous problematic taxa that required further investigation. He did not resolve *K. uvaria* (L.) Oken and allies [*K. rooperi* (Moore) Lem., *K. tysonii* Bak., *K. citrina* Bak. and *K. linearifolia* Bak.] completely. He reluctantly gave each of these taxa species rank. He also noted problems in *K. praecox* Bak.; *K. angustifolia* (Bak.) Codd and *K. ichopensis* Bak. ex Schinz; *K. gracilis* Harv. ex Bak. and *K. laxiflora* Kunth. Codd (1968) grouped taxa into ten informal infrageneric sections based on probable affinity. He saw no advantage in Berger's (1908) sections although he viewed them as sound and did not support *Notosceptrum* as a separate genus.

Marais (1973) revised the tropical African species but did not group taxa into infrageneric sections. Marais (1973), like Codd (1968), found difficulty with some taxa. He found that there were two varieties of *K. thomsonii* Bak. Marais (1973) considered *K. ankaratrensis* Bak. (Madagascar) to be closely related to *K. splendida* E.A.Bruce (southern Africa and Malawi) and that these may be a single species. He also noted that *K. sumarae* Deflers from Yemen is an excellent link between taxa placed in *Notosceptrum* and African species such as *K. pumila* (Ait.) Kunth and *K. foliosa* Hochst. Although Marais did not specify reasons for this opinion, it appears he based this hypothesis on floral characters.

Kativu (1996) treated eight species for the *Flora Zambesiaca* area but failed to include *K. monticola* Blackmore in this treatment. Whitehouse (2002) found that there were eight species of *Kniphofia* for the Flora of Tropical East Africa. He maintained *K. goetzei* Engl. which Marais (1973) sunk under *K. thomsonii* Bak. and noted that there were taxonomic problems between these two species. Furthermore, Whitehouse (2002) maintained *K. paludosa* Engl. which Marais (1973) considered a synonym of *K. kirkii* Bak. Whitehouse (2002) relegated the name *K. kirkii* to *nomen dubium*.

1.1 Generic relationships

Asphodelaceae is currently placed in the order Asparagales and considered a family of the lower asparagoids which are characterised by simultaneous microsporogenesis (Chase *et al.*, 1995; Fay *et al.*, 2000). The family is divided into two subfamilies, Alooideae and Asphodeloideae. Alooideae has a distinct southern African centre of radiation with outliers in Saudi Arabia, Madagascar and the Mascarene Islands. Asphodeloideae has a predominantly Eurasian distribution with significant outliers in Africa, Australia and New Zealand (Treutlein *et al.*, 2003).

Currently the most accepted morphological treatment of Asphodelaceae is the framework of Dahlgren *et al.* (1985). Although this treatment is widely accepted, there have been varying and different views on the relationships of the genera in Asphodelaceae. Despite various attempts to stabilise classification of Asphodelaceae, relationships remain unresolved (Treutlein *et al.,* 2003). Some workers have placed *Kniphofia* within Alooideae based on floral morphology and inflorescence structure (e.g. Cronquist 1981, 1988). However, various studies using phytochemical (Van Staden & Drewes 1994; Van Wyk *et al.*, 1995) and molecular data (Chase *et al.*, 2000; Treutlein *et al.*, 2003) have shown that *Kniphofia* is best placed in Asphodeloideae supporting Dahlgren *et al.* (1985).

Recent molecular studies in Asphodelaceae have been of limited benefit. Chase *et al.* (2000) investigated generic relationships in Asphodelaceae using *rbcL* and *trnL-F* chloroplast DNA (*cp*DNA) sequence data. These authors found that Asphodelaceae *sensu* Dahlgren *et al.* (1985) is monophyletic, and more closely related to Hemerocallidaceae and Xanthorrhoeaceae than the morphologically similar Anthericaceae. Based on *cp*DNA sequence data, *Kniphofia* appears to be better placed in the subfamily Asphodeloideae, however support for two separate subfamilies is lacking. Alooideae appears to be monophyletic, while Asphodeloideae appears paraphyletic. Alooideae is nested within the Asphodeloideae. Furthermore, Chase *et al.* (2000) found that *Kniphofia* is sister to *Bulbinella* Kunth. Molecular studies by Treutlein *et al.* (2003), using *rbcL* and *matK cp*DNA sequence data, concentrated on subfamily Alooideae. They studied all seven currently recognised genera of Alooideae represented by 43 species (and a hybrid, × *Astroworthia bicarinata* (Haw.) G.D.Rowley). These authors (Treutlein *et al.*, 2003) also included representative genera of Asphodeloideae in their analyses which comprised seven genera (11 species) of the presently recognised nine genera (± 300 species) of Asphodeloideae. They found that *Kniphofia* is best placed in Asphodeloideae and is sister to *Bulbinella.* Chase *et al.* (2000) included only a single representative of *Kniphofia* (*K. uvaria*) in their study, while Treutlein *et al.* (2003) included four *Kniphofia spp.* in their study. Thus, phylogenetic relationships at the species level within *Kniphofia* (and many other genera of Asphodelaceae) are still unexplored and unsettled.

In past studies of *Kniphofia* little attempt was made to examine evolutionary relationships or produce a phylogenetic classification. This study utilises DNA sequence data from the chloroplast plastid *trnT-trnL* region in an attempt to elucidate a species level phylogeny. The *trnT-trnL* region consists of an intergenic spacer between *trnT* and the *trnL* 5’ exon which is usually 773 to 833 base pairs (bp) long in angiosperms (Taberlet *et al.*, 1991). It is not as frequently used as the *trnL-trnF* regions for phylogeny reconstruction. However, in several recent studies *trnT-trnL* sequences have been used in combination with sequences from other *cp*DNA regions (particularly adjacent regions) to infer phylogenetic relationships at various levels. Mummenhoff *et al.* (2001) used *trnT-trnL* sequence data to elucidate species relationships in *Lepidium* L.

(Brassicaceae). Razafimandimbison & Bremer (2002) used *trnT-trnL* sequences to infer intertribal relationships in the tribe Naucleeae (Rubiaceae).

Furthermore, we investigated whether leaf surface characters as visible by means of scanning electron microscopy (SEM) were useful in resolving species relationships. Baijnath (1980) investigated the leaf anatomy of 18 *Kniphofia* spp. to access the taxonomic value of anatomical characters. He found that leaf surface and internal anatomy (vascular bundles and crystals) proved to be taxonomically useful characters. Leaf surface anatomical characters were variable and deemed to be potentially phylogenetically useful. Comparisons between the anatomical phylogeny, the molecular phylogeny and the existing morphological classification were made. Here we report on preliminary findings.

2 Materials and methods

2.1 Plant samples

The details of the samples and voucher specimens, which are deposited in the Selmar Schonland Herbarium (GRA), are presented in Appendix 1. All samples were collected in South Africa, except *K. umbrina* Codd from Swaziland. Most samples were collected from the field by the senior author. Some samples were obtained from plants in cultivation, growing at various botanical gardens in South Africa. Twenty-three *Kniphofia* species (40 samples) of the 45 South African species were sampled for molecular studies. These 23 species represented eight of Codd's (1968) ten sections. Thirty-five *Kniphofia* species (46 samples) of the 45 South African species were sampled for anatomical studies. These 35 species represented all ten of Codd's (1968) sections. Seventeen species (18 samples) were complimentary for both studies. Only one species, *K. typhoides* Codd, of the segregate genus *Notosceptrum* was examined.

2.2 DNA extraction, amplification and sequencing

Most leaf samples were dried with silica gel (Chase & Hills, 1991). In some cases plants collected in the field were cultivated and fresh material was used. Total genomic DNA was extracted using the hot CTAB method of Doyle & Doyle (1987). The *trnT-trnL* spacer was initially amplified and sequenced by means of the polymerase chain reaction (PCR) using primers 'A' and 'B' (Taberlet *et al.*, 1991). The forward primer 'A' proved to be problematic in amplification. To circumvent this problem, an alternative internal primer ('Knip1') (5'–CTA CCG GAT CCT AGG TAT–3') was designed by one of us (NPB). 'Knip1' was subsequently used for both amplification and sequencing. This primer represents a successful alternative to the primer 'A' and also worked for *Bulbinella* samples. PCR products were purified by means of the Promega Magic PCR Preps™ or QIAGEN© QIAquick™ PCR purification kits. Purified PCR products were then sequenced using primers 'Knip1' and 'B'. Sequencing was done on a ABI 3100 autosequencer using the ABI PRISM™ Dye Terminator Cycle Sequencing Ready Reaction Kit v. 3.0 or v. 3.1.

2.3 DNA sequence manipulation and alignment

Sequences were assembled, checked and edited using Sequencher™ version 3.1.1 (Gene Codes Corporation). Sequences were imported into the alignment package DAPSA (DNA and Protein Sequence Alignment; written by E.H. Harley, Dept. Chemical Pathology, University of Cape Town Medical School, Observatory, 7935, South Africa). Alignments were done manually. As this study is ongoing, the aligned sequences were not submitted to Genbank, but are available from the senior author upon request.

2.4 DNA sequence data: phylogenetic analysis

Two analyses were undertaken: a neighbour joining analysis (Analysis I) and a parsimony analysis (Analysis II).

Analysis I. Analysis I was conducted with PAUP* version 4.0b3a (Swofford, 2000) using the neighbour joining (NJ) algorithm (Saitou & Nei, 1987), based on distance matrices calculated using the Jukes-Cantor correction (Jukes & Cantor, 1969). This analysis was applied to the full alignment. Gaps were excluded from consideration for each pair-wise comparison when encountered. A NJ bootstrap analysis using 1000 replicates was also conducted with these settings.

Analysis II. Analysis II was a maximum parsimony (MP) analysis using the FULL HEURISTIC search option in PAUP* version 4.0b3a (Swofford, 2000) with TBR branch swapping and MAXTREES were set at 5000. Gaps were treated as missing data and all characters were weighted equally. Gaps (indels) were not coded but mapped onto the tree. *Bulbinella* was used as the outgroup in both the NJ and MP analyses.

2.5 Leaf anatomy

All samples used for the SEM anatomical survey were obtained from fresh material. Mature leaves were sampled midway along the length of the leaf for sampling constancy and fixed in FAA. Leaves were dehydrated through a gradually increasing series of ethanol. Leaves were then critical point-dried, mounted on brass stubs with conductive tape and coated with gold. Both adaxial and abaxial surfaces were examined using a JEOL JSM840 Scanning Electron Microscope. Seventeen characters were coded for phylogenetic analysis. Full details of this data matrix is available from the senior author upon request. This data set was analysed using PAUP* version 4.0b3a (Swofford, 2000) applying the FULL HEURISTIC search option with TBR branch swapping. MAXTREES were set at 5000 and *Bulbinella* was used as the outgroup.

3 Results

3.1 *trnT-trnL* Sequence data

Phylogenetic analyses based on DNA sequences are dependent on sequence alignment, and it is therefore important that the evolutionary events, which cause length variation, are recognised and used during the alignment of length-variable sequences (Asmussen & Chase, 2001). The *trnT-trnL* region in this study was rich in $(AT)_n$ & $(T)_n$ repeats, which proved difficult to align in certain regions. However, even when these areas were excluded from the analyses we obtained the same results. Sequences of the *trnT-trnL* region were obtained for 24 taxa (23 *Kniphofia* spp. and one *Bulbinella* sp.). The complete alignment included 916 nucleotide positions. Of these, 126 were variable, and 32 positions were parsimony-informative.

Analysis I. The NJ analysis (Fig. 1) revealed three groups (designated as Group 1, 2 and 3). These groups correspond to occurrence of insertions in *trnT-trnL* sequences. Group 1 has a nine bp insertion at position 844 of the alignment and Group 3 has a six bp insertion at position 428. Group 2 has neither insertion. With the exception of Group 2, bootstrap values for these groups were less than 50% and groups are thus not supported. The three groups based on molecular data are incongruent with Codd's (1968) informal sections given in parentheses. None of the sections delimited by Codd (1968) correspond to lineages found in our molecular trees.

Analysis II. The parsimony analysis gave similar results to the NJ analysis, resolving the same three groups of samples. Parsimony analysis resulted in excess of 5000 equally parsimonious trees. The trees were 55 steps long (ci = 0.618, ri = 0.867). The strict consensus tree is shown in Fig. 2. Bootstrap percentages are indicated above the branches, but groups with bootstrap percentages less than 50% have not been indicated.

K. typhoides (arrowed in Fig. 1 & 2) of the segregate genus *Notosceptrum* is nested in Group 2, thus not supporting the separation of *Notosceptrum* from *Kniphofia*.

Our results revealed a serious taxonomic problem: where species are represented by multiple samples, they are not resolved as monophyletic. These include *K. linearifolia* (samples placed in Group 1 & 3), *K. triangularis* (samples placed in Group 1 & 3) and *K. uvaria* (samples placed in Group 1 & 2). Some multiple samples are resolved as belonging to one group but even then these species are not monophyletic. These include *K. baurii* (Group 3), *K. laxiflora* (Group 3), *K. ichopensis* (Group 3), *K. tysonii* (Group 3) and *K. caulescens* (Group 1). This is found in the NJ tree and in the largely unresolved consensus tree from the MP analysis. The above results emphasise the importance of using multiple samples in plastid studies of problematic groups.

3.2 Leaf anatomy

The strict consensus tree showed almost no resolution and is not been presented here. This indicated that leaf surface characters fail to provide any unambiguous information on relationships of the species analysed.

As with the molecular data, in taxa with multiple samples, excessive variation was found. *K. uvaria* is used here to demonstrate leaf surface anatomical variability (Fig. 3). Both samples (SR 172 & SR 186) have dimorphic adaxial and abaxial surfaces. *K. uvaria* (SR 172) has rectangular epidermal cells on both surfaces. Longitudinal and transverse striae are absent on the adaxial surface but present on the abaxial surface. Papillae are present on both surfaces. The adaxial stomata are sunken with distinct rims, while the abaxial stomata are more or less level with the leaf surface and lack distinct rims. *K. uvaria* (SR 186) has rectangular epidermal cells on both surfaces. Longitudinal and transverse striae are absent on the adaxial surface. Only longitudinal striae are present on the abaxial surface. Papillae are present on both surfaces. The adaxial and abaxial stomata are sunken with distinct rims. Baijnath (1980) did not use multiple samples for most species examined. Thus, leaf surface anatomical characters, although variable, failed to resolve relationships.

4 Discussion

The above results (both molecular and anatomical) were unexpected. It would be expected for multiple samples of each species to cluster together and form monophyletic groups. However, in both analyses (molecular and anatomical) this was not found. We attribute our results to two factors: reticulation through hybridisation and incomplete lineage sorting.

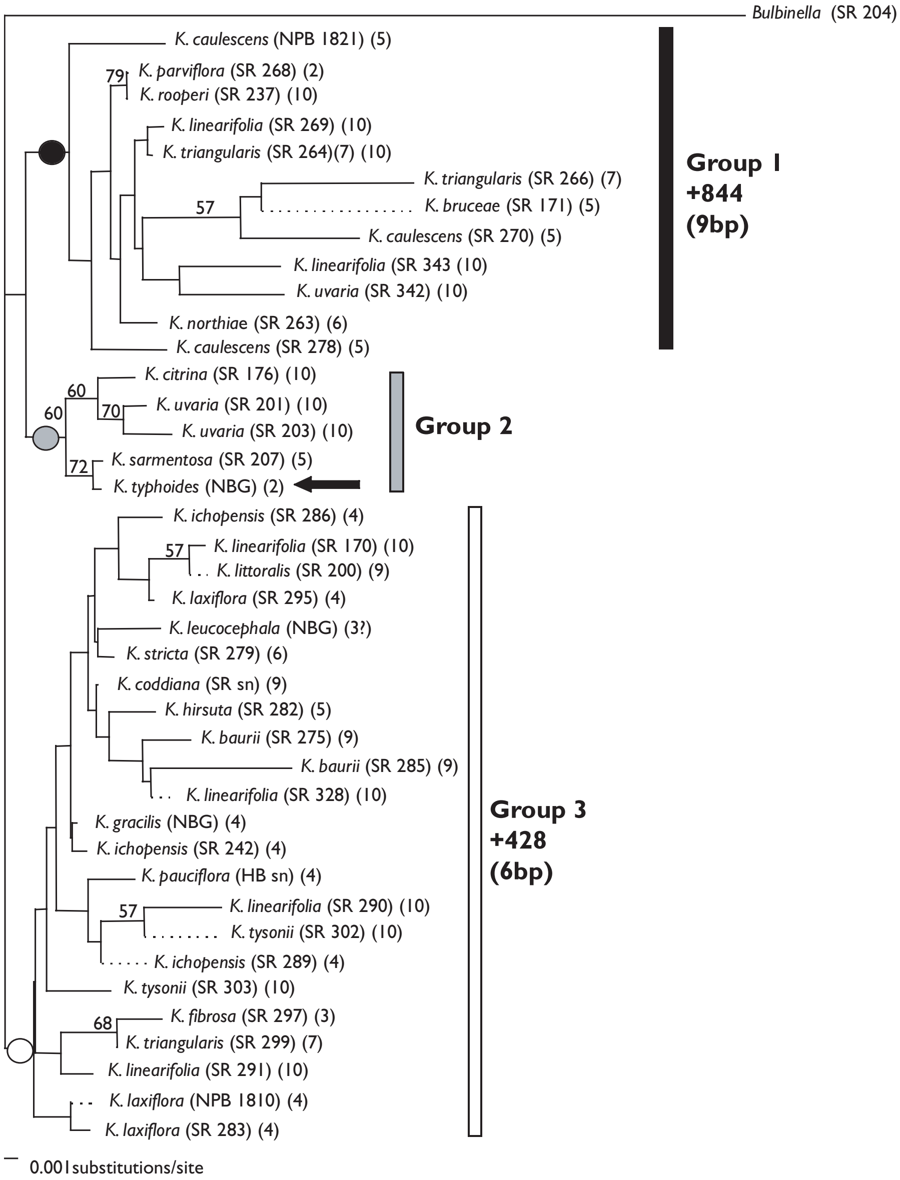

FIG. 1. The neighbour joining tree (using Jukes-Cantor correction) of *trnT-trnL* sequence data. Bootstrap support values are shown above the branches. Codes in parentheses after the taxon names are collection numbers followed by the informal section in which the species has been placed [following Codd (1968); refer to Appendix l.]. Circles indicate groups. The arrow shows *K. typhoides*, previously placed in *Notosceptrum.* Dotted lines imply branch length= 0. Numbers below group indicate position of insertion and the bp size of the insertion in parentheses.

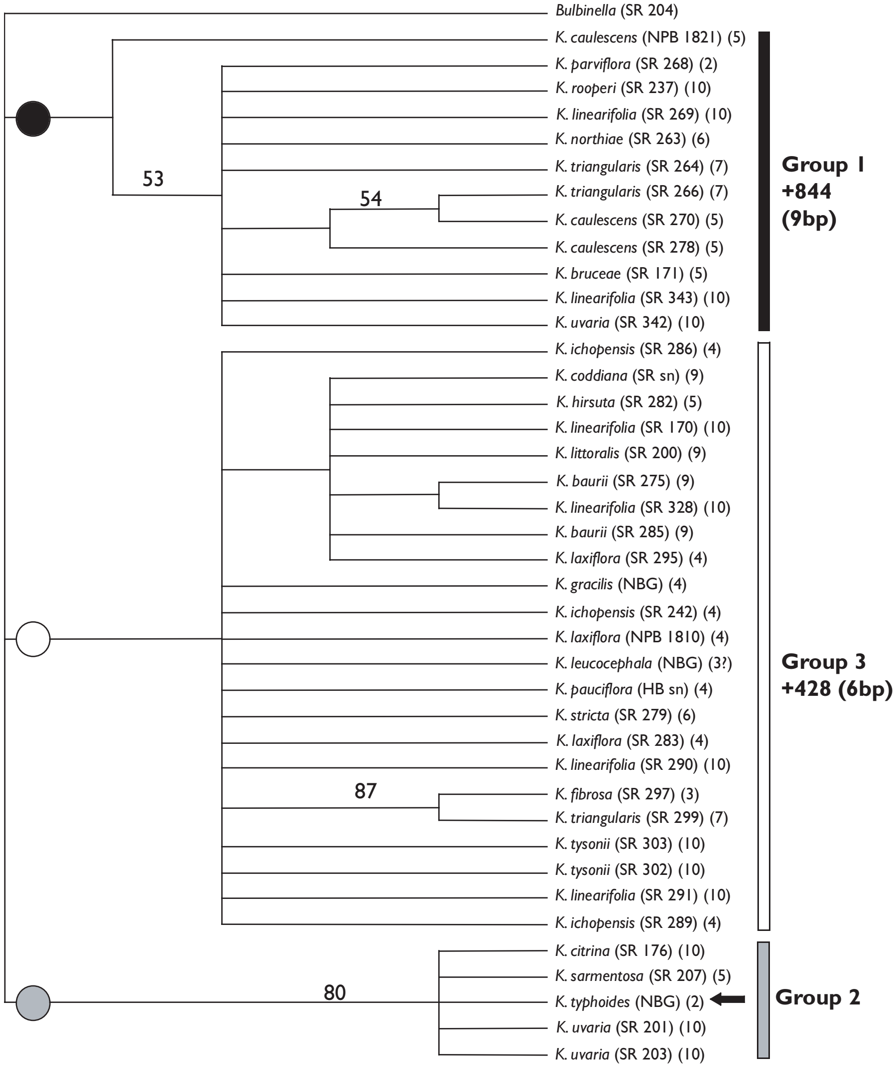

FIG. 2. The strict consensus tree (of most parsimonious trees) of *trnT-trnL* sequence data. Bootstrap support values are shown above the branches. Codes in parentheses after the taxon names are collection numbers followed by the informal section in which the species has been placed [following Codd (1968); refer to Appendix 1.]. Circles indicate groups. The arrow shows *K. typhoides*, previously placed in *Notosceptrum*. Numbers below group indicates position of insertion and the bp size of insertion in parentheses.

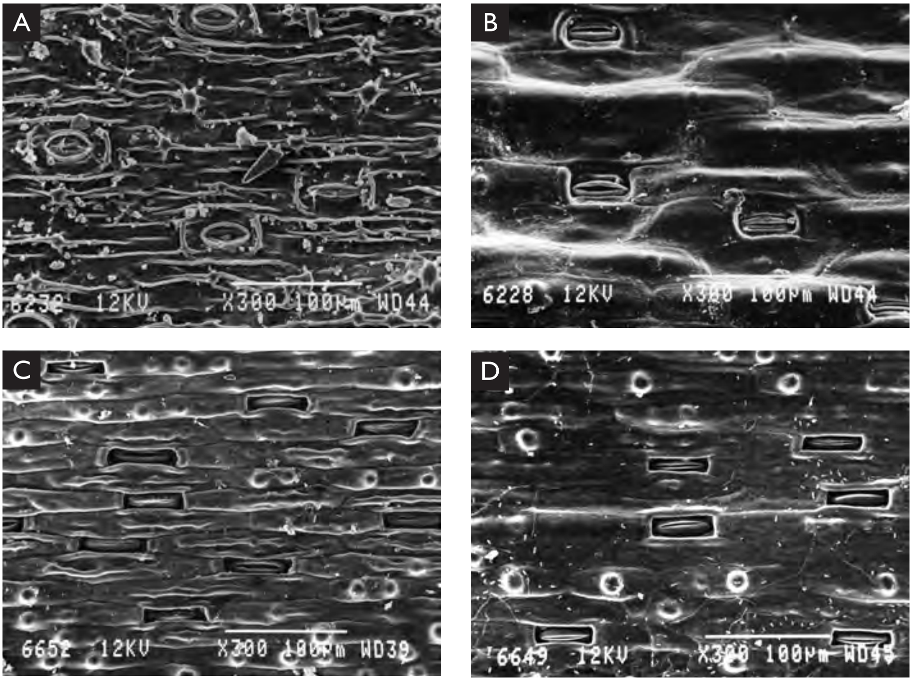

FIG. 3. Leaf surface SEM micrographs of *K. uvaria* showing variation in leaf surface ornamentation and structure (abaxial transverse striae, abaxial stoma position, abaxial stomata rim). **A**, *K. uvaria* (SR 172) adaxial surface; **B**, *K. uvaria* (SR 172) abaxial surface; **C**, *K. uvaria* (SR 186) adaxial surface; **D**, *K. uvaria* (SR 186) abaxial surface.

4.1 Hybridisation (reticulate evolution)

If hybridisation is an important factor in the evolutionary history of a given group then phylogenetic reconstruction using cladistic methods may be questionable and challenges the basis of current taxonomy (McKinnon *et al.*, 1999). At the generic level or below, chloroplast capture resulting from hybridisation can provide a species with a foreign chloroplast genome and could result in a fallacious *cp*DNA phylogeny. A major disadvantage of using *cp*DNA at lower taxonomic levels involves the potential for chloroplast transfer i.e. the movement of a chloroplast genome from one species to the other by introgression (Soltis & Soltis, 1998, also see Harris & Ingram, 1991, Rieseberg & Brunsfeld, 1992). If chloroplast capture is undetected it will bias estimations of phylogeny. However, when recognised it can be very informative about evolutionary processes (Soltis & Soltis, 1998). Also, if chloroplast capture (via hybridisation) does exist, important questions have to considered. Firstly, determining the chloroplast donor; and secondly, determination of what represents the 'true' genome and the 'captured' genome for the species suspected of chloroplast capture (Soltis & Kuzoff, 1995).

Caution is needed when using organellar variation to elucidate phylogeny at lower taxonomic levels in groups noted for hybridisation (Soltis & Kuzoff, 1995). *Kniphofia* is noted for hybridisation in horticulture, contributing to its horticultural appeal. However, there are very few reports of hybrids in the wild. Samples of 'problematic' taxa (*K. linearifolia*, *K. triangularis*, *K. uvaria*, *K. baurii*, *K. laxiflora*, *K. ichopensis*, *K. tysonii*

& *K. caulescens*) were morphologically distinct in both molecular and anatomical analyses. But these samples did not cluster into morphologically supported groups in either analysis. Hybridisation could be more extensive in wild populations than previously thought and could account for the observed results. Hybridisation in these 'problematic' taxa may be followed by introgression possibly following the 'stepping stone' model (Soltis *et al.,* 1991) as taxa on different clades could possibly share the same plastid genome.

Furthermore within several species of *Kniphofia* there is evidence for recent speciation, as many species form species complexes. Some problematic taxa encountered by Codd (1968) were also troublesome in our analyses, most notably *K. uvaria* complex, *K. laxiflora* and *K. ichopensis*. Also, fieldwork revealed that some species are difficult to tell apart with certainty. These include *K. triangularis-K. galpinii* and *K. baurii-K. uvaria*. Thus species limits are questionable for the above taxa. There may be incomplete or weak reproductive barriers in taxa of these complexes, promoting hybridisation. Low levels of floral morphological divergence in these complexes supports hypotheses of recent speciation, with the possible addition of hybridisation and back-crossing to further complicate the issue. Many problematic taxa appear to be either incipient species or populations *sensu* Lu (2001) that are in the process of diverging to the point of speciation but still have the potential to interbreed. Problematic taxa are often wide-ranging species, which are sympatric with other *Kniphofia spp.* This scenario favours natural hybridisation. However, we have not done any artificial hybridisation experiments to test this.

Hybridisation followed by introgression should leave traces of foreign genetic material from the implicated/suspected parental species in the nuclear genome of the putative hybrid/s. In several instances ITS sequence data has been used in proving ancient introgression between species (e.g. Sang *et al.*, 1995; Aguilar *et al.*, 1999) and we intend to commence a sequence study using a nuclear region, such as ITS.

4.2 Lineage sorting

The evolutionary history of *cp*DNA represents one particular 'gene genealogy' (matriarchal phylogeny) within an organismal pedigree. Stochastic matriarchal lineage sorting from a polymorphic ancestral gene pool can account for the discordance between species affiliations and *cp*DNA genotype. Discordance between *cp*DNA and conventional morphological taxon boundaries can therefore be attributed to lineage sorting processes (Avise *et al.*, 1990). It is biologically plausible that some individuals may be more closely related to a member of another species than to their conspecifics, solely due to patterns of maternal lineage survival and extinction accompanying the speciation process (Avise *et al.*, 1987). This is particularly so for species which have separated recently, where a state of monophyly has not yet been achieved. Thus, the results obtained above may also be attributed to incomplete lineage sorting.

4.3 Future work

The results we obtained raise more questions than provide answers. The *trnT-trnL* tree represents the phylogeny of a particular stretch of DNA of the chloroplast genome. It is one of many molecular traces in the evolutionary history of an organism. A single region (or part thereof) may not constitute a reliable source of phylogenetic information. Reeves *et al.* (2001) showed how reliance on a single data set may produce misleading conclusions. In the case of *cp*DNA, it is a history of maternal transmission whose molecular record has not been complicated by recombination. Chloroplast DNA can be considered an example of an asexually transmitted trait within a sexually reproducing species. In contrast, nuclear genes segregate and recombine during each generation of sexual reproduction (Avise *et al.*, 1987). It will be useful to compare the *cp*DNA phylogeny with molecular nuclear phylogenies (e.g. ITS data). When based on a suitable sampling strategy comparisons between nuclear and *cp*DNA data may help to further elucidate species relationships and understand reticulation (via hybridisation and chloroplast capture events) and lineage sorting events.

Increased sampling is needed, especially for problematic species across their entire natural geographic range to better understand variation and factors influencing variation. It will be important to include more species (and additional multiple samples) for poorly sampled sections as well as material from tropical Africa, Madagascar and Yemen to deduce centres of origin and migrations patterns for this genus.

5 Conclusions

There is major discordance between *cp*DNA phylogeny, anatomical phylogeny and the existing species concepts in *Kniphofia*. Chloroplast DNA has proven useful in resolving relationships at higher taxonomic levels in the Asphodelaceae, however, at lower levels discordance exists between *cp*DNA phylogeny and species treatment, suggesting reticulate evolution and/or incomplete lineage sorting. Thus, *cp*DNA may not be useful in phylogenetic reconstruction at species levels in *Kniphofia*. Anatomical data, although variable, failed to resolve species relationships. Furthermore, it could not be correlated with morphological groupings and/or the *cp*DNA phylogeny. Anatomical characters used for this study may, however, be plastic (variable with age and environment). These aspects need to be tested. This study also demonstrates the value of not undertaking single exemplar molecular systematic studies. We suspect that such problems as we encountered here may be more frequent than currently believed and urge the adoption of a multi-exemplar approach.

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Appendix 1. Voucher details of the samples included in this study. All voucher specimens which are deposited in the Selmar Schonland Herbarium (GRA). Key to abbreviations: HB= H. Baijnath; JB= J. Burrows; PBP= P.B. Phillipson; NBG= Natal National Botanical Garden (original locality given in parentheses); NPB= N.P. Barker; RG= R. Gama; *sn*= without number (usually with no accompanying herbarium voucher); SR= S. Ramdhani.

	Taxon	**Coll. No.**	**Locality**	**Section following Codd (1968)**	**SEM Anatomy**	**DNA Sequence**
1	*Bulbinella sp.* 1	SR 204	Citrusdal		X	X
2	*Bulbinella sp.* 2	SR 206	Baviaanshoek		X	
3	*K. albescens* Codd	SR 308	Greytown	2	X	
4	*K. albescens* Codd	SR 314	Dirkiesdorp	2	X	
5	*K. albomontana* Baijnath	SR 149	Greytown	5?	X	
6	*K. baurii* Bak.	SR 174	Humansdorp	9	X	
7	*K. baurii* Bak.	SR 275	Elands Heights	9	X	X
8	*K. baurii* Bak.	SR 285	Naudes Nek	9	X	X
9	*K. breviflora* Harv. ex Bak.	SR *sn*	Greytown	3	X	
10	*K. bruceae* (Codd) Codd	SR 171	Komga	5	X	X
11	*K. buchananii* Bak.	SR 307	Greytown	3	X	
12	*K. coddiana* Cufod.	SR *sn*	Port Edward	9	X	X
13	*K. caulescens* Bak.	SR 270	Elands Heights	5	X	X
14	*K. caulescens* Bak.	SR 278	Naudes Nek	5		X
15	*K. caulescens* Bak.	NPB 1821	Sani Pass	5		X
16	*K. citrina* Bak.	SR 176	Humansdorp	10	X	X
17	*K. ensifolia* Bak.	JB *sn*	Witbank	5	X	
18	*K. fibrosa* Bak.	PBP 5579	Dohne Hill	3	X	
19	*K. fibrosa* Bak.	SR 297	Pervensey	3		X
20	*K. galpinii* Bak.	SR 304	Greytown	8	X	
21	*K. galpinii* Bak.	SR 312	Lydenberg	8	X	
22	*K. gracilis* Harv. ex Bak.	SR 321	Durban	4	X	
23	*K. gracilis* Harv. ex Bak.	NBG	NBG (Umzinto)	4		X
24	*K. hirsuta* Codd	SR 282	Naudes Nek	5	X	X
25	*K. ichopensis* Bak. ex Schinz	SR 242	Nottingham Road	4	X	X
26	*K. ichopensis* Bak. ex Schinz	SR 286	Kamberg	4		X
27	*K. ichopensis* Bak. ex Schinz	SR 289	Catheral Peak	4		X
28	*K. latifolia* Codd	SR *sn*	Greytown	10	X	
29	*K. laxiflora* Kunth	SR 253	Himeville	4	X	
30	*K. laxiflora* Kunth	SR 295	Kamberg	4		X
31	*K. laxiflora* Kunth	SR 283	Naudes Nek	4		X
32	*K. laxiflora* Kunth	NPB 1810	Bushmans Nek	4		X
33	*K. linearifolia* Bak.	SR 311	Lydenberg	10	X	
34	*K. linearifolia* Bak.	SR 170	Komga	10	X	X
35	*K. linearifolia* Bak.	SR 269	Seymour	10		X
36	*K. linearifolia* Bak.	SR 343	Seymour	10		X
37	*K. linearifolia* Bak.	SR 328	Kokstad	10		X
38	*K. linearifolia* Bak.	SR 290	Nottingham Road	10		X
39	*K. linearifolia* Bak.	SR 291	Kamberg	10		X
40	*K. linearifolia* Bak.	SR 182	Knysna	10	X	
41	*K. littoralis* Codd	SR 200	Durban	9	X	X
42	*K. leucocephala* Baijnath	NBG	NBG (Richards Bay)	3?	X	X
43	*K. multiflora* Wood & Evans	SR 310	Lydenberg	1	X	
44	*K. northiae* Bak.	SR 263	Seymour	6	X	X
45	*K. parviflora* Kunth	SR 268	Seymour	2	X	X
46	*K. pauciflora* Bak.	HB *sn*	Durban	4	X	X
47	*K. porphyrantha* Bak.	SR *sn*	Lydenberg	8	X	
48	*K. praecox* Bak.	TD 4461	Port Elizabeth	5	X	
49	*K. rigidifolia* E.A.Bruce	SR *sn*	Dullstroom	10	X	

TABLE 1. continued

	Taxon	**Coll. No.**	**Locality**	**Section following Codd (1968)**	**SEM Anatomy**	**DNA Sequence**
50	*K. rooperii* (Moore) Lem.	SR *sn*	Port Elizabeth	10	X	
51	*K. rooperii* (Moore) Lem.	SR 237	East London	10	X	X
52	*K. sarmentosa* (Andr.) Kunth	SR 207	Matroosberg	5	X	X
53	*K. stricta* Codd	SR 279	Rhodes	6	X	X
54	*K. triangularis* Kunth *triangularis*	SR 264	Seymour	7	X	X
55	*K. triangularis* Kunth *triangularis*	SR 266	Seymour	7		X
56	*K. triangularis* Kunth *triangularis*	SR 299	Pervensey	7		X
57	*K. triangularis* Kunth *obtusiloba* (Berger) Codd	SR *sn*	Lydenberg	7	X	
58	*K. typhoides* Codd	JB 8084	Witbank	2	X	
59	*K. typhoides* Codd	NBG	NBG (Vryheid)	2		X
60	*K. tysonii* Bak.	SR 302	Creighton	10		X
61	*K. tysonii* Bak.	SR 303	Ixopo	10	X	X
62	*K. tysonii* Bak.	SR 199	Port Edward	10	X	
63	*K. umbrina* Codd	RG *sn*	Forbes Reef	2	X	
64	*K. uvaria* (L.) Oken.	SR 165	Colchester	10	X	
65	*K. uvaria* (L.) Oken.	SR 172	Kei Road	10	X	
66	*K. uvaria* (L.) Oken.	SR 186	The Crags	10	X	
67	*K. uvaria* (L.) Oken.	SR 342	Seymour	10		X
68	*K. uvaria* (L.) Oken.	SR 201	Humansdorp	10		X
69	*K. uvaria* (L.) Oken.	SR 203	Elim	10		X

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CHARACTER DELIMITATIONS IN THE FAMILY MESEMBRYANTHEMACEAE: *DELOSPERMA*, A CASE STUDY

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Abstract

The family Mesembryanthemaceae, one of the largest succulent plant families in the world, with ± 1690 species currently grouped into ± 125 genera, is comparable in size to the New World Cactaceae. Virtually endemic to southern Africa with only about 20 species from five genera found outside this core area, Mesembryanthemaceae has had a turbulent history and the vast number of names is a definite challenge to taxonomic progress. Characters used and difficulties encountered in untangling the genus *Delosperma* within the family Mesembryanthemaceae are discussed and are representative of problems within the family as a whole.

Résumé

Délimitation des caractères dans la famille des Mesembryanthemaceae: le cas de *Delosperma*. La famille des Mesembryanthemaceae, une des plus grandes familles de plantes succulentes au monde, avec ± 1690 espèces généralement groupées en ± 125 genres, a une taille comparable aux Cactaceae du Nouveau Monde. Virtuellement endémique d'Afrique australe, avec seulement 20 espèces environ au sein de cinq genres présents hors de cette région, la famille des Mesembryanthemaceae a eu une histoire mouvementée et le grand nombre de noms utilisés est un défi aux progrès en matière de taxonomie. Les caractères utilisés et les difficultés rencontrées en tentant d'y voir clair au sein du genre *Delosperma* sont discutés et reflètent les problèmes au sein de l'ensemble de la famille.

Key words: character delimitation, *Delosperma*, Mesembryanthemaceae/Aizoaceae, southern Africa, taxonomy

1 Introduction

The history of the family Mesembryanthemaceae Fenzl (1836), virtually endemic to South Africa (Fig. 1) is most interesting as it emphasizes the difficulties experienced by students of the group.

First listed by Linnaeus in Species Plantarum (1753) under the genus *Mesembryanthemum* L. were 35 species belonging to this group. Later Haworth (1821) described 310 *Mesembryanthemum* species, grouping them in 69 sections but with the

FIG. 1. Worldwide distribution of Mesembryanthemaceae.

exception of one (Hymenogyne), he never validly published section names. Salm-Reifferscheid-Dyck (1836–63) later compiled a collection of paintings and Latin descriptions upon which some subsequent researchers based their work (Berger, 1908). Succulents tend to make poor herbarium specimens and many paintings of specimens grown under glass at low light levels in northern hemisphere conditions are often also poor sources of information. Thus types of these plants are often atypical for the taxon they represent.

Much later N.E. Brown (1925) initiated the more meaningful fragmentation of the supergenus *Mesembryanthemum* and was joined by G. Schwantes (1947), who provided the first classification of the group, and L. Bolus, who concentrated on descriptions of new taxa (1445 new species between 1928 and 1958, Chesselet *et al.*, 1995). These three prominent taxonomists worked on the group at the same time and often duplicated each other's work. The aftermath of this is still being unravelled to this day.

Hartmann (1988) has since contributed to the knowledge of the group by concentrating on fruit characters. This, however, has produced artificial groupings brought to light by molecular work done by Klak *et al.* (2003a) on the Lampranthus Group in the subfamily Ruschioideae. More recently Chesselet *et al.* (2002) have emphasized the importance of flower morphology (especially nectaries), however, more recent molecular data of Klak *et al.* (2003b) did not support the division of the 'core' Ruschioideae into the tribes Delospermeae (lophomorphic meronectary) and Ruschieae (lophomorphic holonectary) by Chesselet *et al.* (2002).

Molecular studies, however, have only included a few taxa and much work remains to be done on this group. Resolution of recent phylogenetic trees (Reeves *et al.*, 2003) is not good for the core Ruschioideae (Tribe Ruschieae). Molecular studies (Klak *et al.*, 2003b) are largely congruent to phylogenetic trees suggested by Bittrich & Struck (1989) and Bittrich (1990) based on morphological data. The recent diversification of this group of plants (Ihlenfeldt, 1994; Klak *et al.*, 2003b, 2004) may also be the reason why resolution of phylogenetic trees is poor for tribe Ruschieae. Hybridization may also have contributed to speciation in the mesembs and poor resolution of some branches of phylogenetic trees may be a reflection of this.

Another distinct possibility is that the current placing of taxa is erroneous and genus concepts need to be sharpened with some genera possibly redefined. The expansion and re-examination of molecular data may be able to assist this process.

Even 250 years after the initial recognition of this group, a suprageneric classification has not yet been finalized. Only recently a more formal system has been published (Chesselet *et al.*, 2002; Klak *et al.*, 2003b). However, one of the genera (*Mestoklema*) described as having a lophomorphic meronectary upon which this system is based, has been found to possess lophomorphic holonectaries (Table 1). Further investigations would be enlightening.

In the most recent tome on this group (Hartmann, 2001a & b) there are a stunning number of entries of "unknown" or "uncertain", under the headings of ecology and distribution of the taxa. To solve this problem the Mesemb Mapping Project has been conceived (Burgoyne, 2003) but will not be discussed here.

1.1 The genus *Delosperma*

The genus *Delosperma* reflects the history of the Mesembryanthemaceae in many ways. This predominantly summer rainfall genus was established by N.E. Brown (1925) as a result of the fragmentation of the supergenus *Mesembryanthemum*. The genus description was later emended by Lavis. Three sections have been validly described (Lavis, 1966, 1967, 1969) but the genus has never been revised since its inception and is in desperate need of taxonomic attention (Chesselet *et al.*, 1995). Mary O'Connor-Fenton (née Lavis) attempted a revision but her death in 1992 prevented her from completing it.

There are about 150 species in the genus after taxa belonging to two other genera (*Corpuscularia* Schwantes and *Hartmanthus* S.A.Hammer) have been removed from it. Most occur in southern Africa, with a particular concentration of species in the Eastern Cape. The distribution extends northwards (Fig. 2) to Zimbabwe (*D. mahonii* N.E.Br., *D. steytlerae* L.Bolus), East Africa [*D. nakurense* (Engl.) Herre, *D. oehleri* (Engl.) Herre], Ethiopia and Eritrea (*D. abyssinicum* Schwantes, *D. schimperi* (Engl.) H.E.K.Hartmann & I.Niesler) and Yemen (*D. harazianum* (Deflers) Poppend. & Ihlenf.)] with two species confined to Madagascar (*D. bosseranum* Marais) and Réunion (*D. napiforme* Schwantes).

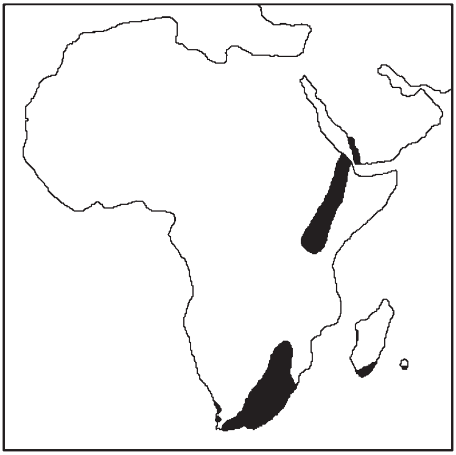

FIG. 2. Distribution of *Delosperma*.

1.2 What defines *Delosperma*?

The absence of covering membranes in the fruit give this genus its name, derived from the Greek words delos (visible) and sperma (seed). However, this is not the only genus with this character as it is shared by *Ectotropis* N.E.Br. and *Trichodiadema* Schwantes.

Establishing the genus *Delosperma*, N.E.Br. (1925), used the following characters to define it: "Perennials; leaves sessile, lanceolate or linear-lanceolate; stigmas and cells of the ovary and fruit 5; capsule with the expanding keels of the valves with membranous marginal wings at their apical part; cells open, no tubercles". Many more characters have been omitted and the following notes show the diversity of this genus.

The plants are perennials and are upright (*D. gratiae* L.Bolus), procumbent (*D. calitzdorpense* L.Bolus) or prostrate [*D. tradescantioides* (A.Berger) L.Bolus], some are even cremophilous, hanging over the edges of cliffs (*D. knox-daviesii* Lavis). They vary from woody (*D. crassum* L.Bolus) to almost herbaceous (*D. karooicum* L.Bolus) and some even boast thick, succulent root systems [*D. sutherlandii* (Hook.f.) N.E.Br.], while others have fine roots or even root at the nodes [*D. lebomboense* (L.Bolus) Lavis]. Leaves are sessile and vary from lanceolate (*D. jansei* N.E.Br.) to ovate (*D. tradescantioides*) or even terete [*D. klinghardtianum* (Dinter) Schwantes], the surfaces finely papillate or sometimes with papillae modified to form hairs. Flowers are solitary or borne in many-flowered cymes. Flower colour varies from pure white, cream, yellow, orange to various shades of pink and even red. Flower size varies greatly and may reach 4 cm in diameter (*D. sutherlandii*). Staminodes are usually present and nectaries are separate (lophomorphic meronectary, Chesselet *et al.*, 2002) but one recent collection had a distinct holonectary (*Burgoyne* 9677, PRE). Capsules, as previously mentioned, are without covering membranes, but the membranes are sometimes reduced to a ledge (Fig. 3). Other capsule characters include prominent valve wings, diverging expanding keels and the absence of a closing body.

1.3 Affinities

Hartmann (1998) proposed informal groups not intended to represent a phylogeny. These included the *Delosperma* Group comprising the genera *Corpuscularia*, *Delosperma* s.str., *Drosanthemum* Schwantes, *Ectotropis*, *Gibbaeum* N.E.Br., *Imitaria* N.E.Br. (now included in *Gibbaeum*), *Lampranthus* N.E.Br. p.p., *Malephora* N.E.Br., *Mestoklema* N.E.Br. ex Glen, *Muiria* N.E.Br. (included in *Gibbaeum* by Thiede & Klak in Goldblatt & Manning, 2000), *Oscularia* Schwantes and *Trichodiadema*. Of the above, only four genera are closely allied to *Delosperma*: *Drosanthemum*, *Ectotropis*, *Mestoklema* and *Trichodiadema* (*Delosperma* Group, Hartmann 1991; with members where bladder cells are absent removed). Table 1 compares characters of the five related genera. Although once included in the genus *Delosperma*, *Corpuscularia* is sufficiently different (epidermis) to be excluded here. *Hartmanthus* also at one time member of *Delosperma*, has closer ties with members of the *Dracophilus* Dinter & Schwantes group (Hartmann, 1998).

A few *Delosperma* species have been described with no localities given. This makes unravelling their identity especially difficult. They are**:** *D. aereum* (L.Bolus) L.Bolus, *D. affine* Lavis, *D. burtoniae* L.Bolus, *D. cronemeyerianum* (A.Berger) H.Jacobsen, *D. erectum* L.Bolus, *D. imbricatum* L.Bolus, *D. incomptum* (Haw.) L.Bolus, *D. invalidum* (N.E.Br.) H.E.K.Hartmann, *D. lineare* L.Bolus, *D. luckhoffii* L.Bolus, *D. monanthemum* Lavis, *D. pallidum* L.Bolus, *D. subpetiolatum* L.Bolus, *D. testaceum* (Haw.) Schwantes and *D. vinaceum* (L.Bolus) L.Bolus. Only through extensive collecting and field work will these species be adequately matched to specimens and localities, so that their true nature and extent of occurrence can be known.

TABLE 1. Comparison of characters for five delospermaceous genera.

	Delosperma	***Drosanthemum***	***Ectotropis*◆**	***Mestoklema***	***Trichodiadema***
Special characteristics	Covering membrane reduced to a ledge or absent	Internodes with elongated bladder cells – prominent on the peduncles	Tiny flowers, fragile tiny capsules	Huge tuberous roots, stems smooth, flowers the smallest in family borne in rich cymes	Characterized by diadems on the leaf-tips*
Growth form	Perennial herbs with soft, succulent leaves	Perennial herbs, upright or mat-forming	Mat-forming, leaves flattish	Stems woody, smooth, shrubby appearance	Perennial herbs, upright or mat-forming
Bladder cells of leaves	level with epidermis/ specialized to form hairs	glassy, resembling a coating of fine sugar	level with epidermis, leaves smooth	very tiny, glassy, dull	specialized with a glaucous, waxy appearance
Flowers	single or in cymes	single	single	tiny, in huge extended cymes	single
Staminodes	present or absent	present or absent	absent	present	forming a central cone with stamens
Nectaries	separate	separate	separate	forming a crenulate ring or separate	5–8, separate
Capsules no. of locules	5	5 (6)	4 (5)	5	5/6
Closing bodies	absent	present	absent?	absent	present or absent#
Valve wings	broad	broad	absent	broad to narrow	broad
Covering membranes	absent or reduced to a ledge	prominent	absent or reduced to a ledge	prominent or reduced	absent or reduced to a ledge

◆ Since preparation of this manuscript *Ectotropis* has been sunk as a *Delosperma* species (Hammer & Dold 2002)

* These may have different forms from only a few specialized hair-like cells to a full diadem.

\# The typical form (Schedule A) has no closing bodies (Niesler 1997).

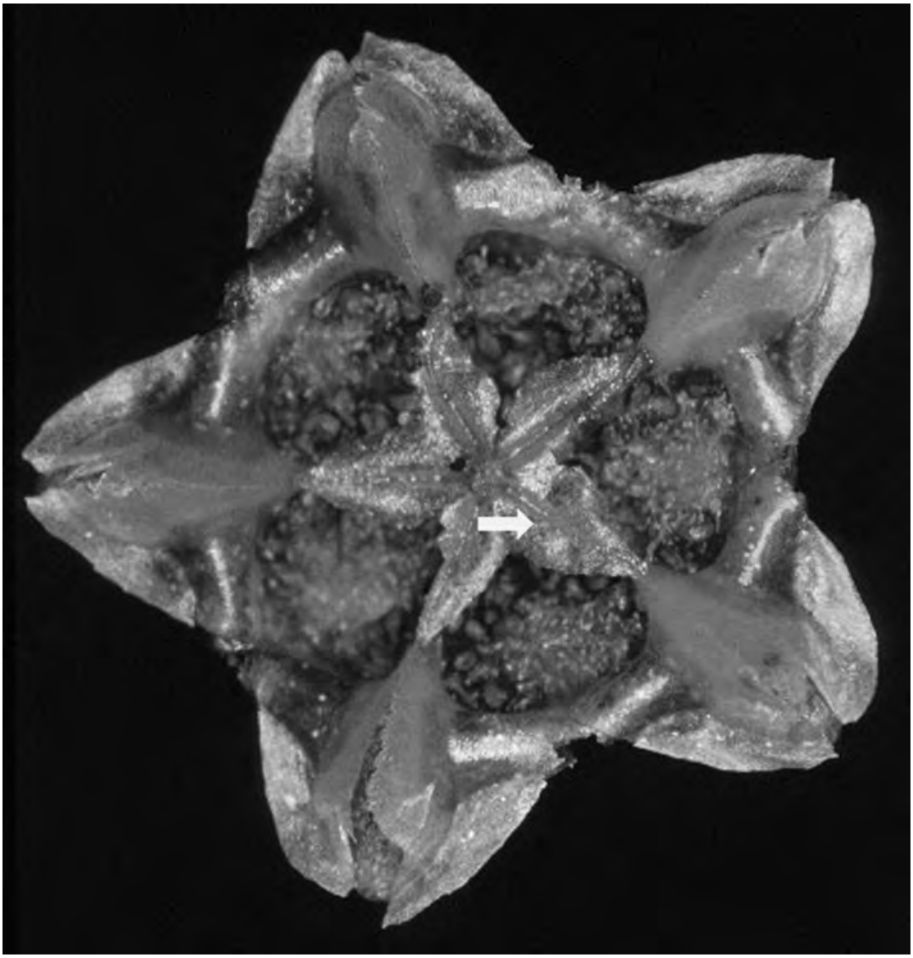

FIG. 3. Capsule of *Delosperma floribundum* [*Burgoyne* 8502 *(PRE)*, arrow indicates covering membranes].

1.4 *Delosperma* …or are they?

Table 2 shows some taxa that have been shuttled between closely related genera. From this we can gather that the experts had difficulty in determining which genus these species belonged to.

2 Progress at the National Herbarium (PRE)

After visiting the Herbarium at Kew and examining *Delosperma* type specimens there, it was found that most of the *Delosperma* species at PRE had been incorrectly identified. Types were requested on loan from the Bolus Herbarium, compared to PRE material and the identity of PRE specimens corrected where necessary. Data from PRE suggest that most species have not been sufficiently collected and some are known only from the type locality. The Red List status of many species is also not known with many species listed as Data Deficient (Burgoyne & Victor, 2003). With *Delosperma* being

TABLE 2. Old and new names of some delospermaceous taxa.

Old name	**New name**
Delosperma asperulum (Salm-Dyck) L.Bolus	***Drosanthemum asperulum*** (Salm-Dyck) Schwantes
Delosperma pubipetalum (L.Bolus) L.Bolus	***Drosanthemum papillatum*** L.Bolus
Delosperma expersum (N.E.Br.) L.Bolus	***Drosanthemum expersum*** (N.E.Br.) Schwantes
Delosperma grandiflorum L.Bolus	***Drosanthemum longipes*** (L.Bolus) H.E.K.Hartmann
Delosperma longipes L.Bolus	***Drosanthemum longipes*** (L.Bolus) H.E.K.Hartmann
Mestoklema macrorhizum (DC.) Schwantes	***Delosperma napiforme*** (N.E.Br.) Schwantes
Mestoklema napiforme N.E.Br.	***Delosperma napiforme*** (N.E.Br.) Schwantes
Delosperma tuberosum (L.) Schwantes	***Mestoklema tuberosum***(L.) N.E.Br. ex Glen
Trichodiadema inornatum L.Bolus	***Drosanthemum inornatum*** (L.Bolus) L.Bolus
Trichodiadema tenue L.Bolus	***Delosperma neethlingiae*** (L.Bolus) Schwantes
Trichodiadema schimperi (Engl.) Herre	***Delosperma schimperi*** (Engl.) H.E.K.Hartmann

predominantly a grassland genus, it is difficult locating small succulent herbs in vast tracts of grassland. This has resulted in poor distribution records, exacerbated by the tendency of succulents to make poor herbarium specimens. The problem of poor succulent herbarium specimens has, however, been solved (Burgoyne & Smith, 1998) and the production of high quality specimens is now possible.

3 Conclusion

It is suspected that with a better understanding of this genus gained from field observations, many of the names now being used will prove to be synonyms of existing species. Some field observations have already proved this (Burgoyne & Victor, 2003). With ample collecting and careful study of all characters (especially flower morphology) the true nature of this genus may be revealed. Eco-versatility must be taken into account as the variability of key visible characters within the species often exceeds that between species, depending on the habitat.

4 Acknowledgements

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SPECIES CONCEPTS IN *CEROPEGIA* L. (APOCYNACEAE – CEROPEGIEAE): A CASE EXAMPLE OF *CEROPEGIA ARISTOLOCHIOIDES* DECNE.

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Abstract

In the genus *Ceropegia* L. *(Apocynaceae: Asclepiadoideae – Ceropegieae),* many species or species complexes, among them *C. aristolochioides* Decne. (African, Arabian), are widely variable and widely distributed. The high variability within and among species and the wide distributions often accompanied by few collections pose problems in species delimitation, thus resulting in often widely differing species concepts. An earlier study based on morphological and RAPD analysis showed that East African *C. seticorona* E.A.Bruce and *C. aristolochioides* should be treated as one species with only two subspecies, one African, with glabrous carpels (subsp. *aristolochioides*) and one Arabian, with pubescent carpels (subsp. *deflersiana*). In the present study, additional morphological and distribution data as well as investigations on the recently described Ethiopian, *C. erergotana* M.G.Gilbert and *C. burgeri* M.G.Gilbert show that the two new species fall within the variation of subsp. *aristolochioides.* The best translation of the complex results into a formal classification lies in the adoption of a broad species concept. It gives a realistic representation of the biological species, because it may be assumed that natural interbreeding takes place between the variants and morphotypes, which may easily pass as distinct taxa when viewed in isolation.

Résumé

Concepts d'espèces chez *Ceropegia* L. (Apocynaceae – Ceropegieae): cas de *Ceropegia aristolochioides* Decne. Au sein du genre *Ceropegia* L. (Apocynaceae: Asclepiadoideae – Ceropegieae), beaucoup d'espèces ou de complexes d'espèces, parmi eux *C. aristolochioides* Decne. (Afrique, Arabie), sont extrêmement variables et largement distribués. La grande variabilité au sein et entre espèces, ainsi que les distributions étendues mais illustrées par un petit nombre de récoltes, posent des problèmes pour la délimitation des espèces et ont pour résultat la définition de complexes d'espèces souvent très différents. Une étude préalable, basée sur l'analyse morphologique et RAPD, a montré que *C. seticorona* E.A.Bruce et *C. aristolochioides* d'Afrique de l'est, pouvaient être traitées comme une seule espèce comprenant seulement deux sous-espèces: la première, africaine, avec des carpelles glabres (subsp. *aristolochioides*) et l'autre, arabe, avec des carpelles pubescents (subsp. *deflersiana*). Pour la présente étude, des données additionnelles concernant la morphologie et la distribution ainsi que des recherches sur *C. erergotana* M.G.Gilbert et *C. burgeri*

M.G.Gilbert, récemment décrits d'Ethiopie, montrent que les deux nouvelles espèces tombent dans la variation de la subsp. *aristolochioides*. La meilleure traduction des résultats complexes en une classification formelle conduit à l'adoption d'un large concept d'espèces. Il donne une représentation réaliste de l'espèce biologique car on peut supposer que l'hybridation naturelle se produit entre les variants et les morphotypes, qui peuvent facilement être assimilés à des taxons distincts lorsqu'ils sont observés isolément.

Key words: Africa, Arabia, *Ceropegia aristolochioides,* distribution, species concept, taxonomy.

1 Introduction

The genus *Ceropegia* L. *(Apocynaceae: Asclepiadoideae – Ceropegieae)* constitutes ± 180 species distributed in the Old World tropics and subtropics. Many species or species complexes, among them *C. aristolochioides* Decne s.l., *C. distincta* N.E.Br. – *C. haygarthii* Schltr.*, C. variegata* Decne.*, C. stenoloba* Hochst. ex Chiov.*, C. carnosa* E.Mey. – *C. racemosa* N.E.Br.*,* and *C. linearis* E.Mey., are widely variable and widely distributed in tropical Africa with some of them extending to Arabia and Madagascar. Such taxa often pose taxonomic problems on the delimitation of species and infraspecific taxa because the variation is difficult to interpret. In the end, numerous taxa of different ranks are recognized due to the often widely differing species concepts among various workers. *Ceropegia aristolochioides* Decne. is a variable and a widely distributed species that is known from Saudi Arabia and North Yemen to Ethiopia, Sudan and Kenya and westwards across tropical Africa to Senegal (Bruyns, 1988; Masinde, 2000; Meve *et al.*, 2001; Meve, 2002). Meve *et al.* (2001) investigated the *C. aristolochioides* complex using morphological and molecular methods and concluded that the well known East African *C. seticorona* E.A.Bruce should be treated as a synonym of *C. aristolochioides*, and that only two subspecies, an African one with glabrous carpels (subsp. *aristolochioides*) and an Arabian one with pubescent carpels (subsp. *deflersiana*) should be recognized. In the same study, it was also concluded that the many variants or morphotypes in eastern Africa that have usually been recognized as species, subspecies or varieties should be relegated to synonyms of subspecies *aristolochioides*. Gilbert (2002) published two new species from Ethiopia, namely *C. erergotana* M.G.Gilbert and *C. burgeri* M.G.Gilbert after the treatment by Meve *et al.* (2001). There is still controversy over the circumscription and classification of the complex. In the present study, further material of *C. aristolochioides* was examined, including that of the new taxa.

2 Materials and methods

All *C. aristolochioides* s.l. specimens at BM, EA, ETH, and K, constituting about 150 specimens, were investigated. Field observations in Kenya as well as investigations of plants in cultivation mostly from Kenya and Arabia were also used. The distribution maps were generated from grid references of herbarium specimens and supplemented by a few *C. aristolochioides* subsp. *deflersiana* specimen citations in Bruyns (1988) for the Arabian Peninsula. In the earlier study (Meve *et al.*, 2001) sampling was mostly in East Africa (Kenya and Tanzania) and Arabia (Saudi Arabia and Yemen). In the present study, increased sampling for carpel characters over the entire geographical range, especially for areas that were previously not sampled, was carried out.

3 Results and discussion

The distribution map for the variants/morphotypes of the *C. aristolochioides* complex shows that there is no geographical pattern as the variants/morphotypes occur sporadically (Fig. 1). This is particularly so in East Africa (central to southern Kenya and northern Tanzania) where nearly all the corolla and corona forms that occur elsewhere, including Arabia, are found. It is only carpel pubescence that reliably separates out the groups and this separation correlates with a geographic pattern (Fig. 2). In the present investigation, corresponding to Meve *et al.* (2001), pubescent carpels have only been found in specimens from the Arabian Peninsula and glabrous ones in specimens from the African continent (Table 1). The island of Socotra is an interesting geographical area as it appears to be a transition zone with an intermediate population with regard to carpel pubescence. A single specimen, *Balfour* 641 (K), collected on Socotra in c. 1880, has only a few hairs at the apex of the carpels but the corolla displays the long slender tubular form with narrow short triangular corolla lobes and thus matches similar forms commonly encountered in north Yemen and occasionally in East Africa.

Corolla morphology provides the most variable characters. All the various parts of the corolla, such as the corolla tube length, diameter and inflation, coloration pattern, corolla lobe shape, size and indumentum, distribution of hairs and colour pattern on the interior of the corolla, are quite variable and sporadically occur across what used to be regarded as distinct species and also across a wide range of geographical regions (cf. Fig. 1). Thus, for example, the long and narrow yellow corolla with narrow corolla lobes ending in a beak-like structure is found in Yemen and East Africa. In East Africa,

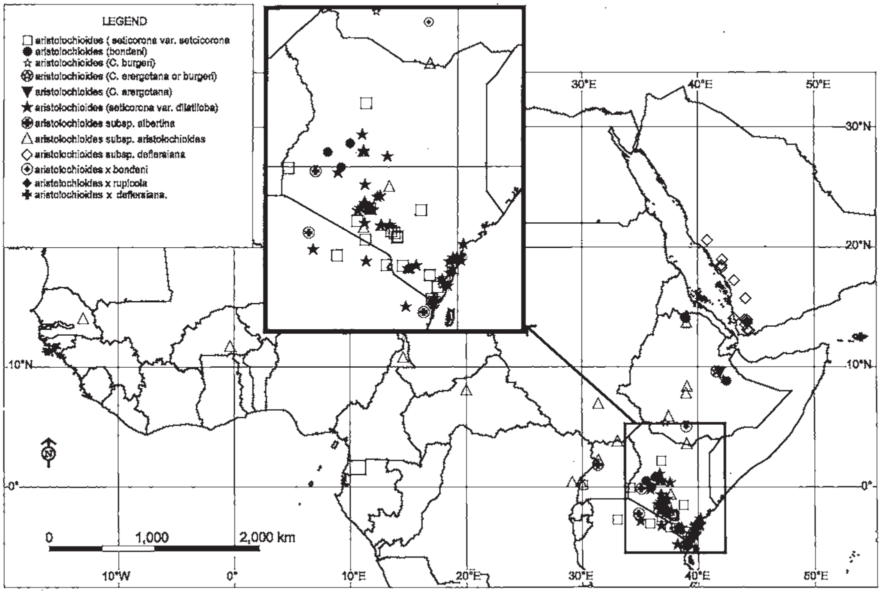

FIG. 1. Distribution of variants/morphotypes in the *C. aristolochioides* complex ("C. bondeni" it is not a validly published name, it has been introduced by Masinde (2000) to describe a significant morphotype).

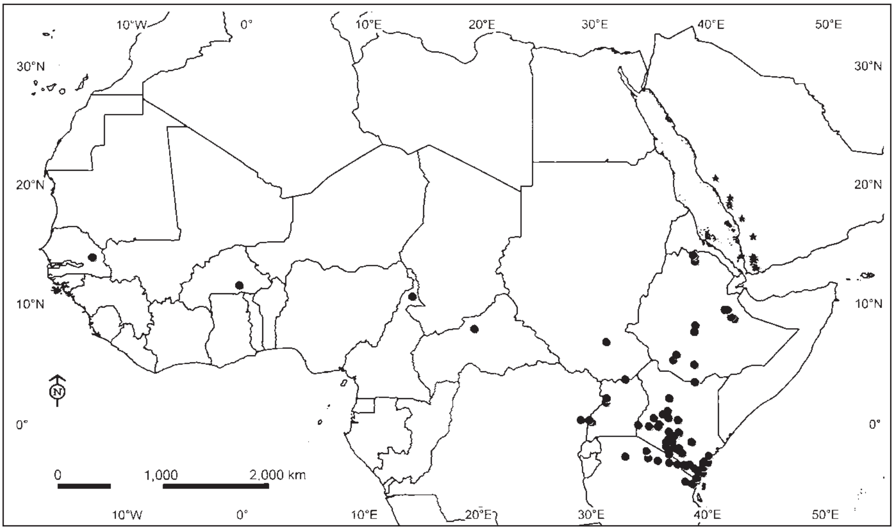

FIG. 2. Distribution of *C. aristolochioides* subsp. *aristolochioides* and subsp. *deflersiana* (★).

these forms were formally regarded as *C. seticorona* var. *seticorona* whereas in Arabia, they were treated as *C. aristolochioides* subsp. *deflersiana.* In earlier investigations based on the analysis of Randomly Amplified Polymorphic DNAs (RAPD) it was shown that corolla morphology, though most conspicuous, provides unreliable characters for sorting out the taxonomy of *C. aristolochioides* complex (Meve *et al.*, 2001). Specimens with very similar corolla morphology and colour such as the yellow forms in Arabia and East Africa clearly separated into two different clades thus showing clear genetic divergence; whereas specimens with highly dissimilar corollas such as the yellow form in East Africa (*C. seticorona* var. *seticorona*) and the typical *C. aristolochioides* subsp. *aristolochioides,* showed hardly any genetic divergence and clustered in the African clade.

The main characters used to distinguish *C. erergotana* and *C. burgeri* from *C. aristolochioides* and '*C. seticorona'* are the corolla morphology, indumentum and color patterns. Specimens with slender corolla tubes and short corolla lobes are also found in north Yemen (cf. ill. in Bruyns, 1988). The only minor difference is that the Yemeni specimens do not have a rounded corolla cage. Many-flowered and branched inflorescences are found in Arabian specimens [e.g. *Collenette* 7762 (K, also observed in cultivation)], in East Africa [e.g. *Masinde* 684 & 813 (EA, K, also observed in cultivation)] and in West Africa [e.g. *Madsen* 5961 (K)]. Specimens with pubescent corolla exteriors are found in Kenya as well as those with a similar corolla form as *C. erergotana.* It is therefore apparent that most corolla features tend to occur sporadically especially in eastern Africa. In Gilbert (2002, 2003), *Gilbert & Thulin* 65 (K), which is *C. erergotana,* is cited twice, under *C. erergotana* and erroneously under *C. burgeri.*

It is here concluded that *C. erergotana* and *C. burgeri* should be treated as synonyms of *C. aristolochioides* subsp. *aristolochioides.* The broad species concept adopted with respect to the *C. aristolochioides* complex gives the best formal classification, as it reflects a realistic representation of the biological species where the variants and/or morphotypes are assumed to interbreed but when viewed in isolation they may easily be confused and considered distinct taxa.

TABLE 1. Representative specimens examined for carpel pubescence and their morphotypic affiliation. Specimens with pubescent carpels are marked with an asterisk (*). Definitions of morphotypes are as in Meve *et al.* (2001).

Origin	**Voucher**	**Morphotypic affiliation**
ARABIA		
Saudi Arabia: Wadi Sakhanah	**Collenette* 7762 (K)	ssp. *deflersiana* (fls large, spotted brown)
Saudi Arabia: Wadi Al Uss	**Collenette* 2111 (K)	ssp. *deflersiana* (fls large, spotted brown)
Yemen (N): Khawlan As Sham	**Wood* 3044 (K)	ssp. *deflersiana* (fls slender, yellowish)
Yemen (N): Taiz	**Wood* 2979 (K)	ssp. *deflersiana* (fls slender, yellowish)
Yemen (N): Jebel Raymah	**Wood* 849 (K)	ssp. *deflersiana* (fls slender, yellowish)
Yemen: Socotra Island	**Balfour* 641 (K), sparse hairs	ssp. *aristolochioides* **?** *deflersiana*? (fls slender, brownish)
AFRICA		
Eritrea: Mereb Valley	*Gilbert & Getachew* 2744 (K, ETH)	ssp. *aristolochioides* (fls large, spotted brown)
Ethiopia: near Arba Minch	*Gilbert & Thulin* 324 (K, ETH)	ssp. *aristolochioides* (fls large, spotted brown)
Ethiopia: Erer, Dire Dawa road	*Gilbert & Thulin* 65 (K)	*C. erergotana* (corolla exterior pubescent)
Ethiopia: no locality	*Gilbert* 7461 (K)	*C. erergotana* (corolla exterior pubescent)
Ethiopia: 23 km Konso–Jinka	*Gilbert & Phillips* 8898 (K)	*C. burgeri* (fls slender, cage small rounded)
Ethiopia: 6 km Konso–Arba Minch	*Gilbert & Phillips* 9138 (K)	*C. burgeri* (fls slender, cage small rounded)
Kenya: Hunters Lodge	*Masinde* 809 (EA, K)	ssp. *aristolochioides* (fls slender, often 2 corolla cages)
Uganda: Butiaba Plain	*Bagshawe* 848 (BM)	ssp. *albertina* (fls slender, long triangular corolla lobes)
Sudan: Nyany Camp	*Lock* 81/142 (K)	ssp. *aristolochioides* (fls large, cage broad)
Cameroon: near Bogo nr Maroua	*Letouzey* 6463 (K)	ssp. *aristolochioides* (fls large, spotted brown)
Burkina Faso: near Tenkodogo	*Madsen* 5961 (K)	ssp. *aristolochioides* (fls large, spotted brown)

3.1 Taxonomy

Key to subspecies of *Ceropegia aristolochioides*

Carpels glabrous . . . . subsp. *aristolochioides*
Carpels hairy . . . . subsp. *deflersiana*

Ceropegia aristolochioides Decne., Ann. Sc. Nat. 9: 263 (1838). Type: Senegal, 1837, *Heudelot* 477 (P, holo; G, iso; K, photo. & pencil ill.!).

Ceropegia aristolochioides Decne. subsp. ***aristolochioides***

C. beccariana Martelli, Florula Bogos 56 (1886); N.E. Br. in Dyer, Fl. Trop. Afr. 4(1): 446 (1903); Werdermann, Bot. Jahrb. Syst. 70: 222 (1939).
C. perrottetii N.E.Br. in Bull. Misc. Inf. Kew 1898: 308 et in Dyer, Fl. Trop. Afr. 4(1): 448 (1903).
C. albertina S.Moore in J. Bot. 45: 51 (1907); Werdermann, Bot. Jahrb. Syst. 70: 222 (1939).
C. aristolochioides Decne. subsp. *albertina* (S. Moore) H. Huber in Mem. Soc. Brot. 12: 92 (1958).
C. crassula Schltr. in Bot. Jahrb. Syst. 51: 152 (1913).
C. aristolochioides var. *wittei* Staner in Bull. Jard. Bot. Etat 15: 237 (1938).
C. seticorona E.A.Bruce, Cact. Succ. J. (US) 13(11): 181 (1941); P.R.O. Bally in Candollea 20: 13–41 (1965) et in Fl. Pl. Afr. 41: t. 1616A & B (1970); Archer in Kenya *Ceropegia* Scrapbook: XXII (1992); Masinde in Cact. Succ. J. (Los Angeles) 6: 107–114 (1998 publ. 1999).
C. seticorona E.A.Bruce var. *dilatiloba* P.R.O.Bally in Candollea 20: 24 (1965).
C. volubilis N.E.Br. var. *crassicaulis* H.Huber in Mem. Soc. Brot. 12: 200 (1958), nomen superfl.
C. maasairum J.J.Halda & B.Prokes, Cactaceae etc. 2(43):43–45 (2000).
C. erergotana M.G.Gilbert in Nord. J. Bot. 22(2): 205–210 (2002 publ. 2003) et in Fl. Ethiopia & Eritrea 4(1): 164 (2003), **syn. nov.**
C. burgeri M.G.Gilbert in Nord. J. Bot. 22(2): 205–210 (2002 publ. 2003) et in Fl. Ethiopia & Eritrea 4(1): 165 (2003), **syn. nov.**
C. baringii P.R.O.Bally *in sched.* [Kenya, Lukenya, 9 Sept. 1954, *Bally* 9891 (K!, G)].

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FLORA OF TROPICAL EAST AFRICA: QUANTITATIVE ANALYSIS OF THE FLORA AND ITS CONSERVATION

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Abstract

Quantitative analysis of the flora of tropical East Africa (taken here to include Uganda, Kenya and Tanzania) shows about 12,154 species of vascular plants in 254 families and 2110 genera. The majority of the families have fewer than 100 species, but there are 7 with more than 500 species, and Leguminosae, if treated as a single family with more than 1000 species. The most species-rich areas lie in the eastern and southern parts of the region. There are 51 genera (in 20 families), and over 1200 species endemic to tropical East Africa with two subdivisions in Tanzania, Tanga and Eastern, containing the highest number of endemic genera. These are followed by the Coastal subdivision of Kenya, the Southern Highlands and Southern and Northern subdivisions of Tanzania. There is a need for Nature Reserves in at least two areas that are regarded as centers of species-richness and endemism, and for Strict Nature Reserves to be designated for conservation and monitoring vegetation dynamics due to environmental changes.

Résumé

'Flora of Tropical East Africa': analyse quantitative de la flore et conservation. L'analyse quantitative de la flore d'Afrique orientale (considérée ici comme comprenant l'Ouganda, le Kenya et la Tanzanie) révèle environ 12.154 espèces de plantes vasculaires dans 254 familles et 2110 genres. La majorité des familles sont constituées de moins de 100 espèces mais sept comprennent plus de 500 espèces et les Leguminosae, si elles étaient traitées comme une seule famille, comprendraient plus de 1000 espèces. Les zones à richesse spécifique la plus élevée se situent dans les parties orientale et australe de la région. Cinquante-et-un genres (dans 20 familles) et environ 1200 espèces sont endémiques d'Afrique de l'est. En Tanzanie, les deux subdivisions Tanga et Eastern, contiennent le plus grand nombre de genres endémiques. Ils sont suivis par la subdivision 'Coastal' du Kenya, les 'Southern Highlands' et les subdivisions 'Southern' et 'Northern' de Tanzanie. Une nécessité de réserves naturelles se fait sentir, au moins dans deux régions considérées comme centres de richesse spécifique et d'endémisme, ainsi que de réserves naturelles strictes qui devraient être établies pour la conservation et pour suivre la dynamique de la végétation provoquée par les changements environnementaux.

Key words: East Africa, quantitative analysis, species richness, endemism, conservation

1 Introduction

The flora of tropical East Africa spreads over a highly diverse landscape and is extremely rich in species. The region of the flora taken here is that of Uganda, Kenya and Tanzania, and the flora as described in the taxonomic treatment of the publication (by families) of Flora of Tropical East Africa (Flora of Tropical East Africa 1952–, hereafter referred to as FTEA). In an area of approximately 1,766,500 km^2 that is tropical East Africa, over 12,000 species (>13,000 taxa) of vascular plants are present, with the Eastern Arc Mountains the tenth most species-rich area in the world both in overall natural and remaining natural vegetation (Brummitt & Lughadha, 2003)

In this paper we summarise the results of a quantitative analysis of the flora, analyse in detail the distribution of the species, and determine areas of high species diversity and endemism in tropical East Africa, and in the light of our results evaluate the significance of the existing national parks and conservation areas in this region.

Geomorphology

Although most of the geomorphological features of eastern Africa have developed over the last 200 million years the geological beginnings of this region lie in the Archaean systems (3800–2500 Mya) forming the central Nyanza Shield. This includes the exposed granites in central Tanzania, and the gneiss complex in northern Uganda. Major geological events that include sedimentation and folding of metamorphic rocks during late pre-Cambrian, erosion, incursion of sea into Gondwana (the present Indian Ocean), uplifting and downfaulting during the mid-Tertiary (30 million years Mya) which formed the central African plateau (including the Kenya highlands) and the Eastern and Western Rift Valleys and the Lake Victoria basin, the vulcanicity in the eastern rift which formed Mt Elgon, Mt Kenya, the Aberdare range, Mt Meru and Mt Kilimanjaro, and fluctuating sea levels up to 0.6 million years ago have resulted in the present land morphology of eastern Africa (Morgan, 1973).

Eastern tropical Africa is characterised by coastal plains that slope gently upwards away from the sea and are interrupted by a series of low hills. A chain of high mountains rise from the central and southern parts of the plains and form some of the highest mountains of the African continent (Kilimanjaro at 5895 m, Mt Kenya at 5169 m). The plains rise steeply at the western end to eventually reach the Central African Plateau which stretches from southern Kenya to Zimbabwe between 1000 m and 1500 m and lies between the two rift valleys. Lake Victoria lies in the northern part of this region. In the north-east of the Central Plateau, the lowlands of Lake Rudolf connect the Eastern Rift Valley in central Kenya with that of Ethiopia. In the floor of the Rift Valley several soda lakes are present as a result of inland draining. In the south and east of the Central Plateau lie the Southern Highlands and in the west the Ufipa plateau, the Usambara, Pare, Kilimanjaro, and Uluguru mountains are located. Uplift along the western margin of the Central Plateau reaches to form the Kigezi-Karagwe Highlands which in the south-west of Uganda includes a small portion of volcanic range associated with the western rift. Several large lakes lie west and south of the Western Rift Valley including Lake Albert, Lake Edward and Lake Tanganyika (the last being the world's second deepest lake with a maximum depth of 1426 m), as well as high mountains such as the Ruwenzori (5120 m) and Muhavura (Virunga Volcanoes).

2 Material and methods

Distribution data (by subdivisions based on colonial administrative units and as used in FTEA, referred to as subdivisions in this paper) were obtained from published literature (Flora of Tropical East Africa (FTEA), 1952–present), Families & Genera of Flowering Plants Database (Brummitt & Brummitt, in prep.); some data were also modified from the distribution database LEAP (List of East African Plants), developed by the East African Herbarium, National Museums of Kenya. Data were analysed variously including the use of Geographical Information System and the database of collection localities in East Africa. Land area was calculated by subtracting the water area (lakes) from total area; correlation for collecting localities was calculated as localities/1000 km^2. For calculating species richness we have excluded data for the two islands, Zanzibar and Pemba, as islands follow a different distribution pattern from the mainland. We did not think it was appropriate to correct our data for correlation of species richness and area, as without the two islands we did not see a linear relationship for our data ($R^2 = 0.033$) (see Fig. 10) (for large non-isolated sample areas the power function $S=cA^z$ is often used, with $z=0.12–0.14$ for correction of a species-area relationship; Rosenzweig, 1995).

3 Results

3.1 Floristics and species richness

A near total of 12,154 species (13,537 taxa) of vascular plants are recorded for tropical East Africa (Table 1, Fig. 3) with the flowering plants comprising approximately 48% of the total flowering plant taxa of tropical Africa (Lebrun & Stork, 1991–7). (These figures are by no means final as several plant families with over 200 species are yet to be treated for FTEA, which will invariably change the final number of known species there). Species recorded so far are distributed in 254 families (Leguminosae taken as single family; Asclepiadaceae included in Apocynaceae) and 2110 genera (Table 2). There are 22 families with more than 100 species, 9 with more than 300 species and 7 with more than 500 species (Tables 3, 4). Leguminosae, if treated as a single family is the only one with more than 1000 species. The majority of the families have fewer than 100 species and 75 families have 20 or more than 20 species. There are 128 families with 10 or fewer than 10 species, and 43 families with only a single species (see also Figs. 1, 2, 3).

In analyzing our data we have seen a low correlation between the number of collection localities (excluding Zanzibar and Pemba) and the number of species per Flora subdivisions ($R^2=0.4298$) (Fig. 4). The Tanga subdivision (T 3) of Tanzania has the most collection localities; for the other subdivisions the number of collections localities are more or less the same except for the Central (T 5) subdivision in Tanzania and the Northern Frontier (K 1) in Kenya where the collecting localities are fewer (Fig. 5). No significant correlation was seen between elevation and the number of species per subdivision ($R^2=0.1046$) (Fig. 6).

In terms of political boundaries, our data shows that Tanzania is the most species-rich with about 82% of the total species found there (Table 1; Figs. 7, 8). As our data on species richness is by subdivisions, we can separate four groups (Table 4; Figs. 7, 8). The most species-rich areas in tropical East Africa lie in the eastern and southern part of the region, whilst the northern and north western areas are relatively lower in diversity.

TABLE 1. Approximate number of species in each country in tropical East Africa (from Beentje *et al.*, 1994).

Country	**Estimated species**	**% total species**
Uganda	5400	44.4
Kenya	6500	53.5
Tanzania	>10,000	>82.3

TABLE 2. Composition of the vascular flora of tropical East Africa (see also Fig. 1). (The numbers of species of ferns and the flowering plants are approximate until the entire flora is described and updated).

	Families	**Genera**	**Species**	**% total species**
Fern & fern allies	31	110	595	4.9
Gymnosperms	3	4	13	0.1
Dicotyledons	179	1597	9071	74.6
Monocotyledons	39	408	2475	20.4
Total species 12,154				
Total taxa 13,537				

TABLE 3. Families with the highest number of species (>500 spp.) in tropical east Africa. (*938, FTEA Compositae I, II, III, 2000–2005)

Families	**No. of species**	**% total spp in tropical East Africa**	**% total spp in respective families in tropical Africa**
Leguminosae	1227	10.1	46.2
Compositae	± 886*	7.3	52.9
Gramineae	864	7.1	58.2
Rubiaceae	756	6.2	43.2
Orchidaceae	628	5.2	54.3
Euphorbiaceae	527	4.3	43.0
Acanthaceae	>500	c. 4.3	not known

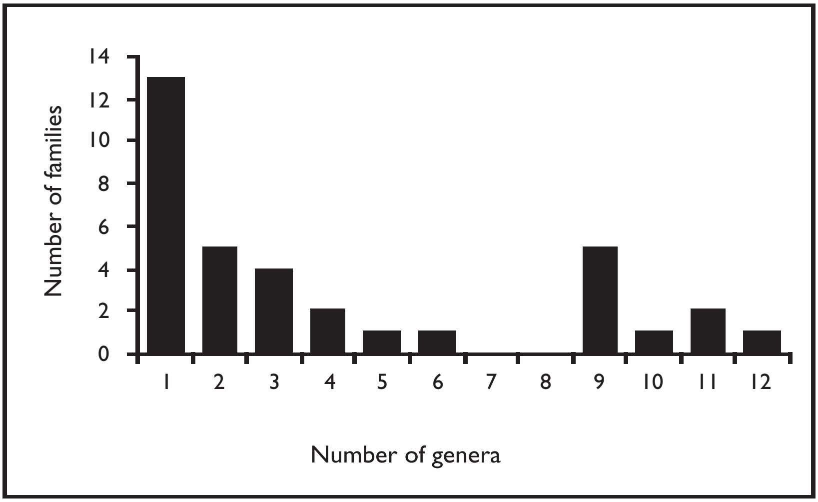

FIG. 1. Number of genera per family in the vascular cryptogams of tropical East Africa.

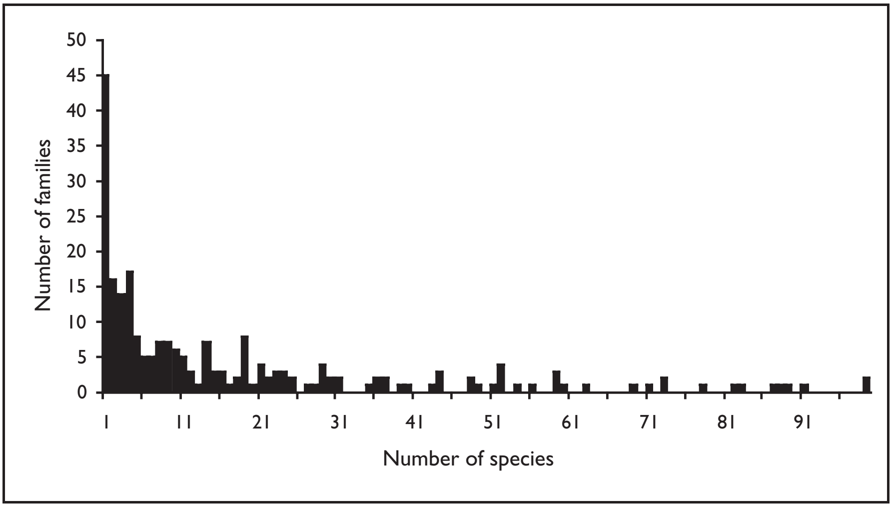

FIG. 2. Number of species per family with 100 or ⩽100 species.

TABLE 4. Number of species per country per province.

>4000 species	Tanzania: Southern Highlands (T7), Eastern Province (T6), Tanga Province (T3) Kenya: Rift Valley (K4), Central Province (K3)
3000–4000 species	Kenya: Coastal (K7), Masai (K6) Tanzania: Western (T4), Northern (T2), Southern (T8) Uganda: Western (U2)
2500–3000 species	Kenya: Nyanza (K5), Northern Frontier (K1) Tanzania: Lake (T1)
1000–2500 species	Uganda: Northern (U1), Buganda (U4), Eastern (U3) Kenya: Turkana (K2) Tanzania: Central (T5)
⩽1,000 species	Tanzania: Zanzibar, Pemba

* Recent surveys show the number of taxa in K7 to be >4000 (Luke, pers.com.)

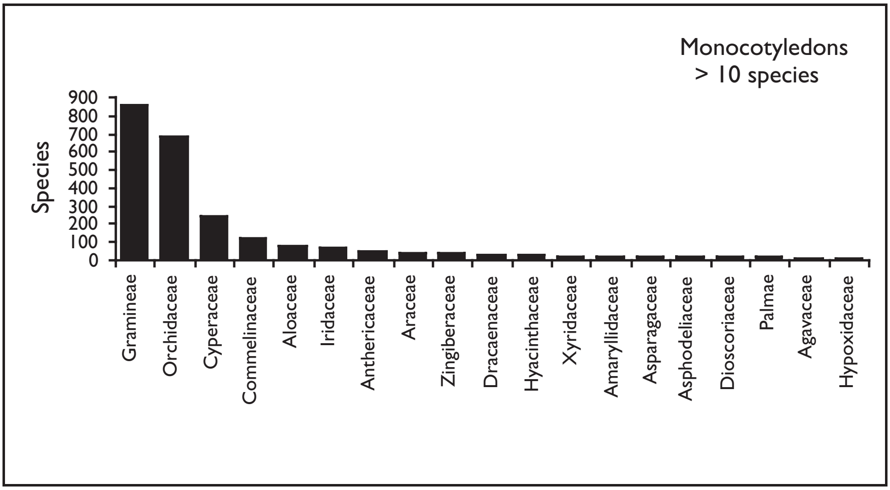

FIG. 3. Number of species per family in the monocotyledonous flora of tropical East Africa.

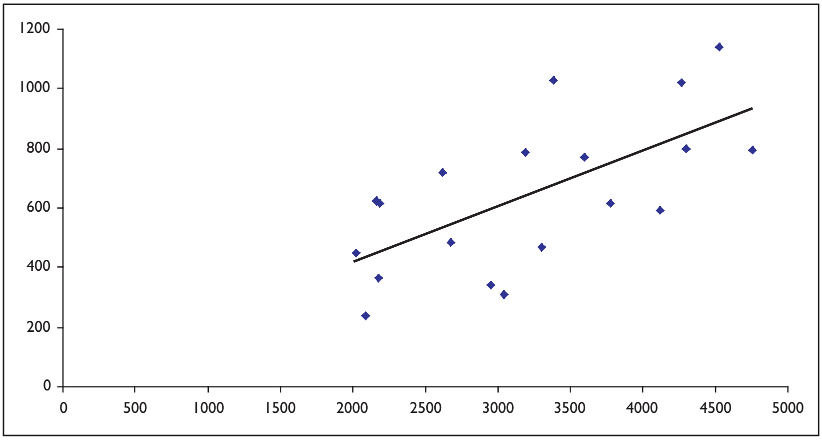

FIG. 4. Correlation of species richness and collection localities in tropical East Africa excluding Zanzibar and Pemba ($R^2 = 0.4298$)

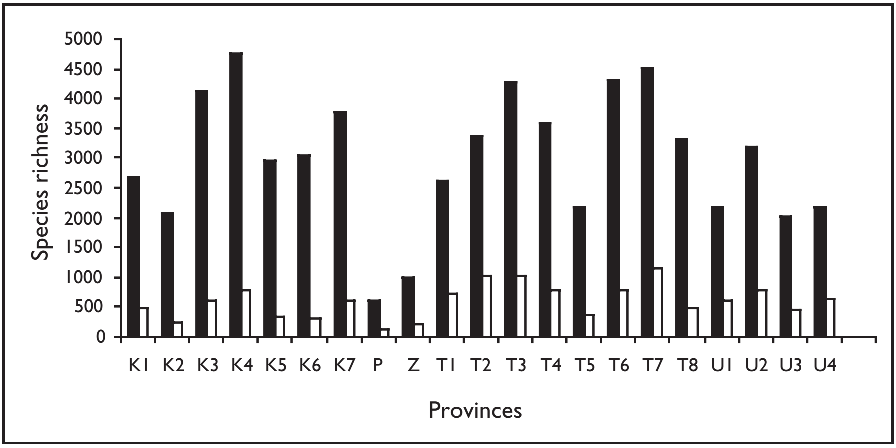

FIG. 5. Number of collection localities and species richness shown by FTEA subdivisions in tropical East Africa including Zanzibar and Pemba.

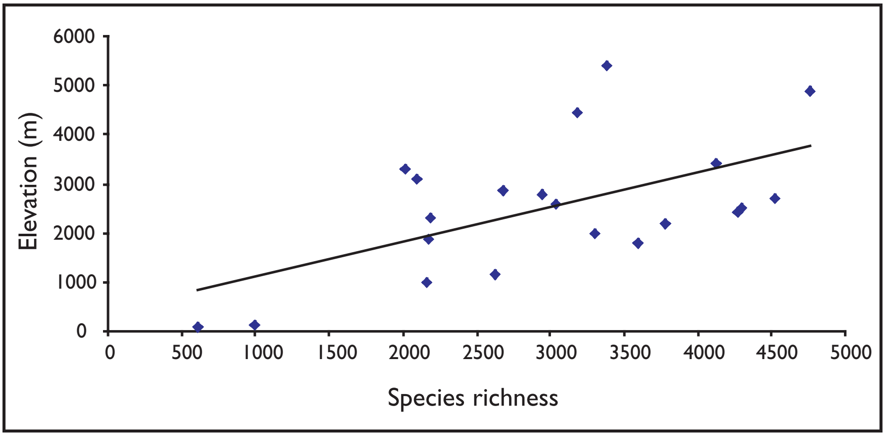

FIG. 6. Correlation of species number and elevation including Zanzibar and Pemba ($R^2 = 0.3384$).

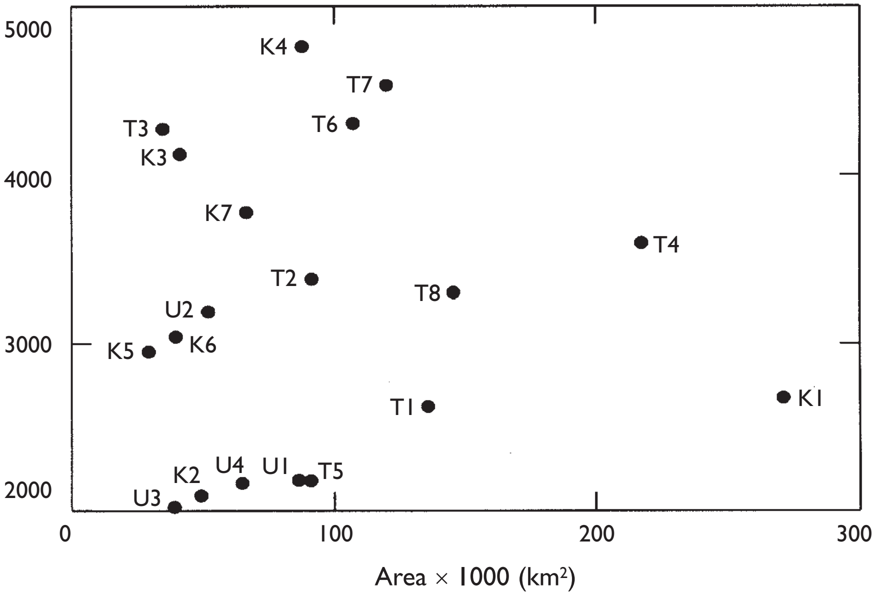

FIG. 7. Species richness by Flora subdivisions in tropical East Africa excluding islands. (For full names of FTEA subdivisions and districts see Appendix 1). Recent surveys show the number of taxa in K7 to be >4000 (Luke, pers.com.).

The eastern and southern regions include:

1. The Rift Valley and associated highlands, comprising four of the highest peaks in East Africa (Kilimanjaro, Mount Kenya, Mount Meru and Mount Elgon), and on the eastern margin of the highlands the more recent volcanic Chyulu and Nyambeni Hills. This region is a part of two phytochoria, the Somalia-Masai regional centre of endemism and the Afromontane Archipelago-like centre of endemism, both recognised for their high alpha diversity and endemism (Hedberg, 1951; White, 1983). Data on species distribution is not available for the whole region but relatively good data exist for Kilimanjaro, Mount Kenya, Mount Elgon and Mount Meru, the former three already listed as local centres of species richness (Beentje *et al.*, 1994) (Table 5).
2. The Eastern Plateau and the coastal hinterland, consisting of vast alluvial plains, and mountain blocks of pre-Cambrian crystalline, mostly metamorphic rocks, including the Mathews Range and Taita Hills in Kenya, and the Usambara, Pare, Uluguru, Nguru, Udzungwa and Mahenge mountains. Also included in this region are the Matumbi Hills and Rondo Plateau in Tanzania. As the Eastern Rift Valley, these regions are also floristically rich with high species diversity and endemism, and several locations in this region are listed as centres of species richness (Brenan, 1978; Lovett, 1993; Burgess & Clarke, 2000) (Table 5).

TABLE 5. Centres of species richness (from Beentje *et al.*, 1994).

Country	**Location (estimated no. of species/endemism)**
Uganda	Bwindi Forest (1000) – U2 Mount Elgon – U3 Ruwenzori Mountains (2000/25–30%) – U2
Kenya	Shimba Hills – K7 (above 1000/30%) Mount Kenya (800 above 2000 m/1.2%) – K4 Mount Elgon – K3 Taita Hills – K7
Tanzania	Itigi thicket – T5 Mahale-Karobwa Hills – T4 Msumbugwe – T3 Puge Hills & Kazimzumbi Forest Reserve – T6 Rondo Plateau (800/25%) – T8 East Usambara Mountains (1500) – T3 Eastern Arc Mts (above 3000/35%) – T3 Kitulo Plateau/Kipengere Mountains – T7

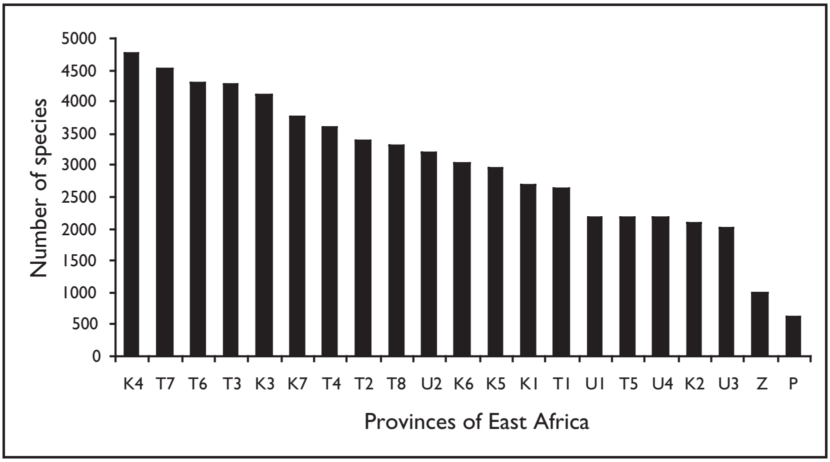

FIG. 8. Species richness by subdivisions in tropical East Africa. (For full names of FTEA subdivisions and districts in tropical East Africa see Appendix 1). Recent surveys show the number of species in K7 to be between 4000 and 4500.

TABLE 6. Endemism per country in tropical East Africa (from Beentje *et al.*, 1994).

Country	**Flowering plants**	**Gymnosperms and ferns**	**Number of endemics**	**% species endemism**
Uganda	5400	406	30	0.6
Kenya	6500	506	265	4.1
Tanzania	>10,000	data incomplete	1122	11.2

TABLE. 7. Local centres of endemism in coastal regions of East Africa (from Clarke *et al.*, 2000).

Area/region	**Endemic genera + near endemic genera/endemic species**
Rondo Forest	2+2/60
Kimboza Forest	2/16
E Usambara (below 400 m)	1/17
Lake Lutamba/Litipo	+1/16
Pugu-Kazimzumbwi Forest	1?/12
Shimba Hills	0/12
Selous Game Reserve	1?/46

3. The Nyasa Highlands, Ufipa Plateau and the Ruaha-Rukwa rift in Tanzania, consisting of a diverse geomorphological region with elevated peneplains reaching up to 2700 m, alluvial plains drained by the Ruaha river, inland drainage of Lake Rukwa and Mount Rungwe at the southern end of the Ruaha-Rukwa rift. Similar in species richness is the uplift along the western margin of the Central Plateau in Uganda which forms the volcanic Muhavura range, and the northerly range of the Western Rift Valley which includes the Ruwenzori, an equatorial mountain chain rising to 5120 m. The main vegetation type of this region falls under the Zambezian regional centre of endemism with several representative areas recognised as centres of species diversity (Beentje *et al.*, 1994; Linder, 1998), (Table 5).
4. The Tana Plains and NE Kenya are the third richest in alpha diversity with 2500 to 3000 species. The region is mainly feature-less peneplains with mount Kulal, the Nyiru and Ndoto Mountains and Mt Marsabit in the north eastern part of this area. Most of the species diversity is found in the mountains (Lusigi *et al.,* 1986). The region falls in the Somalia-Masai regional centre of endemism with *Acacia-Commiphora* deciduous bushland and thicket and grassland as the main vegetation types. Limited data is available for this area, and certain locations are not well known botanically.
5. The least species-rich region on mainland East Africa, in our analysis, is the Ugandan plateau and the Lake Rudolf lowlands. The Turkana escarpment and Cherangani Highlands, and the Lake Victoria basin in Uganda and Tanzania are included in this region. Alpha diversity is between 1000 and 2500 species with grasslands and wooded grassland as the main vegetation types.

One of the main factors determining species diversity in East Africa is the presence/absence of forest. There is a correlation of forest vegetation with mountains which is derived from the presence of rain, relief and reduction in temperature. Most mountain areas of East Africa (e.g. Ruwenzori, Elgon, Aberdare, Kenya, Kilimanjaro, Usambara, Udzungwa) therefore contain forests or forest remnants. This, and the presence of specialised Afroalpine flora on certain mountains, has resulted in the alpha diversity of these regions. Below 1500 m, temperatures are higher, there is more rain, and forests become equatorial rainforests. This zone is prominent in Uganda, where it is heavily populated with much forest clearing and cultivation. With decreasing altitude, rainforest gives way to wooded grassland and grassland where species diversity is relatively lower.

3.2 Endemism

Data are still incomplete on the level of endemism in the three countries. However, published records show that in Uganda 0.6%, in Kenya 4.1%, and in Tanzania 11.2% of the total species are endemic (Table 6). There are 51 genera (in 20 families), and over 1200 species endemic to tropical East Africa (Beentje & Smith, 2001) (Figs. 9, 10). Two subdivisions in Tanzania, Tanga and Eastern have the highest number of endemic genera, followed by the Coastal subdivision of Kenya, and the Southern Highlands and Southern and Northern subdivisions of Tanzania; the Central and Masai in Kenya are next, followed by the Central subdivision of Tanzania. Tanzania is the richest in endemic genera, which are found throughout the country (including Zanzibar and Pemba). Kenya is second highest, whilst Uganda is least genera-rich with the Western and Northern subdivisions including 4 and 2 genera respectively. The poorest in generic endemism is the Nyanza subdivision of Kenya with a single genus. Endemism in the coastal forests of East Africa is discussed in detail by Clarke *et al.* (2000) (see also Table 7).

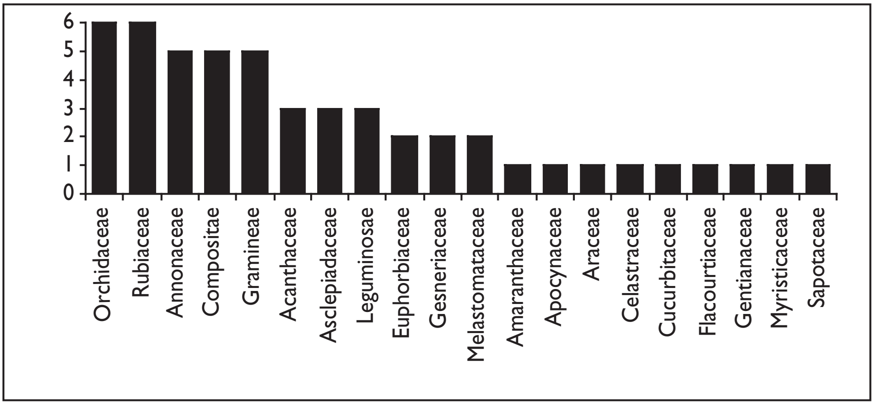

FIG. 9. Number of endemic genera per family.

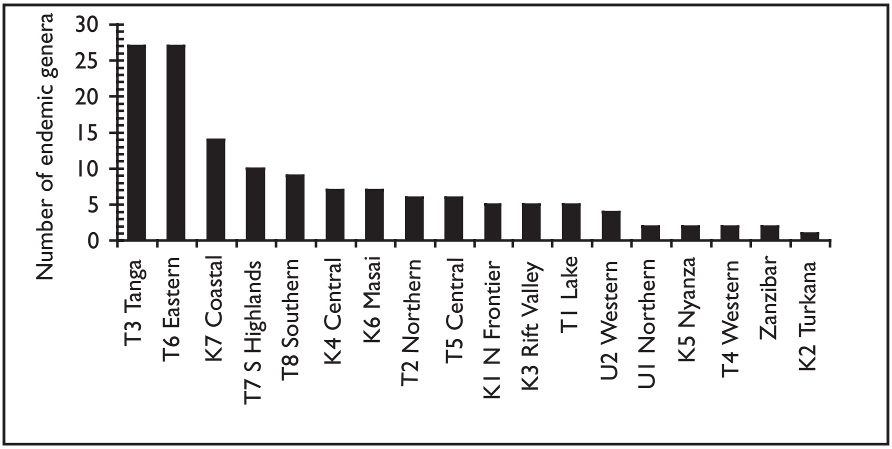

FIG. 10. Number of endemic genera in tropical East Africa shown by FTEA subdivisions.

3.3 Conservation

National Parks and protected areas

Apart from the recently gazetted Kitulo National Park in Tanzania (413 km^2 established 2004), as far as we are aware, there are no national parks for the protection of plant species *per se* in tropical East Africa. However, the most species-rich areas fall within gazetted national parks or forest reserves. There are six categories of management of protected areas defined in the 1997 UN list of National Parks and Protected Areas (IUCN 1998). See Table 8 for definition of these categories and the number of protected areas in each country.

In addition the UNESCO programme on Man and Biosphere (MAB) for the development of sustainable use and conservation of biological diversity, have identified nine biosphere reserves in East Africa spanning across the major ecosystems in this region (Table 9; Fig. 11).

TABLE 8. Protected areas in tropical East Africa and their management categories (IUCN 1997).

Category Ia:	Strict Nature Reserve: protected area managed mainly for science
Ib:	Wilderness Area: protected area managed mainly for wilderness protection
Category II:	National Park: protected area managed mainly for ecosystem protection and recreation
Category III:	Natural Monument: protected area managed mainly for conservation of specific natural features
Category IV:	Habitat/Species Management Area: protected area managed mainly for conservation through management intervention
Category V:	Protected Landscape/Seascape: protected area managed mainly for landscape/seascape conservation and recreation
Category VI:	Managed Resource Protected Area: protected area managed mainly for the sustainable use of natural ecosystems

	Ia or 1b	II	III	IV	V	VI	Protected area % of total area
Uganda	0	7	0	23	2	16	9.2%
Kenya	0	33	0	4	0	18	15.5%
Tanzania	0	12	0	18	0	48	6.1%

There are no Strict Nature Reserves (Category 1a or 1b) in East Africa, but several in Categories II, IV and VI. We have taken Category II, which is a National Park designated mainly for the protection of "... ecological integrity of one or more ecosystems for present and future generations" "... exclude exploitation" "... provide a foundation for spiritual, scientific, educational, recreational, and visitor opportunities ..." (IUCN 1998) as representative of an area which would offer the most protection to a habitat, and protection and conservation of plant species within. It is clear from Tables 8 and 9 and Fig. 10, that protected areas of this nature are wanting in at least two areas that are centres of species richness and endemism: the southern subdivision of Tanzania (T 8) and the coastal regions in Kenya and Tanzania (T 3, K 7). There are several Forest Nature Reserves (Category IV) that are managed nature reserves of which the Amani Forest Nature Reserve established by the Tanzanian Government in 1997 for the protection of the flora and fauna of east Usambara, and the Shimba Hills National Reserve established in 1968, fall in the T 3 and K 7 regions respectively.

Clarke (1998) found high endemism in the vascular flora of the Zanzibar-Inhambane regional mosaic of White (White, 1983), and suggested that the northern part of the Zanzibar-Inhambane regional mosaic be re-classified as a new Regional Centre of Endemism, the Swahilian Regional Centre of Endemism. His proposed phytochorion contains an estimated 1200 endemic and 287 near endemic species, and 25 endemic and 8 near endemic genera. With an estimated 4500 species and high endemism it ranks one of the most species-rich areas in tropical East Africa (see also Clarke *et al.*, 2000). Somewhat similar results were obtained by Brenan (1978) and Linder (1998) who also suggested that the centre of endemism ranges along the coast from southern Kenya to northern Mozambique and emphasised the richness of

TABLE 9. Biosphere Reserves established by the UNESCO programme on Man and Biosphere (MAB).

Country	Biosphere Reserve	Established	Ecosystem(s)
Uganda	Ruwenzori National Park	1979	Tropical montane
Kenya	Mount Kulal	1978	Semi-desert and desert; lake
	Mount Kenya	1978	Montane and highland
	Amboseli	1980	Tropical grassland
	Kiunga	1980	Coastal
	Malindi-Watamu	1979	Coastal
Tanzania	Serengeti-Ngorongoro	1981	Tropical grassland
	Lake Manyara	1981	Tropical dry or deciduous ground water forest and soda lake
	E Usambara	2000	Tropical montane rainforest

biological diversity in this region. Robertson & Luke (1993) in their report on the coastal forests of Kenya had arrived at similar conclusions and recommended several Nature Reserves to be established in this region. Clarke *et al.* (2000 and references therein) examined published accounts of the flora of Tanzania and identified the Lindi area as a local centre of endemism in Tanzania, with Rondo, Noto, Litipo, and Chitoa forest areas especially rich in plant species and endemism (Clarke, 2001).

The main threats to the biological diversity of tropical eastern Africa are population growth and the requirement for housing and farming which is compensated through forest clearing. Increased clearings have led to soil degradation and invasion of exotic species. In Kenya, Robertson & Luke (1993) surveyed about 68 small coastal forest sites (the Mijikenda Kayas) that were of religious significance and protected through local customs, but saw an increased encroachment of the sites; in Tanzania several earlier protected sites were degazetted to building and planting pressure for an expanding population, for example the larger forests of Matumbi Hills, Rondo Plateau and Makonde Plateau have been cleared for farming and logging.

In addition to the increasing population pressure and shift from traditional farming practices in eastern Africa, global warming has resulted in environmental changes which will consequently have a marked effect on vegetation and biological diversity. There is evidence of receding glaciers and shrinking ice-cap on Mt Kenya, Kilimanjaro and Ruwenzori, with 92% of Mt Kenya's Lewis glacier melting in the last 100 years, and about 75% of the glacier area on Ruwenzori decreasing since the 1990s. On Kilimanjaro, it is projected that ice will disappear by 2020 (82% of Kilimanjaro's ice has disappeared since 1912, with about one-third melting in just the last twelve or so years) (Hasternath, 1991; Kaser, 1999; IPCC, 2001; Hardy, 2002). It is hypothesised that less snow on the mountains during the rainy season will decrease the surface reflectiveness and will lead to higher rates of heat absorption. This will result in an increase in local temperatures, an increased melting of ice and changes in microclimate. As a consequence of warming, the range of the natural vegetation will shift, together with a shift of its biota, (Epstein *et al.*, 1998), and where the vegetation is already degraded, this will result in an increased invasion and establishment by non-native species and a consequent loss in the native biological diversity.

Despite the fact that there are two Biosphere Reserves on coastal Kenya, there is still an urgent need for designated Nature Parks to protect and conserve the rich coastal habitats. And even though there are forest reserves recently set up by the

Wildlife Conservation Society of Tanzania (WCST), supported by the UNDP Global Environmental Facility (GEF) to manage the forest areas in the coastal hinterland, National Parks are still needed to protect the diversity of plants, mammals, birds, reptiles, amphibians and invertebrates that are endemic and forest-dependent in this region (Burgess & Clarke, 2000). In addition, Strict Nature Reserves need to be designated in this and other habitats to reduce the degradation of natural vegetation and incursion of non-native species; Strict Nature Reserves are also necessary to monitor changes in vegetation resulting from environmental changes related to global warming.

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Appendix 1. Flora and Districts subdivisions of tropical East Africa.

UGANDA

Abbr.	Flora subdivisions	Flora Districts
U1	Northern	W Nile, Acholi, Lango, Karamoja
U2	Western	Bunyoro, Toro, Ankole, Kigezi
U3	Eastern	Teso, Busoga, Mbale
U4	Buganda	Masaka, Mengo, Mubende

KENYA

Abbr.	Flora subdivisions	Flora Districts
K1	Northern Frontier	Isiolo, Samburu, Marsabit, Mandera, Wajir, Garissa
K2	Turkana	Turkana, W Pokot
K3	Rift Valley	Trans-Nzoia, Uasin Gishu, Nandi, Elgeyo, Baringo, Laikipia, Nakuru, Naivasha
K4	Central	N Nyeri, S Nyeri, Muranga, Kiambu, Nairobi, Meru, Embu, Machakos, Kitui
K5	Nyanza	Busia, Kakamega, Siaya, Kisumu, Kisii, S.Nyanza
K6	Masai	Kajiado, Narok
K7	Coast	Taita, Kwale, Mombasa, Kilifi, Malindi, Tana River, Lamu

TANZANIA

Abbr.	Flora subdivisions	Flora Districts
T1	Lake	Bukoba, Biharamulo, Ngara, Mwanza, Kwimba, Shinyanga, Maswa, Musoma, N Mara
T2	Northern	Masai, Mbulu, Arusha, Moshi
T3	Tanga	Pare, Lushoto, Handeni, Tanga, Pangani
T4	Western	Buha, Kahama, Nzega, Kigoma, Tabora, Mpanda, Ufipa
T5	Central	Singida, Kondoa, Dodoma, Mpwapwa
T6	Eastern	Kilosa, Morogoro, Bagamoyo, Uzaramo, Rufiji, Ulanga
T7	Southern Highlands	Chunya, Mbeya, Iringa, Rungwe, Njombe
T8	Southern	Songea, Kilwa, Tunduru, Masai, Lindi, Newala, Mikindani
Z	Zanzibar Island	Zanzibar
P	Pemba Island	Pemba

Onana, J.M., Achoundong, G., Ghogue, J.P. & Tadjouteu, F. (2006). Progrès de l'étude de la Flore du Cameroun. In: S.A. Ghazanfar & H.J. Beentje (eds), Taxonomy and ecology of African plants, their conservation and sustainable use, pp. 609–612. Royal Botanic Gardens, Kew.

PROGRÈS DE L'ÉTUDE DE LA FLORE DU CAMEROUN

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Résumé

Au mois de Septembre 2003, la flore camerounaise est connue d'une collection de 65,100 spécimens effectivement incorporés à l'Herbier National Camerounais (YA), de 37 volumes de la série "Flore du Cameroun" et de diverses publications. En outre, une base de données informatique appelée "Letouzey" en vue d'un échange d'information grâce aux nouvelles technologies de l'information et de la communication est en cours d'élaboration.

Abstract

The flora of Cameroon is known from a collection of 65,100 specimens so far incorporated in the National Herbarium of Cameroon (YA), 37 volumes of the series "Flore du Cameroun" and other publications. A database named "Letouzey" has been set up for the exchange of information through the Internet.

Key words: Cameroon, flora, database

1 Introduction

Dès 1963, paraît le premier volume de la série "Flore du Cameroun". Aujourd'hui en 2003, 37 volumes ont été publiés. Les études se poursuivent pour beaucoup de taxa et les résultats sont publiés dans diverses revues scientifiques. Aussi, les récoltes de nouveau matériel d'herbier ont enrichi la collection de l'Herbier National Camerounais (YA). Une base de données électronique en vue de la diffusion des informations par les nouvelles technologies de l'information et de la communication a été lancée. Nous présentons ici les principaux résultats obtenus.

2 Situation de la collection

Au mois de Septembre 2003, 65,100 échantillons ont été enregistrés et incorporés à YA. Ce sont surtout des échantillons secs en herbier, mais aussi des fruits en carpothèque, des fleurs en anthothèque et des cals de bois en xylothèque. Sur la base de Satabié (1999), après une mise à jour des statistiques consécutive aux nouveautés taxonomiques apparus depuis lors, il apparaît que ces échantillons représentent:

- 243 familles: pas de famille nouvelle décrite, mais 8 (9) nouveautés taxonomiques issues d'exclusions lors des révisions ou études des familles déjà existantes (Anthericaceae (excl. Liliaceae); Buddlejaceae (excl. Loganiaceae); Costaceae (excl. Zingiberaceae); Draceanaceae (excl. Agavaceae); Mendonciaceae (excl. Acanthaceae); Viscaceae (excl. Loranthaceae); probablement Memecylaceae (excl. Melastomaceae); Pteridaceae (excl. Adiantaceae); Woodsiaceae (excl. Athyriaceae).
- environ 1800 genres (exactement 1760 selon Satabié, 1981) : 6 genres nouveaux décrits depuis 1985 (*Djinga* et *Winklerella* (Podostemaceae), *Korupodendron* (Vochysiaceae), *Kupea* (Triuridaceae), *Namatea* (Sapindaceae) et *Ossiculum* (Orchidaceae);
- environ 8500 espèces : plus d'une centaine d'espèces décrites à partir de récoltes récentes par divers auteurs et près de 300 à 400 échantillons difficiles à identifier et qui pourraient être pour la plupart des taxons nouveaux ou connus ailleurs et récoltés pour la première fois au Cameroun (cas des 48 espèces signalées par Martin Cheek (com. pers.) ou des 132 par Thomas *et al.* 2003).

La collection de YA compte à ce jour 110 types, pour la plupart des isotypes.

3 Situation des publications

3.1 Série «Flore du Cameroun»

Depuis l'an 2000, trois fascicules de la Flore du Cameroun ont été publiés. Il s'agit des volumes 35 (Tome II Orchidacées), du volume 36 (Tome III Orchidacées), et volume 37 (Dichapetalacées).

L'édition de ces volumes a été rendue possible grâce à un financement du BSP (Biodiversity Support Program) du CARPE (Programme Régional de l'Afrique Centrale pour l'Environnement). Ceux-ci viennent à la suite du volume 34 (Tome I Orchidacées) paru en 1998 après 7 ans d'interruption.
Au 30 Octobre 2003, 37 volumes ont été effectivement édités. Ceux-ci représentent:

- 116 familles (dont 30 de Ptéridophytes), soit 48%;
- 622 genres (dont 68 de Ptéridophytes), soit environ 35%;
- 2249 espèces (dont 257 de Ptéridophytes), soit environ 28%.

Parmi les plantes déjà décrites, les taxa endémiques sont représentés par:

- aucune famille;
- 6 (sous) genres;
- et plus de 160 espèces.

Ce travail est l'œuvre de 39 auteurs de 15 nationalités différentes et appartenant à diverses institutions du monde.

3.2 Flores régionales

Des listes documentées de plantes ou *check-list* selon les ditions ont été éditées:

- Cable & Cheek (1998): 2435 espèces dans la région du Mont Cameroun (aire de 2700 km^2)
- Cheek *et al.* (2000): 920 espèces dans la région du Mont Oku (aire de 1550 km^2).

3.3 Articles dans les journaux scientifiques

De nombreux auteurs ont décrit effectivement depuis 1999:

- 2 genres nouveaux dont 1 appartenant à une famille déjà publiée (Sapindaceae);
- au moins 32 taxa infra-génériques, dont 6 espèces appartenant à des familles déjà publiées (1 Balsaminaceae, 1 Ebenaceae, 2 Orchidaceae et 2 Sapindaceae).

4 Bases de données "Letouzey"

Depuis Octobre 2000, avec l'appui technique et financier de l'Institut de Recherche pour le Développement (IRD – ex-ORSTOM), l'élaboration d'une base de données dénommée "Letouzey" a été lancée dans le cadre du projet d'informatisation de YA. Ce projet est en fait la première étape vers la mise en place d'un Réseau Informatique des Herbiers Africains (RIHA) qui mettra à la disposition des scientifiques l'information sur la flore africaine à travers les nouvelles technologies de l'information et de la communication .

Les fiches d'herbier accompagnant l'échantillon sont la principale source pour cette base de données. Ainsi au 30 Octobre 2003, ont été enregistés 8100 spécimens (environ 13,500 parts) représentant 851 genres et 12 familles: Annonaceae, Apocynaceae, Begoniaceae, Burseraceae, Combretaceae, Cucurbitaceae, Leguminosae-Caesalpinoïdae, Moraceae, Ochnaceae, Podostemaceae, Rutaceae, Scrophulariaceae et Zingiberaceae (incl. Costaceae). Le nombre de taxa infra génériques n'est pas connu.

5 Perspectives

5.1 Prospections phytogéographiques et récoltes d'échantillons botaniques

On estime que 90% de taxa présents au Cameroun sont représentés à YA. De nombreux sites restent mal connus et sont des sites potentiels de prospection. Nous citons ci-après quelques-uns (Letouzey 1968):

- Nord: rives du Logone, Mont Alantika, Monts de Poli, région de Rey-Bouba;
- Plateau de l'Adamaoua: Tchabal Mbabo;
- Sud: région Ndikinimeki-Yabassi, abords du Mbam, alentours d'Ebolowa, région de Campo, mangrove littorale, pointe sud-est ;
- Ouest: Monts Rumpi, extrême nord du Cameroun occidental (zone Akwaya-Wum-Nkambé).

5.2 Publication de la Flore du Cameroun

Aujourd'hui, à notre connaissance, 2 manuscrits ont été déposés par les auteurs (Leguminosae-Mimosoïdae, Irvingiaceae).

Les recherches se poursuivent et la rédaction est en cours pour les Burseraceae et les Violaceae.

La plupart des familles (soit près de 120) ne sont pas attribuées à des spécialistes. Pour certaines, ces derniers ont ralenti ou même arrêté leur collaboration souvent à cause des difficultés logistiques et financières de YA (exemples: Apocynaceae, Convolvulaceae, Ochnaceae, Leguminosae-Papillionoïdae).

6 Conclusion

L'étude de la flore camerounaise se poursuit malgré les irrégularités et difficultés d'édition des fascicules de la série "Flore du Cameroun". Près de 50% des familles et 65% d'espèces ne sont pas encore publiées. Les botanistes spécialistes de ces familles sont alors invités à s'intéresser à cette riche biodiversité (c'est la troisième en Afrique) malgré tout encore peu connue. Les flores régionales de parution récente, en tenant compte du statut de conservation des espèces apportent des arguments scientifiques pour la conservation et la gestion rationnelles des écosystèmes forestiers, permettront ainsi de sauver de nombreuses espèces encore inconnues.

Remerciements

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A CATALOGUE OF THE VASCULAR PLANTS OF MADAGASCAR

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Abstract

Madagascar is regarded as a globally significant biodiversity hotspot, and the conservation of its unique but threatened flora and ecosystems is of paramount importance. The Malagasy flora is remarkable in terms of its species richness, high level of endemism and complex biogeographic relationships. Efforts to produce a complete Flora started many decades ago, but progress in completing this work is slow, and many of the older treatments are now drastically out-dated. On the other hand, efforts to document the flora through renewed inventory work and modern systematic research are providing new data and insights. Experience in other countries has shown that detailed floras and monographic treatments often fail to provide the data urgently required by conservation agencies and national decision-makers, and it is argued that the time is ripe for the compilation of a catalogue of Malagasy plants. This project is envisaged as a collaborative work that will provide printed and electronic products containing basic information on taxonomy, geographical distribution and conservation status of all naturally occurring vascular plant taxa in Madagascar. It also aims to provide a framework for ongoing inventory work, and to stimulate systematic and other research in poorly documented components of the flora.

Résumé

Un catalogue des plantes vasculaires de Madagascar. Madagascar est considéré comme un 'hotspot' de biodiversité d'importance mondiale et la conservation de sa flore, unique mais menacée, est de la plus haute importance. La flore malgache est remarquable en termes de richesse spécifique, de fort taux d'endémisme et de relations biogéographiques complexes. Les efforts consentis pour produire une Flore complète ont débuté il y a plusieurs décennies mais l'avancement de ce travail est lent et nombreux sont les traitements antérieurs qui devraient être remis à jour. Par ailleurs, efforts pour documenter la flore que constituent les nouveaux travaux d'inventaire et les recherches systématiques modernes ont fourni des données et de conceptions nouvelles. Dans d'autres pays l'expérience a montré que les flores détaillées et les traitements monographiques ne fournissent pas les données attendues d'urgence par les agences de conservation et les décideurs nationaux et que le moment est venu de compiler les données pour créer un catalogue des plantes malgaches. Ce projet est le fruit d'une collaboration qui permettra la diffusion de produits imprimés et électroniques contenant l'information taxonomique de base, la distribution géographique et le statut de conservation de tous les taxons de plantes vasculaires présents naturellement à Madagascar. Il a également l'ambition de fournir un cadre pour les inventaires en cours et de stimulera la recherche, notamment en systématique, sur des composantes de la flore mal documentées.

Key words: biodiversity, conservation, electronic publication, flora, hotspot, Madagascar

1 Introduction

The compilation of a listing of species for a particular area, country or region serves a need for basic data on plant biodiversity and biogeography and provides a taxonomic framework in the form of an authoritative list of "names in current use". Such information is important for a wide range of botanical and related activities because "a plant's name is the key to its literature" (Davis & Heywood, 1973). In particular, effective conservation planning at local, national and global levels inevitably depends in part on acquiring and integrating reliable information regarding the flora and fauna of the area in question. Annotated checklists have become well established in the literature, in which complementary information of various kinds adds value to the basic list of taxa. However, with the availability of modern databasing programs and internet technology, it is now possible to go well beyond the conventional "annotated checklist" to produce a more robust electronic "catalogue" containing far more information, and serving a broader set of users. While checklists and catalogues cannot replace detailed floras and monographs, which remain the cornerstones of plant taxonomy and phytogeography, they can be valuable products that efficiently document the state of our knowledge of the plants in a particular area.

Madagascar is widely recognized as a centre of botanical diversity and endemism of global importance. The total number of vascular plant species has been estimated at between 7,900 (Humbert, 1959) and 12,000 species (see Schatz, 2001), although our current estimate is that the total may in fact approach 14,000 species, of which more than 90% are endemic to Madagascar. However, precise figures are not available, largely because the existing literature is widely dispersed and because much of it is now outdated (Morat & Lowry, 1997). Madagascar has also been widely regarded as one of the world's most critical biodiversity hotspots (Myers *et al.*, 2000; Mittermeier *et al.*, 2005), and, as such, merits urgent conservation action. But the process of identifying conservation priorities and targeting actions has been hampered, among other things, by a lack of up-to-date information on the flora as a whole, and on the occurrence of species within specific areas such as national parks and reserves, and by a shortage of conservation status assessments. This is the direct result at least in part by too many out-of-date or inadequate taxonomic treatments, and by incomplete botanical inventory.

In many parts of the world, the compilation of checklists has proved to be of enormous benefit to the scientific and conservation communities, providing basic data about plant species and their occurrence in a relatively short period of time compared to that required to produce a comprehensive Flora. Examples of this include the annotated checklist of plants of southern Africa, now in its fourth iteration (Germishuizen & Meyer, 2003) and the catalogue and red data list of vascular plant for Ecuador (Jørgensen, 1999). National and regional Flora projects in Africa, as elsewhere, have required large amounts of financial and human resources, and in many cases have spanned periods of more than 40 years or more (Morat & Lowry, 1997), and even then some have never reached completion. Furthermore, ongoing botanical exploration and changing taxonomic concepts have rendered the early volumes of many Floras out-of-date. In Africa, annotated checklists have been produced recently for southern Africa (Germishuizen & Meyer, 2003), Tropical Africa (Lebrun & Stork, 1991–1997) and the Mediterranean region (Greuter *et al.*, 1984, 1986, 1989). These lists are now linked to ongoing computer databasing efforts (for example http://www.euromed.org.uk/), which enables easy printing of regularly updated versions that reflect taxonomic changes and can include additional data fields.

Our efforts in Madagascar to provide a comprehensive compilation of the flora clearly lag behind those for continental Africa. While the *Flore de Madagascar et des Comores* project has to date treated about 75% of the plant families traditionally recognized in the country (see below), this amounts to approximately 6500 species, perhaps no more than 50% of the total species diversity. It is one of the oldest flora projects in Africa, dating back to 1936. The production rate of new treatments has been very slow over the last decade, with only 11 families published since 1990, covering a mere 387 species. Furthermore, many of the older treatments have been at least partially superceded by more recent taxonomic revisions, and others are critically in need of an update (see discussion below). In many cases this can be accomplished by means of synoptic revisions, a series of which has recently been published on genera in Madagascar's endemic families (Lowry *et al.,* 1999, 2000, 2002; Randrianasolo & Miller, 1999; Schatz *et al.*, 1999a, 1999b, 2000, 2001).

The TROPICOS database, developed and maintained by the Missouri Botanical Garden, includes a vast amount of data on the flora of Madagascar painstakingly compiled over the last decade. The database includes information on plant names (i.e., nomenclatural data) and specimen data. To date (Sept. 2005) approximately 23,500 name records have been captured that refer to Malagasy plants (including synonyms) and the database contains approximately 107,000 specimen records. Information in TROPICOS is available in the public domain through the internet via a hypertext (HTML) interface (http://mobot.mobot.org/W3T/Search/vast.html). TROPICOS is, however, essentially a research tool for plant taxonomy, and thus does not provide an integrated and user-friendly means for extracting information on, for example, the plants of a particular area or habitat type, even though much of the relevant information has been captured. Checklist and flora projects for other parts of the world have used TROPICOS as a platform for providing information delivered through an HTML interface, including:

Catalogue of New World Grasses
    (http://mobot.mobot.org/W3T/Search/nwgc.html)
Catalogue of the Vascular Plants of Ecuador
    (http://www.mobot.org/MOBOT/research/ecuador/welcome.shtml)
Checklist and Descriptions for the Flora de Nicaragua
    (http://www.mobot.org/MOBOT/research/nicaragua/welcome.shtml)
Flora Mesoamerica Checklist (http://www.mobot.org/MOBOT/fm/welcome.html)
Flora of China Checklist (http://mobot.mobot.org/W3T/Search/foc.html)
Flora of Madidi National Park (Bolivia)
    (http://mobot.mobot.org/W3T/Search/madidi/madidifr.html)
Flora of Panama Checklist (http://mobot.mobot.org/W3T/Search/panama.html)
Peru Checklist (http://mobot.mobot.org/W3T/Search/peru.html)

Building on these models, we have now begun a 5-year project that will make use of modern information technology to produce a "Catalogue of the Vascular Plants of Madagascar", in both printed and on-line versions.

2 Discussion

2.1 The Flora of Madagascar and synoptic revisions

To date 165 of the 222 traditionally recognised plant families (75%) in Madagascar have been treated for the *Flore de Madagascar et des Comores* series, and an additional 14 families (6%) are expected to be published in the next three years. Full or partial taxonomic treatments for some of the other outstanding families have also been published elsewhere, and researchers at various institutions are currently working on revisions of some of the genera that have not been treated in the *Flore*. Our knowledge of the flora of Madagascar is thus advancing steadily. However, many of the treatments in earlier volumes are now badly outdated and of little use today. This can be seen clearly for groups that were treated for the *Flore* and which have been studied again recently, such as the Palm family (Arecaceae), in which a recent monograph for Madagascar (Dransfield & Beentje, 1995) contained major generic level changes and a total of 80 (46%) newly described species. In the case of the family Iridaceae, the original treatment for the *Flore* (Perrier de la Bâthie, 1946) recognized 11 species, while a completely new *Flore* treatment written for the family by Goldblatt (1991) accepted 21 species, the additional 10 species including seven newly described locally endemic species. Other examples include the ongoing synoptic revisions of Madagascar's endemic families, in which drastic changes in delimitation have increased the number of recognised species from 48 to 81 (69% increase) (see Table 1). Some other recent generic revisions have resulted in even more drastic changes, such as in *Buxus*, with a single species recognised in the *Flore* (Perrier de la Bâthie, 1952) a second described several years later (Capuron, 1960), but with a total of nine species recognised in the new treatment (Schatz & Lowry, 2002); *Prockiopsis*, which expanded from a single species in the *Flore* (1946) treatment to three (Schatz & Lowry, 2003); *Tacca*, with two species accepted in the *Flore*, an additional species described by Bardot-Vaucoulon (1997), and six in a new revision (Phillipson *et al.*, in prep.); and, most extreme of all, *Xerophyta*, from three species

TABLE 1. Changes in taxonomic treatments of genera in three endemic families between *Flore de Madagascar et des Comores* and recent revisions - new species published in recent treatments: A = no. of spp. in *Flore de Madagascar* treatment; B = New spp. published in recent revision; C = Total number of spp. accepted in recent revision; D = % increase since *Flore* treatment (Miller & Randrianasolo, 1999; Schatz *et al.*, 1999, 2000, 2001, 2002).

Family	**Genus**	**Revision**	**A**	**B**	**C**	**D**
Asteropeiaceae	*Asteropeia*	Schatz *et al.* 1999a	5	2	8	60%
Sarcolaenaceae	*Eremolaena*	Lowry *et al.*, 2000	2	0	2	0%
Sarcolaenaceae	*Leptolaena (s.s.)*	Schatz *et al.*, 2001	3	5	7	133%
Sarcolaenaceae	*Pentachlaena*	Lowry *et al.*, 2000	1	1	3	200%
Sarcolaenaceae	*Perrierodendron*	Lowry *et al.*, 2000	1	4	5	400%
Sarcolaenaceae	*Rhodolaena*	Schatz *et al.*, 2000	4	3	7	75%
Sarcolaenaceae	*Sarcolaena*	Randrianasolo & Miller 1999	7	1	8	14%
Sarcolaenaceae	*Schizolaena*	Lowry *et al.*, 1999	8	8	18	125%
Sarcolaenaceae	*Xyloolaena*	Lowry *et al.*, 2002	3	2	5	67%
Sphaerosepalaceae	*Dialyceras*	Schatz *et al.*, 1999b	1	0	3	200%
Sphaerosepalaceae	*Rhopalocarpus*	Schatz *et al.*, 1999b	13	0	15	15%
	Totals		**48**	**26**	**81**	**69%**

in the *Flore* treatment (Perrier de la Bâthie, 1950) to 27 species (Phillipson & Lowry, in prep.). In taxa that have never been treated in the *Flore* similar results can be seen, for example in the genus *Chouxia*, there has been an increase from a single species (Capuron, 1969) to five species (Schatz *et al.*, 1999a); and in *Brexia*, from eight species (Perrier de la Bâthie, 1933, 1942) to 11 (Schatz & Lowry, 2004). In most of these cases a series of closely related locally endemic species had previously been placed together into what was perceived as widespread and variable one. A pattern is now emerging in which careful re-examination of the available herbarium material and consideration of eco-geographic parameters such as bioclimate and geological substrate generally results in substantially modified species circumscriptions. Consequently, it is obvious that conservation priorities cannot be based on the distribution patterns of species as they were defined in older taxonomic treatments, as this would inevitably lead to erroneous conclusions about areas of local endemism, high species diversity, and which taxa are most critically threatened.

While the publication of comprehensive monographic revisions might be the ideal way to develop a full understanding of the entire Malagasy flora, it would take many decades to complete the task given the human and financial resources now available. Significant progress can, however, be made through synoptic revisions prepared by experienced taxonomists who are familiar with the flora, vegetation and geography of Madagascar. Typically a synoptic revision involves the following steps:

- Rapidly evaluate herbarium specimens of the taxa currently recognised in Madagascar
- Confirm the typification of published names
- Verify or correct the identification of material not seen be previous authors
- Determine which species or groups of species appear to be variable in terms of their diagnostic characters and/or eco-geographic range, and sort these into "morpho-species"
- Refine these groups on the basis of morphological characters and eco-geographic distribution patterns
- Compare each of the potential taxa recognised in Madagascar with their congeners from elsewhere (if any)
- Undertake (if necessary) targeted field work to resolve uncertainty
- Publish new species and nomenclatural changes in a revision that includes at least a diagnostic description of the novelties and an identification key.

Although synoptic revisions are not intended to provide the "last word" on the taxonomy and evolution of a particular group, they allow us to make major advances in our understanding more rapidly than through traditional approaches, such as detailed monographic work, an essential consideration if we are to be able to complete the Catalogue project in a timely manner. Synoptic revisions have the added advantage of providing an ideal training opportunity for Malagasy botanists and students who wish to contribute to the study of their flora. Our ability to use this approach successfully is due in large part to the facts that (1) the flora of Madagascar is largely endemic, reducing the need for extensive comparisons with that of other areas such as Africa and Asia; (2) much of the representative herbarium material, including types, is present in a single herbarium (P), with significant holdings in Madagascar (TAN and TEF); and (3) most species in Madagascar have distribution patterns that are strongly correlated with reasonably well understood eco-geographic parameters. It should be noted, however, that not all taxa are can be resolved adequately using this approach – in some groups, patterns of diversity are too complex to be assessed rapidly, and will thus require longer term studies to evaluate species limits.

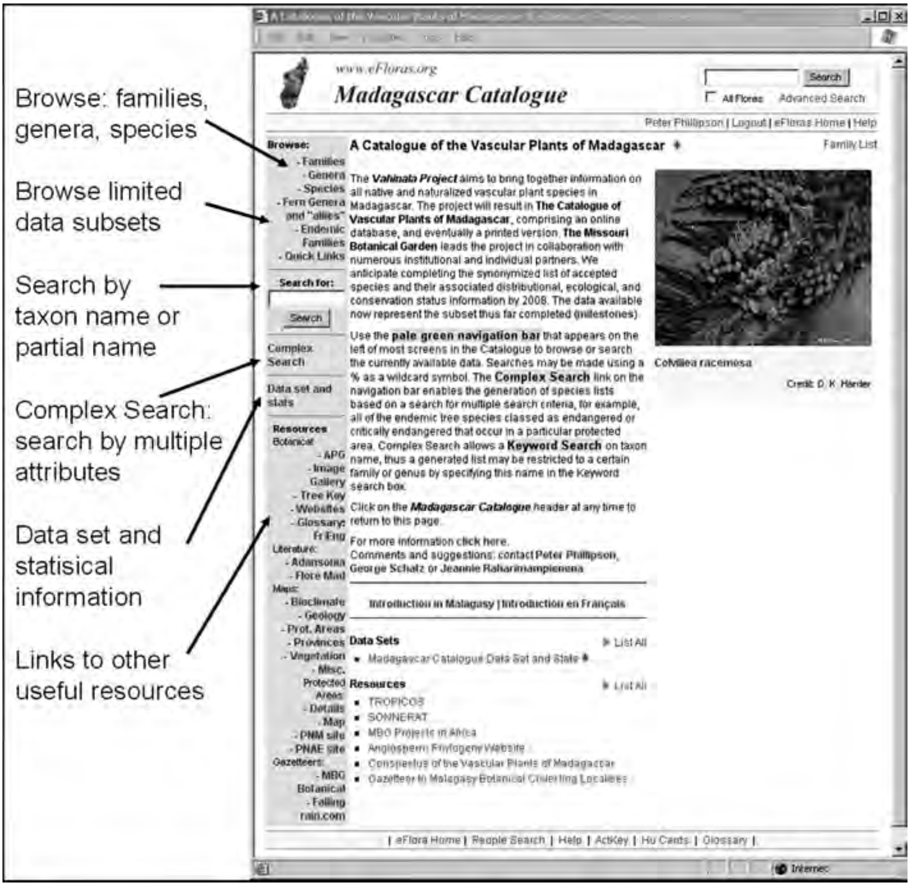
For the Madagascar Catalogue Project we will examine each genus of vascular plants in order first to assess the value of the currently available taxonomic treatments (if any). This will result in six possible scenarios, as follows:

1. The taxonomy of the genus may be sound and we will be able to adopt the existing treatment with little or no modification, and merely capture the relevant data electronically.
2. The species-level taxonomy may be sound, but taxonomic changes to generic delimitation in other parts of the world may require re-evaluation of the Malagasy taxa and the creation of new combinations for them.
3. Nomenclatural work may be necessary, such as the lectotypification of taxa based on syntypes or the correction of invalid names.
4. The species level taxonomy may need some revision, such as the recognition of a few new species, the placement of taxa into synonymy or the change in rank of some taxa.
5. "Problem taxa" for which the taxonomy may need substantial revision at species and/or other levels.
6. "Problem taxa" which have never been the subject of a revision or flora treatment.

For those groups currently under study by colleagues, we will seek their collaboration and input, especially in the cases of Scenarios 5 and 6. For the other taxa, we intend to tackle as much of the needed work as possible ourselves during the time span of the Catalogue project. In some cases this will be accomplished by mentoring Malagasy students who wish to undertake taxonomic projects, who will gain valuable experience and contribute significantly to the task in hand. Using this diversified approach, we will produce numerous revisions, descriptions of new species, and other relevant articles, often in collaboration with co-workers, including at least synoptic revisions for many of the genera that fall into Scenarios 4, 5 and 6. While it may not be possible to carry out a full taxonomic revision of a few of the largest and most complex groups, we will at the very least compile information on all of the currently recognized species and provide an estimate of the number of additional taxa that remain to be described.

2.2 Catalogue versus checklist

A checklist of species is a static product, usually arranged in alphabetical order or according to an accepted taxonomic sequence, with each entry accompanied by a limited amount of additional information. By contrast, the kind of Catalogue we envision for Madagascar will be a more dynamic product containing a broad range of information that can be accessed in a variety of ways. For the Madagascar Catalogue this will include "red" data for all indigenous species in the form of preliminary assessments of conservation status based on known-distribution data or based on more rigorous data if this is available. Modern databasing technology lends itself perfectly to such an approach, especially when accessed through the internet. Biologists have thus far only made limited use of these techniques, but with broader and more rapid access to the internet, on-line access will increasingly be available to botanists throughout the world, including those in developing countries. In order to make full use of this powerful new tool, we have designed HTML interfaces that permit both interactive browsing and searching through tens of thousands of records to generate online results containing taxonomic, nomenclatural, phylogenetic, biogeographic, and conservation information, along with


Browse: families, genera, species

Browse limited data subsets

Search by taxon name or partial name

Complex Search: search by multiple attributes

Data set and statisical information

Links to other useful resources

A Catalogue of the Vascular Plants of Madagascar

The ***Vahinala Project*** aims to bring together information on all native and naturalized vascular plant species in Madagascar. The project will result in **The Catalogue of Vascular Plants of Madagascar**, comprising an online database, and eventually a printed version. **The Missouri Botanical Garden** leads the project in collaboration with numerous institutional and individual partners. We anticipate completing the synonymized list of accepted species and their associated distributional, ecological, and conservation status information by 2008. The data available now represent the subset thus far completed (milestones).

Use the **pale green navigation bar** that appears on the left of most screens in the Catalogue to browse or search the currently available data. Searches may be made using a % as a wildcard symbol. The **Complex Search** link on the navigation bar enables the generation of species lists based on a search for multiple search criteria, for example, all of the endemic tree species classed as endangered or critically endangered that occur in a particular protected area. Complex Search allows a **Keyword Search** on taxon name, thus a generated list may be restricted to a certain family or genus by specifying this name in the Keyword search box.

Click on the ***Madagascar Catalogue*** header at any time to return to this page.

For more information click here.
Comments and suggestions: contact **Peter Phillipson, George Schatz** or **Jeannie Raharimampionona**

Introduction in Malagasy | Introduction en Français

Data Sets ▶ List All
- Madagascar Catalogue Data Set and Stats

Resources ▶ List All
- TROPICOS
- SONNERAT
- MBG Projects in Africa
- Angiosperm Phylogeny Website
- Conspectus of the Vascular Plants of Madagascar
- Gazetteer to Malagasy Botanical Collecting Localities

FIG. 1. Catalogue web interface – Welcome page with Browse/Search tools on the left.

images and maps, and also some descriptive data, all linked to the core TROPICOS database for the vascular plants of Madagascar. A sample data-set using a prototype interface went live on the Worldwide Web on 18 June 2004 on the efloras.org site (http://www.efloras.org), and since that time the interface has been further developed and additional data added (Fig. 1). The Catalogue database we have developed provides a framework for ongoing data capture and the web interface offers an efficient way to access information on groups that have been treated for the project. The full Catalogue will be completed and published in 2008, but the web site will enable us to make results available progressively group by group as the project proceeds.

In addition to the interactive database (i.e., the Catalogue itself), we also plan to produce a number of other products, including:

- a printed, annotated version of the Catalogue
- a synopsis of the flora at the levels of family and genus
- a series of synoptic revisions, descriptions of new taxa, and other publications
- a collection of representative images on CD-ROM, including colour photos, scanned images of types and other selected specimens, and line drawings

By making these products available rapidly, we will be able to facilitate a number of urgent activities, such as:

- efforts to address some of the key targets of the Global Strategy for Plant Conservation (GSPC)
- decision-making in the areas of conservation planning and natural resource management that incorporates information on patterns of plant distribution and on threatened plant taxa

We also anticipate that the Catalogue will stimulate research by highlighting gaps in our knowledge of the flora, facilitating access to information contained in the dispersed literature and other sources, and presenting a broad range of data in a user-friendly, public domain interface.

2.3 The printed Catalogue

The printed version of the Catalogue will contain summary information on the numbers of genera in each family present in Madagascar, the numbers of species in each genus, generic synonyms, and key literature references. For each accepted species the follow data fields will be provided (where appropriate):

Synonym(s) (limited to those that have been applied to Malagasy material)

Habit (herb, shrub, tree, vine, liana, epiphyte, hemiepiphyte, parasite, saprophyte, submerged aquatic, emergent aquatic, rheophyte, leaf succulent, stem succulent, halophyte, geophyte)

Status of occurrence (endemic, or presence also in some or all of the following areas: Comoros, Mascarenes, Seychelles, Africa, Europe, Asia, Australasia/Pacific, New World, or naturalized)

Bioclimate (humid, subhumid, montane, dry, subarid)

Vegetation formation (grassland, wooded grassland, shrubland, bushland, thicket, woodland, forest, mangrove, freshwater wetland, saline wetland, marine, inselberg/rock face, anthropic)

Elevation (in 500 m increments)

Province (Antananarivo, Antsiranana, Fianarantsoa, Mahajanga, Toamasina, Toliara)

Protected areas (Ambatovaky, Ambohijanahary, Ambohitantely, Analamazaotra-Périnet, Analamerana, Andohahela, Andranomena, Andringitra, Anjanaharibe-Sud, Ankarafantsika, Ankarana, Baie de Baly, Bemaraha, Bemarivo, Betampona, Bezaha Mahafaly, Bora, Cap Sainte Marie, Fôret d'Ambre, Isalo, Kalambatritra, Kasijy, Kirindy-Mitea, Lokobe, Mananara-Nord, Mangerivola, Maningoza, Manombo, Manongarivo, Mantadia, Marojejy, Marotandrano, Masoala, Midongy du Sud, Montagne d'Ambre, Namoroka, Nosy Mangabe, Pic d'Ivohibe, Ranomafana, Tampoketsa d'Analamaitso, Tsaratanana, Tsimanampetsotsa, Zahamena, Zombitsy/Vohibasia)

Conservation status (using IUCN threat categories: extinct, extinct in the wild, critically endangered, endangered, vulnerable, near threatened, least concern, data deficient, not evaluated)

Type specimen(s) (label data and places of deposit)

Voucher specimen(s) (label data and places of deposit)

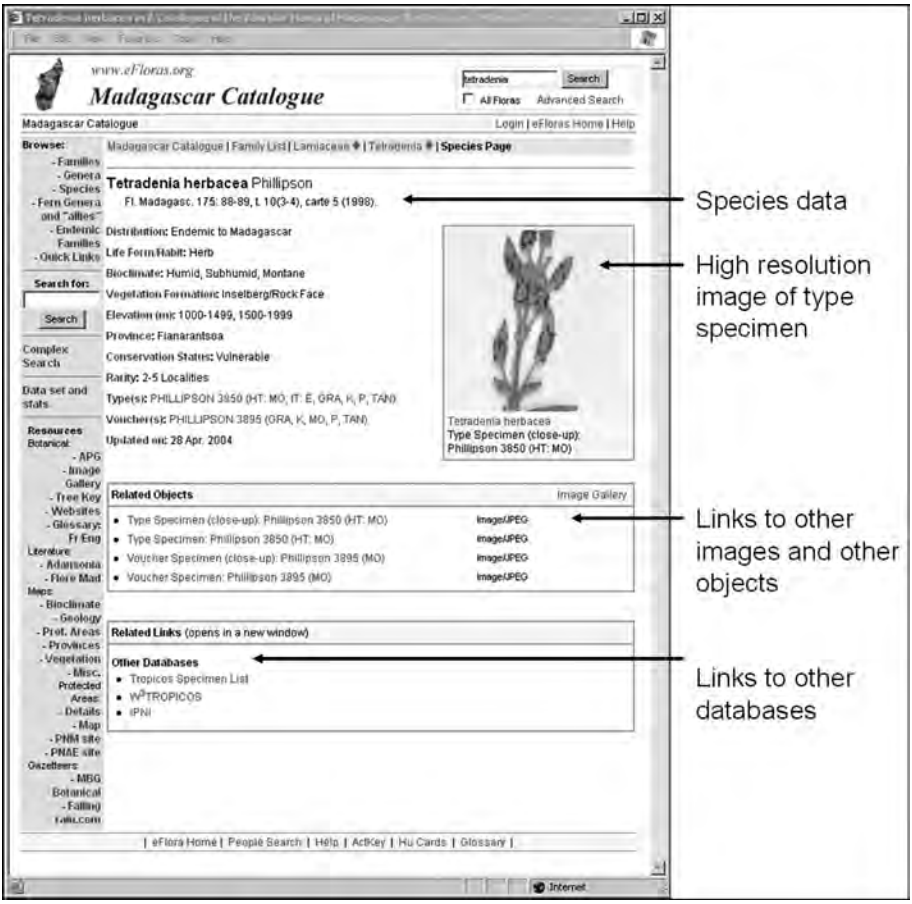
Notes (including a list of any accepted infraspecific taxa)

A sample treatment for the endemic family Asteropeiaceae is given in Appendix 1.

The printed version of the Catalogue will be published in a loose bound form. The treatment of each family or genus will be paginated separately and the date of publication will be indicated so that a user can easily print and insert an up-dated version when it becomes available. These updates will be distributed as downloadable files in "pdf" format and will be made available for each taxon (genus or family) through a link on the corresponding web page. The printed version of the Catalogue will also contain summary data on the number of endemic species in Madagascar and in each geographical area (e.g., Province, Protected Area, etc.) as well as information on red-listed species.

2.4 The internet interface

As outlined above, the web version of the Catalogue comprises a browseable and searchable database. Access to the data can be gained in the following ways: by browsing or searching for a family, genus or species name, or by searching on individual or multiple taxon attributes (see Fig. 1). We anticipate providing a built-in GIS module and a 'Phylogeny Interface' in the future that will provide alternative ways of accessing and visualising the data.



Tetradenia herbacea Phillipson

Fl. Madagasc. 175: 88-89, t. 10(3-4), carte 5 (1998).

Distribution: Endemic to Madagascar

Life Form/Habit: Herb

Bioclimate: Humid, Subhumid, Montane

Vegetation Formation: Inselberg/Rock Face

Elevation (m): 1000-1499, 1500-1999

Province: Fianarantsoa

Conservation Status: Vulnerable

Rarity: 2-5 Localities

Type(s): PHILLIPSON 3850 (HT: MO; IT: E, GRA, K, P, TAN)

Voucher(s): PHILLIPSON 3895 (GRA, K, MO, P, TAN)

Updated on: 28 Apr. 2004

Tetradenia herbacea
Type Specimen (close-up):
Phillipson 3850 (HT: MO)

Related Objects Image Gallery

- Type Specimen (close-up): Phillipson 3850 (HT: MO) Image/JPEG
- Type Specimen: Phillipson 3850 (HT: MO) Image/JPEG
- Voucher Specimen (close-up): Phillipson 3895 (MO) Image/JPEG
- Voucher Specimen: Phillipson 3895 (MO) Image/JPEG

Related Links (opens in a new window)

Other Databases

- Tropicos Specimen List
- W³TROPICOS
- IPNI

FIG. 2. Web interface – Species page.

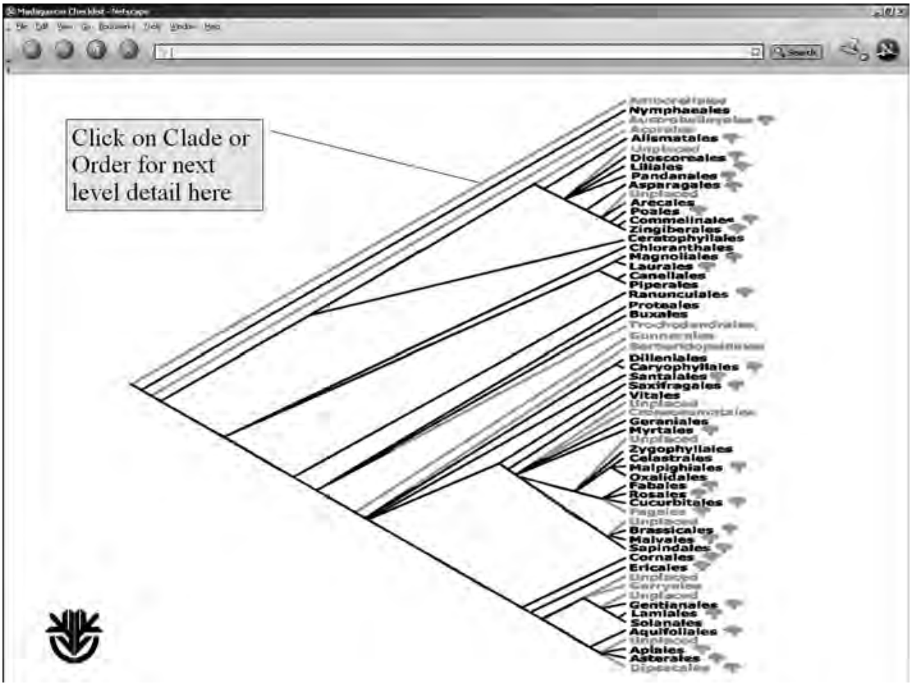
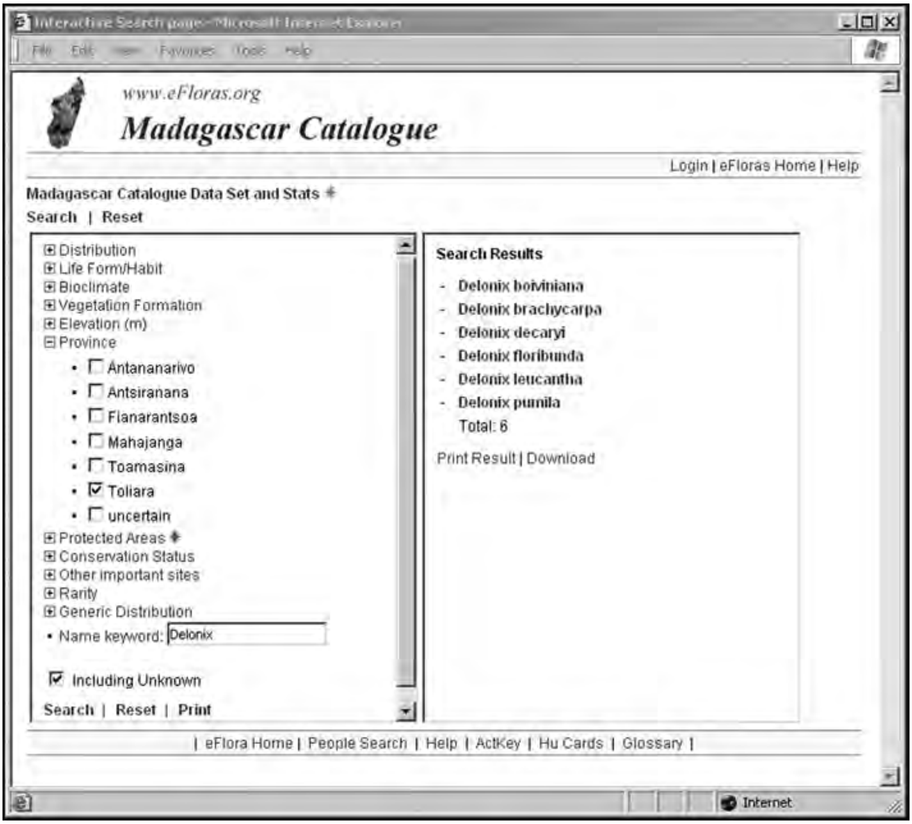


FIG. 3. Web interface – Ordinal level: Malagasy Clades and Orders in black. Tree icons indicate orders with family level trees.

2.5 Data browsing

Hypertext links lead to a series of alphabetic lists from which the user can select the taxon required. For example, selecting a particular name from a family list will lead the user to a corresponding page which will contain information about the family, including a list of accepted and synonymous genera, with links to each. Similarly, each genus page contains a list of all species, each of which is linked to a data page for each accepted species. Browsing the data in this way can be initiated at the family, genus or species level, or by accessing a number of pre-defined restricted subsets of the data, for example: fern genera and Malagasy endemic families. Each taxon page provides a list of synonyms, a list of subordinate taxa and contains all of the captured data for the fields listed above (Section 2.3). In addition, 'thumbnail' images of the type and of selected voucher specimens, and of plants in their wild habitat are provided when available (Fig. 2). The thumbnail images are linked to high resolution versions. Links to other resources such as 'pdf' files and links to corresponding data in other databases are also provided. We also envisage a "phylogeny interface" that will allow the user access to the data by browsing a series of cladograms based on the Angiosperm Phylogeny Website (APG) (http://www.mobot.org/MOBOT/Research/APweb/welcome.html) in which clades containing Malagasy representatives are highlighted, thus providing a graphic visualisation of the relationships of the Malagasy flora (Fig. 3). Links to geographical areas (Bioclimate, Province and Protected Area) will provide access to lists of species recorded from the area selected. For example, selecting Isalo National Park (INP) will generate a species list for that area. Data on the conservation status of species in each area can also be accessed directly to generate a list of species assigned to each of the IUCN threat categories.



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Madagascar Catalogue

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Madagascar Catalogue Data Set and Stats

Search | Reset

⊞ Distribution
⊞ Life Form/Habit
⊞ Bioclimate
⊞ Vegetation Formation
⊞ Elevation (m)
⊟ Province
- ☐ Antananarivo
- ☐ Antsiranana
- ☐ Fianarantsoa
- ☐ Mahajanga
- ☐ Toamasina
- ☑ Toliara
- ☐ uncertain

⊞ Protected Areas
⊞ Conservation Status
⊞ Other important sites
⊞ Rarity
⊞ Generic Distribution
- Name keyword: Delonix

☑ Including Unknown

Search | Reset | Print

Search Results

- **Delonix boiviniana**
- **Delonix brachycarpa**
- **Delonix decaryi**
- **Delonix floribunda**
- **Delonix leucantha**
- **Delonix pumila**

Total: 6

Print Result | Download

| eFlora Home | People Search | Help | ActKey | Hu Cards | Glossary |

FIG. 4. Complex search page, species of *Delonix* from Toliara Province selected on the left, and results posted on the right.

2.6 Data searching

In addition to these browseable links, the on-line database can be searched by complete or partial family or genus name, or by epithet species (Fig. 1). Complex searches based on multiple attributes such as geographic distribution and conservation status, which may be combined with higher taxon restriction will also be possible, such as a search for all species of *Delonix* recorded from Toliara Province (Fig. 4).

2.7 Data links

All of the data pages available through the web interface are cross-linked to one another as appropriate. Links from relevant Catalogue pages are also provided to the corresponding TROPICOS web interface to allow the generation of specimen lists and distribution maps for particular species based on the exsiccatae data available in TROPICOS. We plan to complete the web-based Catalogue by the end of 2008, but the process of updating information will continue beyond that as new data become available.

2.8 Family and genus level synopsis

Since the original list of families was drawn up for the *Flore de Madagascar et des Comores* over half a century ago, family circumscriptions and the placement of many genera have changed dramatically and continue to evolve as a result of modern phylogenetic studies. Modern family placements will be used for the Madagascar Catalogue based on the APG system. In order to facilitate the use of this system, especially by those not familiar with the many changes it includes, we will publish a synopsis of the families and genera currently recognised in Madagascar. This will also serve as an index to the printed version of the Catalogue. A draft synopsis will be available by end-2005, and the final version will be published at the end of 2008. Revision to this will be made available online.

3 Conclusions

While the Madagascar Catalogue project is very ambitious and the products available at the end of 2008 will inevitably contain some imperfections, we are confident that this endeavour will make an important contribution to the study of the flora of Madagascar. It will provide a reliable basis for calculating up-to-date statistics about the size of the flora, levels of endemism, etc. Moreover, the Catalogue will highlight gaps in our knowledge and, we hope, stimulate future generations of botanists to continue improving our understanding of the flora. Finally, the project should also stimulate the conservation community, decision makers and funding agencies to recognise fully the importance of the Malagasy flora and the need to pursue basic plant biodiversity research in order to achieve sound management and lasting protection of this critically important portion of global biodiversity.

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APPENDIX 1. Sample treatment of Asteropeiaceae for the printed checklist.

Asteropeiaceae

1 endemic genus, 8 endemic species.

***Asteropeia* Thouars**
Syn.: *Rhodoclada* Baker
8 endemic species.
Ref.: Schatz *et al.*, 1999.

***Asteropeia amblyocarpa* Tul.**
Syn.: *Asteropeia amblyocarpa* Tul. var. *longifolia* H. Perrier, nomen inval.; *Asteropeia rhopaloides* (Baker) Baill. var. *angustata* H. Perrier, nomen inval., pro parte.
Endemic. Shrub or tree. Subhumid and Dry, Forest and Woodland. 0–2000 m.
Prov.: ANTA, ANTS, FIAN, MAHA, TOLI
PA: Andohahela, Andringitra, Ankarafantsika
Cons. Stat.: LC
Type: BERNIER 281 (HT: P; IT: P)
Voucher: C. BIRKINSHAW *ET AL.*, 725 (MO, P, TAN).

Asteropeia amblyocarpa Tul. var. *longifolia* H. Perrier, nomen inval. = ***Asteropeia amblyocarpa* Tul.**
Asteropeia amblyocarpa Tul. var. *matrambody* Capuron = ***Asteropeia matrambody* (Capuron) G.E. Schatz, Lowry & A.-E. Wolf**
Asteropeia bakeri Scott Elliot = ***Asteropeia multiflora* Thouars**

***Asteropeia densiflora* Baker**
Syn.: *Asteropeia sphaerocarpa* Baker; *Asteropeia rhopaloides* (Baker) Baill. var. *angustata* H. Perrier, nomen inval., pro parte.
Endemic. Shrub or tree. Subhumid and Montane, Forest and Woodland. 1000-2000 m.
Prov.: ANTA, FIAN
PA: Andringitra
Cons. Stat.: VU (B1ab2ab)
Type: BARON 40 (HT: K; IT: P)
Voucher: G.E. SCHATZ *ET AL.*, 3965 (MO, P, TEF).

***Asteropeia labatii* G.E. Schatz, Lowry & A.-E. Wolf**
Syn.: *Asteropeia micraster* H. Hallier var. *angustifolia* H. Perrier, nomen inval.
Endemic. Shrub or tree. Subhumid and Dry, Forest and Woodland. 500-2000 m.
Prov.: FIAN, TOLI
PA: Andringitra, Isalo
Cons. Stat.: LC
Type: LABAT, DU PUY, & ANDRIANTIANA 2411 (HT: P; IT: K, MO, TAN, TEF, WAG).
Voucher: G.E. SCHATZ *ET AL.*, 3971 (MO, P, TEF).

***Asteropeia matrambody* (Capuron) G.E. Schatz, Lowry & A.-E. Wolf**
Syn.: *Asteropeia amblyocarpa* Tul. var. *matrambody* Capuron
Endemic. Tree. Humid, Forest. 0-500 m.
Prov.: ANTS, TOAM
PA: Ambatovaky, Betampona, Masoala
Cons. Stat.: VU (B1ab2ab)
Type: SERVICE FORESTIER 8304 (HT: P; IT: K, MO, P, TEF).
Voucher: N.M. ANDRIANJAFY *ET AL.*, 78 (MO, P, TAN, TEF).

***Asteropeia mcphersonii* G.E. Schatz, Lowry & A.-E. Wolf**
Endemic. Shrub or tree. Humid and Subhumid, Forest. 500–1500 m.
Prov.: TOAM
PA: Analamazaotra-Périnet, Zahamena
Cons. Stat.: EN
Type: MCPHERSON 17528 (HT: MO; IT: K, P, TAN, WAG).
Voucher: J. RABENANTOANDRO *ET AL.*, 136 (MO, P, TAN).

***Asteropeia micraster* H. Hallier**
Endemic. Shrub or tree. Humid, Forest. 0–500 m.
Prov.: FIAN, TOAM, TOLI
PA: none
Cons. Stat.: VU
Type: SCOTT-ELLIOT 2514 (HT: P; IT: K)
Voucher: J.L. ZARUCCHI *ET AL.*, 7610 (K, MO, P, TAN).

Asteropeia micraster H. Hallier var. *angustifolia* H. Perrier, nomen inval. = ***Asteropeia labatii* G.E. Schatz, Lowry & A.-E. Wolf**

***Asteropeia multiflora* Thouars**
Syn.: *Asteropeia bakeri* Scott Elliot
Endemic. Shrub or tree. Humid and Subhumid, Forest. 0–1000 m.
Prov.: ANTS, FIAN, MAHA, TOAM, TOLI
PA: Mananara, Manombo, Masoala, Zahamena
Cons. Stat.: LC
Type: DU PETIT-THOUARS S.N. (HT: P; IT: P).
Voucher: G.E. SCHATZ *ET AL.* 1960 (MO, TAN, WAG).

***Asteropeia rhopaloides* (Baker) Baill.**
Syn.: *Rhodoclada rhopaloides* Baker
Endemic. Tree. Humid and Subhumid, Forest. 500–1500 m.
Prov.: ANTA, ANTS, TOAM, TOLI
PA: Analamazaotra-Périnet, Manongarivo, Masoala
Cons. Stat.: LC
Type: BARON 3096 (LT, Schatz *et al.*, 1999: K; ILT: K)
Voucher: G.E. SCHATZ *ET AL.*, 3513 (MO, P, TAN).

Asteropeia rhopaloides (Baker) Baill. var. *angustata* H. Perrier, nomen inval. = ***Asteropeia densiflora* Baker**, pro parte; ***Asteropeia amblyocarpa* Tul.**, pro parte.

Asteropeia sphaerocarpa Baker = ***Asteropeia densiflora* Baker**

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MERGING TROPICAL AND SOUTHERN AFRICAN FLOWERING PLANT DATA: THE AFRICAN PLANT DATABASE PROJECT

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Abstract

A global perspective of the botanical knowledge of Africa will enhance, among other things, conservation and biodiversity management on the continent. It is thus important to have an updated index of current names and synonyms and exact information on the number of taxa for the African flora south of the Sahara. Developments in information technology make it possible to store information in databases with the advantage of continual updating, thus providing current information. A joint project between the National Herbarium, Pretoria (PRE) and Conservatoire et Jardin botaniques de la Ville de Genève (CJBG) is combining existing datasets of the *Flora of southern Africa* (FSA) and *Enumération des plantes à fleurs d'Afrique tropicale* (EPFAT) to produce an angiosperm database and checklist for sub-Saharan Africa. Although there is still much work to be done, the African Plant Database (APD) is progressing well. Merging the two datasets is not a straightforward process and it is important to bear in mind that the aim of the APD is not to solve taxonomic problems. It rather highlights discrepancies, providing useful information about problematic taxa where revision and further study are necessary. The end products of the APD project will be a hardcopy checklist, an electronic version accessible through the internet, and possibly a CD. The APD is a first important step towards a more comprehensive database that can include other information such as maps, illustrations, ecological information, etc.

Résumé

Mise en commun des données sur les plantes à fleurs d'Afrique tropicale et australe: le projet 'African Plant Database'. Une perspective globale de la connaissance botanique de l'Afrique mettra en valeur, entre autres, la conservation et la gestion de la biodiversité sur le continent. Par conséquent, il est important de disposer d'un index mis à jour des noms courants et des synonymes ainsi que de l'information exacte concernant le nombre de taxons constituant la flore de l'Afrique sub-saharienne. Les développements de la technologie de l'information rendent possible le stockage d'informations sous forme de bases de données avec l'avantage d'une mise à jour continue qui permet de fournir l'information actuelle. Un projet mené conjointement par le 'National Herbarium', Pretoria (PRE) et les 'Conservatoire et Jardin botaniques de la Ville de Genève' (CJBG) combine les données existantes de la 'Flora of southern Africa' (FSA) et de l'Enumération des plantes à fleurs d'Afrique tropicale (EPFAT) pour produire une base de données des angiospermes et une check-list pour l'Afrique sub-saharienne. Bien qu'il reste beaucoup de travail, l''African Plant Database' (APD) progresse bien. Fusionner les deux jeux de données n'est pas un processus évident et il est important de tenir compte du fait que l'objectif d'APD n'est pas de résoudre des problèmes taxonomiques. Elle met plutôt en lumière les désaccords et fournit l'information utile au sujet des taxons problématiques pour lesquels une révision et des études ultérieures sont nécessaires. Les produits finaux du projet APD seront une check-list imprimée, une version électronique accessible via internet, et vraisemblablement un CD. L'APD est un premier pas important vers une base de données détaillée qui peut fournir d'autres types d'informations comme des cartes, des illustrations, de l'information écologique, etc.

Key words: Checklist, database, internet access, Southern Africa, Tropical Africa.

1 Introduction

Before the biodiversity of an area can be properly managed and conserved, it is important to know what species occur in the area. Thus, the first step towards conservation should be the production of a species inventory or checklist. Furthermore, the name of an organism is the key to all accumulated information regarding that organism. Despite the obvious value of inventories and checklists, very few complete checklists exist for most areas of the world.

Several international thrusts are in place to try and rectify this situation. Some are focussing on specific taxa, for instance the Species Plantarum Programme with its aim to produce a World Flora; the Global Plant Conservation Strategy (www.biodiv.org/doc/meetings/sbstta/sbstta-07/official/sbstta-07-10-en.doc) aiming to halt the current and continuing loss of plant diversity, with one of its objectives to document the plant diversity of the world; and the Global Plant Checklist (www.bgbm3.bgbm.fu-berlin.de/iopi/gpc) which intends to produce a checklist of the plants of the world that will provide a backbone to which users can append their more specialised information. Other thrusts have more ambitious goals to include all life forms into their inventories and checklists. These include the All Species Project (www.all-species.org) with the grand aim of recording and genetically sampling every living species of life on earth within one human generation; Species 2000 (www.sp2000.org) that has the objective of enumerating all known species of plants, animals, fungi and microbes on earth as the baseline dataset for studies of global biodiversity; and the Global Biodiversity Information Facility (www.gbif.org) which will be an interactive network of biodiversity databases and information technology tools enabling users to navigate and put to use the world's vast quantities of information on biodiversity.

Most of these thrusts depend on partnerships with other institutions and organisations worldwide to obtain the necessary information and link to databases kept by their collaborators. They also encourage the completion of subtargets or milestones consisting of regional components that can later be consolidated into a global whole. In this respect the African Plant Database (APD) project, which is described in this paper, can play an important role as a regional component of a global angiosperm database and checklist.

2 The floristic diversity of Africa

Despite the fact that our knowledge of the extremely diverse African flora is far from complete, the available information base is still more advanced than those for either tropical America or Asia (Morat & Lowry, 1997). The continent, excluding Madagascar, is home to 271 vascular plant families (including 31 pteridophyte families) of which 27 are endemic (10% endemism). These 271 families are represented by 3750 genera, with ± 224 of these being continental endemics (± 6% endemism). Africa harbours 40,000–50,000 vascular plant species, and possibly as many as ± 60,000 species (Beentje *et al.*, 1994; Global Environment Outlook, 2000). However, certain estimates go as high as 74,000 species (Govaerts, 2001). Around 35,000 species are endemic to the continent, giving a species endemism of 58–88% (Beentje *et al.*, 1994; Klopper *et al.*, 2002).

Although the African flora is very distinct at the genus and species levels, the continent has fewer species than either South America or Asia, and many species are relatively widely distributed within the continent. Representation of certain plant families, such as Lauraceae and Palmae, is relatively poor in Africa. Furthermore, the continent also has fewer species of epiphytes compared to South America and Indomalaysia. A drier climate, losses due to past climatic fluctuations and long-term human influence are among the reasons for this relative impoverishment of the tropical African flora compared to those of South America and Asia (Beentje *et al.*, 1994; Klopper *et al.*, 2002).

Traditionally, the documentation of Africa's plant diversity has been through a number of so-called Flora products, based on Flora regions that were defined during colonial times (Klopper *et al.,* 2002). The *Enumération des plantes à fleurs d'Afrique tropicale* (EPFAT) has served to provide a single integrated list of flowering plant species for the countries south of the Sahara, southwards to and including the *Flora Zambesiaca* area. It deals with ± 26,300 taxa. The APD aims to combine the EPFAT list with that of the PRECIS (Pretoria Computerised Information System) database maintained by the National Botanical Institute (NBI) of South Africa (now the South African National Biodiversity Institute) for the Flora of southern Africa region (FSA), which comprises ± 23,000 taxa. This will produce a complete database for the angiosperm flora of sub-Saharan Africa.

3 History of the African Plant Database initiative

The concept of jointly producing an African Plant Database and Checklist was conceived about nine years ago at the XIVth Congress of the Association pour l'Etude Taxonomique de la Flore d'Afrique Tropicale (AETFAT) held at the Wageningen Agricultural University in the Netherlands from 22 to 27 August 1994. At that time one of us (GFS) had preliminary and informal discussions with A. Stork and J.-P. Lebrun on initiating such a project. Subsequently the outline of the basic concept was jointly developed and resulted in the following draft treatment for three fictional accepted species within the genus *Salacia*, with their respective synonyms and basionym:

T – SALACIA ALATA De Wild.
syn.: S. africana Willd.; S. natalensis Acocks
TS – AQUIFOLIA L.
syn.: S. keniensis Pic.-Serm.
T – CONVOLVULOIDES (L.) Acocks
Bas.: Physalis convolvuloides L.

The "T" indicates the presence of the species in tropical Africa only, while "TS" indicates its presence in both southern and tropical Africa. Such references to the respective regions of occurrence of a taxon therefore guide the reader to sourcing the appropriate literature.

The concept of the content of the APD has not changed essentially from the above over the past nine years, as its intention has deliberately been not to duplicate the Lebrun & Stork (1991, 1992, 1995, 1997, 2003) and PRECIS (Arnold & De Wet, 1993; Germishuizen & Meyer, 2003) series of publications. This brand new, significant hardcopy publication and web-based product should rather provide a first step towards accessing the considerably more comprehensive information sets held in these publications.

The reason why the timing was ripe for discussing this joint project in 1994 was that the National Botanical Institute (NBI) had just published a further approximation in its annotated southern African plant checklist series (Arnold & De Wet, 1993), while the annotated tropical African floristic checklist had just seen the first two numbers (Lebrun & Stork, 1991, 1992) in its multivolume series through the press and onto bookshelves. Both products comprehensively dealt with the indigenous and naturalised floras of the regions they treated. With these projects in place, at Pretoria and Geneva respectively, and the publications available, the stage was set to foster closer collaboration between the NBI and the Conservatoire et Jardin botaniques de la Ville de Genève (CJBG), with a view to compiling a near-complete continental angiosperm checklist for Africa south of the Sahara. Shortly thereafter formal contact was established with the CJBG and in Pretoria a start was made with the computerisation of the set of tropical African plant names.

Over the next few years the NBI in Pretoria made slow but steady progress with computerising the names included in the early parts of the tropical African checklist series (Lebrun & Stork, 1991, 1992), while the authors steadily expanded the tropical African project to its logical, four-volume conclusion (Lebrun & Stork, 1995, 1997). By the end of 2000 the NBI's process of computerising the comprehensive set of tropical plant names was complete. Throughout this period the NBI also kept its database of southern African plants current, through selectively accommodating name changes proposed for components of the FSA flora.

The collaboration that initially started as an informal activity was now ready to be elevated to a formal level. Following negotiations between the NBI and CJBG in March 2002, a mutually beneficial agreement was signed between the two organisations. The electronic EPFAT database, held in Pretoria, was presented to the CJBG at that stage. At that time the FSA and EPFAT name databases existed as two separate electronic entities in Pretoria, requiring harmonisation before further development could be contemplated.

4 The southern African component: PRECIS

Over the past 30 years southern African plant taxonomists and environmental planners have been fortunate in having PRECIS at their disposal to facilitate plant systematic research and informed environmental decision-making. From its inception the PRECIS database has covered the FSA region, i.e. Namibia, Botswana, Swaziland, Lesotho and South Africa. The plant name component of this database therefore carries information on about 24,000 taxa. Development of PRECIS began in the early 1970s with the computerisation of the herbarium collections of the National Herbarium (PRE). This was coupled with the adoption of a quarter degree grid reference system for specimen localities. The focus was predominantly collection-based with the database structured in such a way as to also facilitate information retrieval at the taxon level. The initial phase of encoding continued into the mid-1970s by which time computerisation of the 450,000 existing specimens held at PRE was completed. Encoding of new specimens accessioned into the herbarium was carried out concurrently with the encoding of existing specimens and has continued uninterrupted until the present. Today PRECIS holds information on nearly 800,000 collections representing over 20,000 indigenous Southern African plant taxa housed at PRE.

Restructuring of PRECIS took place on three occasions in order to make information in the system more easily accessible to users and, more recently, to provide extended coverage by including data at the taxon level. The development of PC-based satellite systems also took place to allow for the use of selected components, such as the specimen component, by other herbaria throughout the subregion. Today this particular component is used and supported at over 25 herbaria in 11 countries throughout southern Africa. The use of PRECIS has become an invaluable tool throughout the region, providing access to critical information on the botanical resources of the region. It has considerably streamlined both herbarium curation and taxonomic research. PRECIS, maintained primarily by the NBI's Northern Data Management Unit and taxonomists of the National Herbarium in Pretoria, has developed into a comprehensive system of linked literature, taxon and specimen components. Annually, over 450 requests are processed at the NBI's Data Unit for PRECIS information, both from local and overseas users. PRECIS information has proved to be invaluable at all levels of environment assessment and resource management.

At present, PRECIS includes detailed coverage of descriptive morphology, literature, plant uses, conservation data and some general taxonomic information only for a small subset of about 300 important indigenous medicinal plant taxa. Much of this information resides in a stand-alone database still to be incorporated into the main centralised PRECIS system. A current development in the expansion of the system at the taxon level is the production of the Concise Flora of Southern Africa. Forming the nucleus of this project is the list of current and alternative names (synonyms) housed in the Plant Names (Nomenclatural) component of PRECIS. This project will link basic ecological, morphological and regional distribution data to current names for the full complement of southern African plant taxa.

This comprehensive database system represents one of the most powerful research tools available to plant scientists working on the rich southern African flora and vegetation. However, computerisation of a plant checklist is not seen as an end in itself. The acquired capacity in capturing and analysing fundamental botanical data serves as a catalyst for promoting associated botanical activities. The PRECIS system represents a technological breakthrough that will ultimately combine the power of the computer with the contents of the most representative southern African collections of preserved plant specimens.

5 The tropical African component: EPFAT and its updates

Despite the fact that the Geneva Herbarium (G) houses significant African plant collections, this is not its main strength and consequently, until the mid-1960s, African studies were not its main focus. When Professor J. Miège became the director of the CJBG, he brought with him a vision to develop African botany at the institute. In 1974, the AETFAT Congress took place in Geneva and A. Stork has been employed since 1973 to help with the preparation of this congress. She already had an African background from her previous position in the Museum of Natural History in Stockholm, where she was also responsible for the management of species distribution maps.

J.-P. Lebrun was active as botanist at the IEMVT in Maisons-Alfort, Paris, from 1962 to 1997, where, as curator of the herbarium, he identified about 80,000 specimens from tropical Africa. The immense botanical knowledge he developed was first published as country checklists (Boudet *et al.*, 1986; Lebrun, 1973; Lebrun *et al.*, 1972, 1990; Peyre de Fabergues & Lebrun, 1976), with numerous updates (see Lebrun & Stork, 1991 for further references).

With this background, it was clear that a fruitful collaboration was possible. The first task they addressed was a list of distribution maps of African vascular plants (Lebrun & Stork, 1977; Stork & Lebrun, 1981, 1988). A further collaboration, together with P. Bamps, resulted in an Iconographical Index for African plants (Bamps *et al.*, 1981, 1983, 1984, 1988). The following, logical, step was the publication of a continental checklist of plants for tropical Africa: the *Enumération des plantes à fleurs d'Afrique tropicale* (Lebrun & Stork, 1991, 1992, 1995, 1997).

The precise limits are not the geographical Tropics, but are based on political boundaries reflecting also the existing major floras and plant checklists. The northernmost countries included are, from west to east: Mauritania, Mali, Niger, Chad and the Sudan. The southernmost countries are Angola, Zambia, Zimbabwe and Mozambique. It is thus complementary to the FSA component.

The *Enumération* is a critical checklist, which means that it is not only a list of names, but also (to some extent) an index of synonyms. Further information included in this work consists of bibliographic references at the family and generic levels, main floras in which a species is cited, and reference to illustrations. The number of species per family and genera is given, for the first time allowing an accurate estimate of tropical African plant diversity: 246 families, 2773 genera and c. 26,300 species.

Thinking that these two indefatigable authors would remain idle after this incredible accomplishment would be wrong. Since then, they have undertaken a new task: *Tropical African flowering plants, Ecology and Distribution*, which documents all tropical African flowering plant species, including information on habit and the vegetation type in which they are found, and which provides rough distribution maps for tropical Africa. The work will comprise six volumes, the first one was published recently (Lebrun & Stork, 2003) and the second is at the manuscript stage.

In the meantime, botanical work on Africa at Geneva had also developed in a project concerning Côte d'Ivoire, incorporating modern techniques such as electronic databases and GIS (Gautier *et al.*, 1999). Taking into account the experience in database management accumulated, it seemed logical to accommodate the Lebrun and Stork efforts in a global database. However, for several reasons, including the methodology of the authors, such a step was not straightforward. All the *Enumération* manuscripts had not been captured in a way that allows a simple transformation into a database. Several attempts have been made from the word processor files as well as from scans of the printed pages, but too much editing work would be required for this to be feasible. The G team came to a stage at which it was considering the possibility of capturing all the information manually. Then G became aware that these data had already been captured by PRE.

In March, 2002, the EPFAT database compiled by PRE on the basis of the four volumes of the *Enumération des plantes à fleurs d'Afrique tropicale*, was forwarded to G for improvement. The EPFAT database compiled at PRE, although being an immense and time-consuming task, was not suitable for a straightforward merging with the FSA data. Numerous problems, hidden in the text form, but incompatible with a database format, had to be solved, including:

- Standardisation of author names
- Data discrepancies, such as circular synonyms, etc.
- Encoding in a standard way taxonomic problems that could not be solved
- Dealing with misapplied names

Furthermore, the G team endeavoured to update the data to some extent by taking into account the newly published information included in the first volume of the *Tropical African flowering plants, Ecology and Distribution* (Lebrun & Stork, 2003) and in recently published taxonomic revisions.

6 The role of the SABONET

The Southern African Botanical Diversity Network Project (SABONET) is a donor-funded programme aimed at strengthening the level of botanical expertise, expanding and improving herbarium and botanical garden collections, and fostering closer collaborative links among botanists in the southern African subcontinent. SABONET is funded by the Global Environment Facility (GEF)/United Nations Development Programme (UNDP) and co-funded by the United States Agency for International Development (USAID)/World Conservation Union–Regional Office for southern Africa (IUCN-ROSA).

The main objective of SABONET is to develop a strong core of professional botanists, taxonomists, horticulturists and plant diversity specialists within the ten countries of southern Africa (Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland, Zambia and Zimbabwe), competent to inventory, monitor, evaluate, and conserve the botanical diversity of the region in the face of specific development challenges, and to respond to the technical and scientific needs of the Convention on Biological Diversity (Huntley *et al.,* 1998).

To enhance the human resource capacity and infrastructure available in the region, SABONET offers regional training courses and workshops, internship programmes to collaborate with centres of excellence, and collaborative expeditions to under-collected areas (Huntley *et al.,* 2002). In addition to this, SABONET has purchased the necessary capital equipment such as computers, printers, microscopes and cameras to aid botanical research. All sponsorship is geared towards achieving two of the major outputs of the Project, namely computerising herbarium specimens (Smith *et al.,* 2003) and compiling national plant checklists (Siebert & Smith, 2004).

Up to March 2003, the 16 participating southern African herbaria (GAB, LMA, LMU, LUAI, MAL, MASE, NBG, NH, PRE, PSUB, ROML, SDNH, SRGH, UCBG, UZL and WIND) have computerised 430,000 herbarium specimens using PRECIS; this excludes the 760,000 herbarium specimens computerised by the National Herbarium (PRE) before the SABONET Project was initiated. The computerisation rate in the participating herbaria stands at 150,000 specimens per annum, which means that 600 specimens have been computerised per working day in southern Africa with SABONET funding (Arnold & Siebert, 2002). This process of documenting plant life is probably one of the most affordable endeavours of its kind in the world (Smith *et al.,* 2003).

In November 1999 the first SABONET-supported national plant checklist was published for one of the participating southern African countries (Craven, 1999). This publication documented for the first time the 4200 vascular plants of Namibia. Since then, checklists for the grasses of Zimbabwe (540 taxa; Chapano, 2002), Lesotho (300 taxa; Kobisi & Kose, 2003) and Namibia (426 taxa; Klaassen & Craven, 2003) and the trees of Botswana (440 taxa; Setshogo & Venter, 2003) were also published. At present, one of the main drives of the project is to publish the reviewed vascular plant checklist of Zimbabwe consisting of approximately 6000 known plant species and infraspecific taxa. Currently country-level checklists are also being prepared for Botswana, Lesotho, Malawi, Mozambique, South Africa, Swaziland and Zambia. By delivering these products the Project commits itself to the expectations of the donor agency to meet priority outputs that will regularly make available botanical information to stakeholders (Siebert & Smith, 2004). Given the priorities of the SABONET Project, it was a natural expansion of its functions to also encompass the production of a joint African Plant Checklist for the continent south of the Sahara and SABONET is proud to be associated with this initiative.

7 Combining the two taxon lists: problems and challenges

Combining the two taxon lists in the two databases is not a straightforward process. Once a family is updated in both original databases, the EPFAT data are sent to PRE to undergo the merging process. In most cases, numerous discrepancies arise. They are summarised in a merging report sent to G as a text-file. On this basis, the G team endeavours to solve part of these discrepancies, annotating the report. An annotated report and the new set of data are sent back to PRE, for further examination and improvement of FSA data. The merging process is repeated with the new set of data. If the result is still not considered satisfactory, the cycling of information is repeated. When the merge is considered satisfactory, the merged data are sent to G where they are incorporated into the final merged database.

We are not going to enter into the details of the IT problems we met and solved. Suffice it to say that although both datasets exist in the form of MS-Access 2000 databases, the merging and follow-up of corrections is a challenging task. We will rather concentrate here on the nomenclatural and taxonomic issues raised by the process.

The main categories of problems encountered when merging the two lists are:

7.1 Nomenclatural problems

- Spelling of names

Most of the spelling discrepancies can be solved either by referring to a commonly accepted standard (for genera: ING (Farr *et al.*, 1979, 1986)) or by consulting the original publication.

- Authors of names

The accepted standard is *Authors of plant names* (Brummitt & Powell, 1992). However, discrepancies often arise when comparing the two lists because of different origins of the data. Once again, coming back to the original publication may help solving these discrepancies. It should be noted that although a mismatch in publication authors can generally be solved by the simple application of the nomenclatural code, most of the remaining discrepancies originate from the inclusion of “ex” authors and their confusion with “in” authors, and their different placement in relation to the primary author of the taxon. As there is a general tendency to omit these authors, the possibility of doing this systematically should be considered in the future, but one must be very careful not to discard the primary author in error.

7.2 Taxonomic problems

- Family concept: attribution of genera to families

There are discrepancies as to family concepts between FSA and EPFAT. However, families are principally a practical means of arranging binomials, and besides, they are subject to numerous changes, especially nowadays. In this respect, the use of a standard (Brummitt, 1992) emerges as the simplest way of handling this problem. Therefore, when the family concepts of the two datasets are similar, that view is followed, but where the concepts differ, Brummitt (1992) is followed.

- Generic concept: attribution of species to genera, synonyms

As both lists are critical (i.e. intending to have only one current name per taxon), the generic concepts adopted, as well as the taxonomic treatments followed, are of primary importance. Since both lists depend on treatments that are often limited geographically, it is clear that in many cases there is no general consensus on which name is current, and which is a synonym. The problem raised here is of course not specific to this merging of two separate checklists, but is general in botany and is, for instance, raised daily when curating a herbarium with worldwide collections. The present work does not pretend to solve these discrepancies, and the anticipated outputs are being designed to reflect the FSA and EPFAT taxonomic views in parallel, and in some instances even propose alternate views as remarks or footnotes. In this way, it should help pointing out areas for future research in taxonomy. The evolving nature of modern access to data (website) allows future changes to be implemented and available instantly for the user.

- Infraspecific level

Merging the two lists has also revealed an immense area for discrepancies at the infraspecific level. These include:

- Species subdivided into infraspecifics in one list, but not in the other.
- Species subdivided at a different level, e.g. subspecies vs. varieties.
- Infraspecific cascades (i.e. species in which both subspecies and varietal levels are accepted in one or both lists).
- Synonymy: to which infraspecific does a heterotypic synonym apply?
- Once more, the database is designed to present both views, waiting for a future taxonomic treatment to solve these issues.

As a whole, and from a practical point of view, discrepancies can be classified as follows:

- Problems that can be solved rapidly by access to literature (most of them are nomenclatural). They will be solved in the editing process.
- Problems that need more time/work than we can allow, but that can nevertheless be solved through literature. They will be marked, but solved later.
- Problems that are of a taxonomic nature and need field/herbarium work. The resolution of these problems will depend on external work and the solutions will be incorporated as they become available.

8 Present state of the work

Currently (March 2004), all FSA families have been updated by PRE. In addition 213 EPFAT families (representing c. 79% of the families) have been updated by G and are ready to be merged. On this basis, the merging process has already been carried out on 149 families, of which 63 have reached the final stage. For the families that have been completely merged a family report for the hardcopy publication has been finalised. Furthermore, the merged database component of these families and the additional morphological and distribution data from PRECIS have been forwarded to G to meet the corresponding data from tropical Africa and will be incorporated into the website at a further stage.

9 The outputs

The outputs of the APD project will be:

- A hardcopy publication of the checklist.
- A website based on the merged database component that will also include additional morphological and distribution data for all taxa.
- A CD containing similar information.

The hardcopy publication will be funded by SABONET and is a milestone, to be published only once at the end of the merging process. It will consist of family reports arranged alphabetically, first the dicotyledons and then the monocotyledons. Each current name and synonym will be preceded by a flora code (S or T or both), indicating the origin of the name as discussed in the initial concept. An asterisk attached to this flora code will indicate a naturalised taxon. Although hybrids and certain cultivated taxa are included in the database, a decision has been made to omit these taxa from the hardcopy publication. Discrepancies between FSA and EPFAT will be highlighted to allow easy identification of such existing problems.

Once the final merge has been completed and the hardcopy published, the electronic version of the final merged database will be housed at G. On a monthly basis, an extraction of this Access database will be translated in Oracle 9i, which will be the user database. Access to the database will be free, through the Internet. Queries will be processed using a PHP interface, in English and French. A first screen will allow entering of simple queries based on a scientific name (family, genus, or binomial) or even on an authority. If the query is unequivocal and applies to a unique accepted name, the data of the corresponding taxon will be directly provided: accepted name, family, synonyms relevant for FSA and EPFAT, and ecological information (distribution, habit, vegetation type) where available. When a query gives several results (query based on a genus name for example, but also in cases when a misapplication has been commonly used and is thus recorded in the database), an intermediate screen will display the various possibilities corresponding to the query, so that the user can choose the taxon for which detailed information is required. When the original query of the user leads to a name that is not accepted, a second intermediate screen will appear showing the synonymy and allowing a link with a corresponding accepted name, leading to the final screen. It is also through this intermediate screen that conflicting taxonomic views between EPFAT and FSA are handled.

Unlike the hardcopy, which is only a milestone in the process, the electronic version is the long-term goal of the project and will be regularly updated, incorporating additions and corrections as well as other types of data (images, ecological information) at a further stage.

The third product foreseen is a CD, incorporating the dataset together with the query tool. It will be much less bulky than the book, but will of course require a computer, but no internet access. Such a product might prove useful in countries with problematic internet access, as well as for remote research stations. Depending on the interest of users, this CD could be up-dated annually.

10 The future

As mentioned above, the next logical step will be to incorporate ecological data in the database: for tropical Africa such data are currently being captured by J.-P. Lebrun and A.L. Stork in their new series: *Tropical African flowering plants: Ecology and distribution* (Lebrun & Stork, 2003). For southern Africa, these data are mostly already available in PRECIS. The distribution data will be standardised to a rather rough scale and taxa will be considered as recorded or not in a cross-table of political units (countries) and phytogeographic units (main chorologic divisions of Africa, adapted from White, 1983). Habit data will be given using main types of life forms and an additional free text field. Habitat data will include main vegetation types in which the taxon is present, also with an additional free text field.

The bilateral consortium consisting of the NBI and CJBG is also in the process of developing a funding proposal to enable both partners to participate equally in a project aimed at generating electronic images of the type specimens of all the widely accepted names of African plants. This proposed project will build on the E-Type Initiative of the ALL Species Project (Smith & Klopper, 2002; Smith, 2003).

Geographical coverage of the database will also be extended in order to include the islands directly surrounding Africa, which are not included in the EPFAT, like Bioco, São Tomé & Principe, and possibly Socotra. Extension to include Northern Africa is not foreseen, the Sahara being a strong phytogeographical barrier and Northern Africa being included in the Med-Checklist. A much more logical step could be to include the Western Indian Ocean islands (Madagascar, the Comoros and Seychelles and the Mascarenes).

11 Conclusion

Although there is still much work to be done before the APD can see the light, the project is well under way and showing good progress. Because of discrepancies and some other problems, the merging process is not straightforward and can be very time-consuming, depending on the family. Nevertheless, one of the immediate benefits resulting from this collaboration is an improvement of the quality of both original datasets. The checklist does not aim to solve taxonomic problems, but will rather highlight taxa for which future research is necessary, as a second main result. At the end of the process, the database will, for the first time, give a good indication of the number of angiosperm taxa in sub-Saharan Africa. The end products of the APD project will be invaluable to taxonomists working on the African flora and will probably represent a critical step towards a better understanding of the African flora. The APD will serve as a backbone for further developments as mentioned earlier, like integrating ecological information and type images. It can also be used as a shared platform for regional specimen-based databases.

Note Since August 2005, the African Plant Database is available online and can be consulted at http//www.ville-ge.ch/cjb/bd/africa/index.php. The hard copy publication of the checklist is in the final proof stage.

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RIHA, A DATABASE ON PLANT BIODIVERSITY IN WESTERN AND CENTRAL AFRICA: FIRST STEP FOR A NETWORKING OF AFRICAN HERBARIA

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Abstract

RIHA (Réseau Informatique des Herbiers d'Afrique) aims to provide a gateway to information on herbarium collections of Cameroon, Senegal and Togo, and, in the mid term, to other collections in the region. It links data related to plant biodiversity through standardised and coherent units containing information on hierarchial taxon names, collectors, localities, as well as eco-biogeographic and conservation status. Thus, the RIHA model allows access to synthetic information on higher plants of the region. Accessibility of these data via the internet will facilitate the dissemination, processing and interpretation of this knowledge.

Résumé

RIHA, une base de données sur la biodiversité végétale en Afrique de l'Ouest et centrale: première étape vers un réseau d'herbiers africains. RIHA (Réseau Informatique des Herbiers d'Afrique) a pour objectif de fournir un accès à l'information relative aux collections d'herbier du Cameroun, du Sénégal et du Togo et, à moyen terme, à d'autres collections de la région. Elle lie des données relatives à la biodiversité végétale à travers des unités standardisées et cohérentes contenant l'information sur les noms de taxons hiérarchiques, les récolteurs, les localités ainsi que le statut éco-biogéographique et de conservation. Ainsi, le modèle RIHA permet l'accès à l'information synthétique sur les plantes supérieures de la région. L'accessibilité de ces données via internet facilitera la diffusion, le traitement et l'interprétation de ces connaissances.

Key words: Cameroon**,** herbarium collections, linking data, regional network, Senegal, Togo

1 Introduction

Numerous botanical databases have been developed in the last decade, several of which are accessible on-line (Wilson, 1993). Broad models (Berendsohn *et al.*, 1999) permit the manipulation of all types of biodiversity objects, including herbarium collections, living plants, taxonomic treatments and identifications, and geographic analyses; one can be found in Gautier *et al.* (1999), an application using botanical database at country level (Ivory Coast), in a GIS approach. However, we have chosen to adopt a model in which herbarium specimens serve as the source for multiple treatments (Hoff *et al.*, 1989) and where the names of taxa are linked to a single hierarchical classification (Badré *et al.*, 1985). The model presented here is focused on the use of botanical data for African countries such as Senegal, Togo and Cameroon (https://www.orleans.ird.fr/letouzey/). Establishing a network among these herbaria would enable them to share data on the geographic distribution of specific and infraspecific taxa and their current or potential use. By providing access to taxonomic and nomenclatural data from bibliographic sources RIHA should improve the management and the protection of plant biodiversity in this region. This information database for the entire region could then be linked to larger networks throughout tropical Africa.

1.1 Structure of the database

For pragmatic reasons, the model proposed here deals exclusively with the objects traditionally managed by a herbarium:

i) Herbarium specimens
ii) Wood collections
iii) Spirit collections

Several questions may arise when using the herbarium specimens' names including:

The accuracy of the specimens' identification
The correctness and the legitimacy of the plant name, i.e. whether it is in conformity with the International Code of Botanical Nomenclature (Greuter *et al.*, 2000)

Despite the views of Pullan *et al.* (2000), a taxonomic consensus can also be considered as a viable solution when faced with a multiple classification (MCM). The goal is to provide a more or less stable nomenclature even if, for example, this requires long and time-consuming updates. In the end, we have selected the most recent taxonomic opinion as the criterion to be used. From a practical perspective, this is no more time-consuming than an MCM, since updates provided by taxonomic revisions are handled only by the person responsible for the taxonomic thesaurus.

1.1.1 Thesauri

Building of thesauri involves standardization of all data, synonyms for persons, plant names, and localities, and hierarchy for the latter two categories.

Botanical databases are designed to organise data obtained from multiple sources (collections, bibliographic data, ethnobotanical data, etc.) and to establish new links between various domains (nomenclature, descriptive botany, forestry, species conservation, ethnopharmacology, etc.), which must be accommodated in the initial structure before the pertaining data can be incorporated. The same is true for the names of collectors, persons making identifications, and authors of botanical publications. Standardisation implies bringing various functions into a single model, such as the management of synonyms. In addition to synonymy of plant names, this could also involve names of persons, localities, or countries. Although this kind of homogenisation may impose a constraint, it is nevertheless essential for establishing a regional network of herbaria ("Réseau Informatique des Herbiers d'Afrique"), because information exchange requires use of a common language.

For example, the name of a plant is traced by its taxonomic rank, links to higher taxa, and its taxonomic position relative to names at the same or different ranks (in which case they must conform to the Code). Several equivalent names will apply to a single biological entity through synonymy. The tables that determine the principal relations linking specimens to plant names or localities are particularly important and constitute the thesauri.

1.1.2 The plant name thesauri

All the names on herbarium sheets are compiled in the table "herbarium names" that is related to a taxonomic thesaurus by an equivalence link (which does not necessarily have a one to one relationship), which indicates synonyms or correct names (Fig. 1). First, this catalogue makes it possible to arrange the names that appear physically on specimens, since only correct plant names or synonyms will appear, along with their nomenclatural status. Development of this reference base primarily involves compilation from the bibliography, with at least the taxon diagnosis. This thesaurus contains the accepted names as found in Lebrun & Stork (1991, 1992, 1995, 1997) or more recent monographs, where necessary. It is always linked to a higher taxon, and it also reflects the adopted classification for (supra) generic taxa (Cronquist, 1988; Kramer & Green, 1990; APG, 1998). A name is also linked to its synonyms, if any. These data are thus arranged in a hierarchy and all synonyms are given (as before). The system contains not only information concerning classification, but also on distribution by country, bibliography, vernacular names, biological status and IUCN category which are directly associated (Fig. 2).

1.1.3 Locality table

Locality data are derived from a gazetteer, a reference base of all the names that appear on the maps of a given country. Each name corresponds to geographic coordinates expressed in degrees, minutes and seconds. The source can be indicated by providing the name of the corresponding map.

Synonymy can be handled for orthographic variants, translations of local names, etc. This table is associated to collections (Fig. 3).

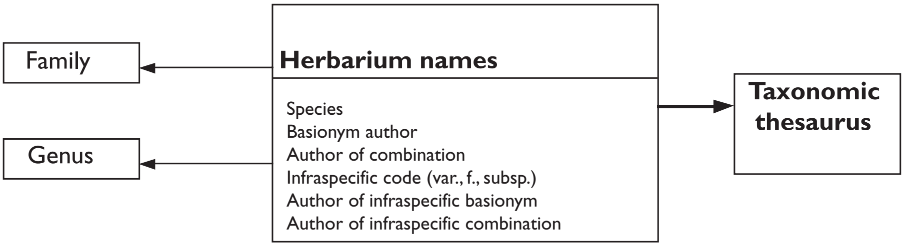

FIG. 1. Contents of the "Herbarium names" entity and its association to family, genus and the "Taxonomic thesaurus".

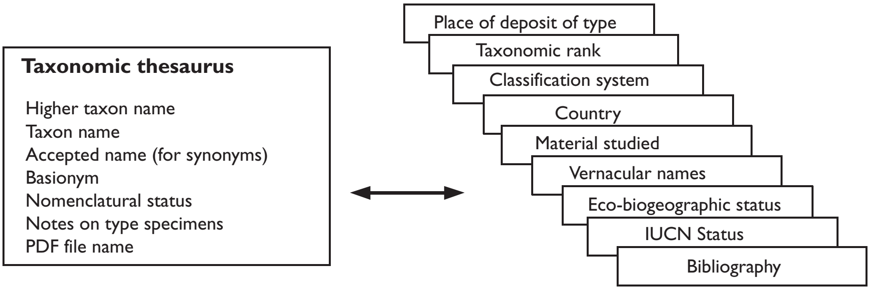

FIG. 2. Contents of the "Taxonomic thesaurus" unit and its various associations.

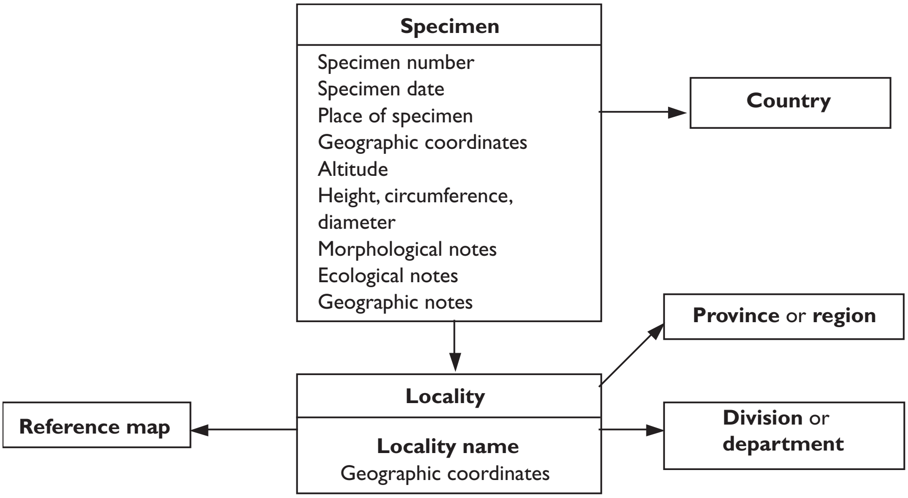

FIG. 3. Scheme of data relating to geographic locality.

1.1.4 The persons table

This table consists of all plants' author names included in the taxonomic thesaurus and the bibliography, as well as the collectors' names and/or the determinavit. Standardisation of persons' names is accomplished by using catalogues and other existing work. Brummit and Powell (1992, also accessible on the Web at the IPNI site: http://www.ipni.org/) is used for authors' names, "Index Herbariorum – Collectors parts" (Lanjouw & Stafleu, 1954; Chaudri *et al.*, 1972; Vegter, 1976, 1983, 1986,1988) is used for collectors' names. For this table, we have decided that, for a first name, we will use the initials followed by the full family name (Fig. 4).

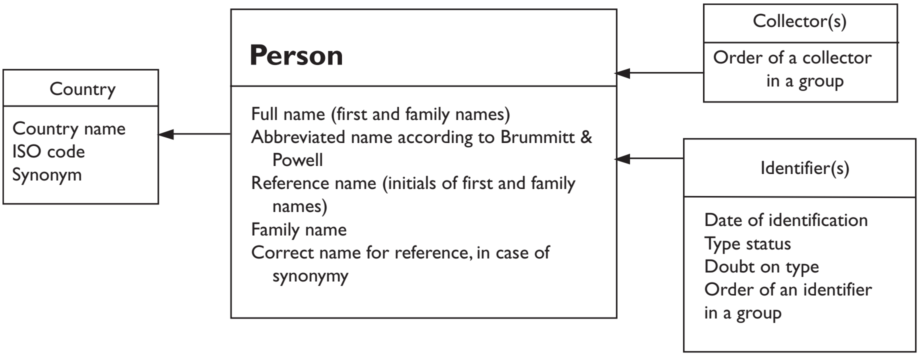

FIG. 4. Contents of the "Persons" unit and its association to collectors, person(s) making identification, and country.

This type of table is not hierarchical, as all the person names are at the same rank; it, however, gives all synonymy. Synonymy is necessary in order to deal with orthographic variants, names changing (for married women for instance, or those who use different transcriptions, such as for Chinese names), which can appear on specimen labels as well as in bibliography. When data are being entered, a single person's name should be used, whether for collectors or for authors of botanical publications.

1.1.5 Country table

Countries are associated with localities, persons and IUCN eco-biogeographic status.

1.1.6 Bibliography

Titles of books follow Stafleu & Cowan (1976–1988) and Stafleu & Mennega (1992–2000). Periodical names follow Lawrence *et al.* (1968) and Bridson & Smith (1991). Bibliographic references contain specimens citations for a particular taxon in a given publication, references to diagnoses with data concerning the type, its status and where it is deposited (Fig. 5).

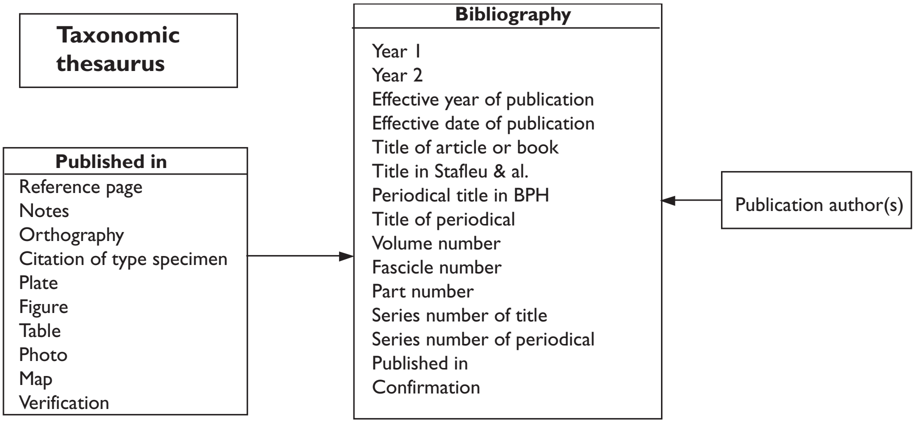

FIG. 5. The "Published in" link ensures a connection between the "Reference system taxon" and the "Bibliography" units. It contains bibliographic data specific to each taxon (page of publication, spelling, type citation, plate, figure, table, photo, map, etc.).

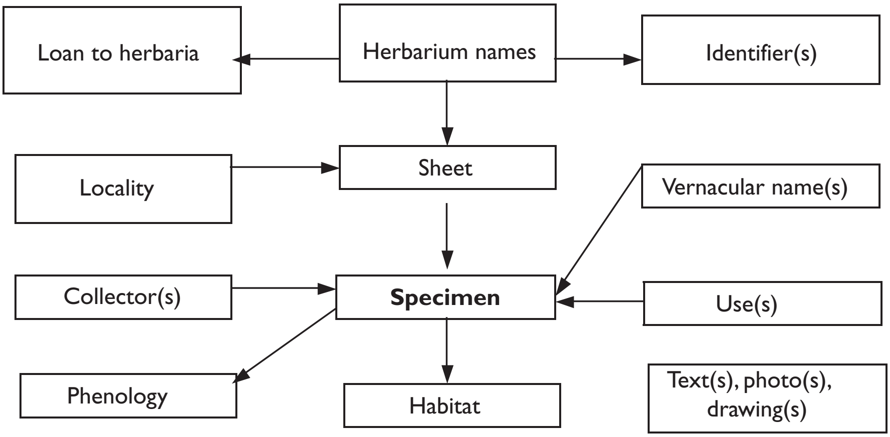

FIG. 6. Distribution of specimen or sample data among several elements of the model.

1.2. Data linked to specimens

Data directly linked to a specimen or a sample are partitioned into several fields, the contents of which are presented above (see Fig. 6).

2 Results

At present the database includes about 45,000 specimens: 35,000 mainly from Yaoundé (YA), 5000 from Dakar (IFAN), and about 5000 each from Lomé (TOGO) and Paris (P). Major families like Caesalpiniaceae, Annonaceae, Apocynaceae, Asteraceae, Cyperaceae, Euphorbiaceae, Lamiaceae, Poaceae and Moraceae are now fully computerized at YA; other families such as Begoniaceae, Burseraceae, Cucurbitaceae, Scrophulariaceae and Zingiberaceae are also databased.

These specimens are linked to over 19,000 localities in the Cameroon's gazetteer, and ± 7500 in Togo's, 11,000 names on labels (herbarium names thesaurus), 3100 taxa names in the taxonomic thesaurus, 23,000 names of collectors and authors, 3600 vernacular names, and 1200 bibliographic references.

3 Conclusion

At this critical time for the conservation of biodiversity, 2005 is the thirteenth anniversary of the Rio Convention. It is important that governments and organisations responsible for managing and protecting biodiversity, along with scientists who are responsible for characterising biodiversity, have ready access to base-line data on taxon names, taxonomy, bibliography, distribution, local diversity and threats, traditional uses or potential for sustainable exploitation. Linking information contained in collections with that obtained from the botanical literature can only contribute to creating a valuable synergy among all of the stake holders. It is hoped that with the establishment of a network in next five years, several tropical African herbaria will be linked via the internet sharing the same thesauri described above. This network will help taxonomic revisions and contribute towards on-line teaching of new African taxonomists; in the medium term, the management of data using GIS technology will also greatly facilitate the analysis and interpretation of botanical data.

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SYNTHÈSE DES INVENTAIRES RÉALISÉS SUR LES ORCHIDACEAE DANS LE CADRE DU PROJET D'EVALUATION DES AIRES PROTÉGÉES DU GABON

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Résumé

Depuis plus de deux ans, la diversité des Orchidaceae gabonaises fait l'objet d'une étude réalisée dans le cadre du projet d'évaluation des aires protégées du Gabon. Des inventaires ont ainsi été réalisés dans 23 sites, principalement au nord du Gabon. Au total, 1024 échantillons d'Orchidaceae ont été mis en culture, ce qui a permis la collecte de 762 échantillons d'herbiers déterminés au rang spécifique ou inférieur. Parmi les 212 taxons répertoriés, 51 sont nouveaux pour le Gabon. Ce pays compte entre 400 et 500 taxons d'Orchidaceae dont 6% d'endémiques. La richesse spécifique est plus importante dans les sites côtiers et dans les Monts de Cristal que dans la partie continentale. La distribution de cette famille au Gabon se répartit selon un gradient d'humidité. La présence dans les Monts de Cristal d'un type de végétation à affinité submontagnarde et doté d'un endémisme propre en Orchidaceae, confirme la présence d'un refuge de forêt montagnard dans cette région. Nous supposons que ce refuge s'étend vers le nord, dans le Parc de Monte Alén, et vers le sud dans le Massif du Chaillu et les Monts Doudou.

Abstract

During more than two years the diversity of Gabonese Orchidaceae has been studied within the framework of the project 'Evaluation of protected areas in Gabon'. Inventories have been made in 23 sites, mainly in the north of Gabon. A total of 1024 orchid specimens have been taken into cultivation, allowing the collection of 762 herbarium specimens identified to species level or below. Among the list of 212 taxa, 51 are new for Gabon. This country has between 400 and 500 orchid species, of which 6% are endemic. Species richness is higher in coastal sites and in the Crystal Mountains than in continental sires. The distribution of this family is correlated with a humidity gradient. The presence of a vegetation type with submontane affinities and with high endemism of orchids in the Crystal Mountains, confirms the presence of a montane forest refuge in this region. We suppose this refuge stretches to the north into the Monte Alén park and to the south into the Chaillu Massif and the Doudou Mountains.

Key words: Orchidaceae, Gabon, Crystal Mountains, endemism, forest refuges

1 Introduction

Le Gabon possède une flore fortement diversifiée qui s'explique par son appartenance à l'une des zones les plus riches d'Afrique, le domaine bas-guinéen défini par White (1983). La flore gabonaise est estimée à plus de 7000 espèces, dont 22% sont endémiques (Brenan, 1978). Devant cette diversité, la nécessité d'un réseau d'aires protégées qui assurerait sa conservation est apparue (Wilks, 1990, Brugière, 1998, Doumenge *et al.*, 2001, 2003a et b). Un projet d'évaluation des Aires protégées du Gabon a été mis en place pour localiser les zones critiques de conservation et estimer l'impact de ce réseau pour la conservation. Le projet a été initié par le Ministère gabonais des Eaux et Forêts à travers la Direction de la Faune et de la Chasse (DFC), en collaboration avec différents partenaires impliqués dans la conservation: Wildlife Conservation Society, WCS, le Fonds Mondial pour la Nature, WWF, et le Centre National de la Recherche Scientifique et Technologique, CENAREST. De nombreux inventaires botaniques et fauniques ont ainsi été réalisés durant les années 2000 à 2002. Ils ont abouti à la création de treize parcs nationaux (Quammen, 2003). Cette étude constitue une première synthèse des inventaires consacrés aux Orchidaceae.

Différents travaux traitant de la flore du Gabon mentionnent des Orchidaceae. La liste des plantes récoltées au nord-est du Gabon (Hallé, 1965a; Hallé & Le Thomas, 1967, 1970; Hladik & Hallé, 1973; Florence & Hladik, 1980) énumère 22 taxons d'Orchidaceae. Le guide de la végétation de La Lopé (White & Abernethy, 1997) signale la présence de 16 espèces et fournit quelques indications sur leur écologie. Sosef *et al.* (2004) signalent 28 espèces dans le refuge forestier des Monts Doudou. Raponda-Walker & Sillans (1961) nous renseignent sur les caractéristiques pharmacologiques et ornementales de 27 Orchidaceae gabonaises. Les travaux consacrés exclusivement aux Orchidaceae sont rares: Cribb *et al.* (1989) ont décrit deux espèces nouvelles du nord du Gabon, Szlachetko & Olszewski (1998a), un nouveau genre et Stévart *et al.* (2003), une espèce nouvelle. Hallé (1965b) s'est intéressé à deux espèces peu connues du Gabon. Un livret présentant les caractéristiques écologiques de 18 Orchidaceae a récemment été publié (Biteau *et al.*, 2001). Par ailleurs, la flore des Orchidaceae du Gabon est en cours de préparation par Szlachetko & Olszewski.

Différentes régions situées dans des pays limitrophes du Gabon ont fait récemment l'objet d'inventaires (Stévart 2003). D'après cet auteur, la richesse spécifique en Orchidaceae du Rio Muni (partie continentale de la Guinée Equatoriale) est de 182, celle de São Tomé et Príncipe atteint 132 et la région de la Réserve de Faune du Dja au sud du Cameroun compte 121 taxa.

2 Méthodologie

2.1 Cadre de l'étude

Le Gabon est situé dans le Golfe de Guinée entre 3°N et 4°S, et 9°O et 14°30'E. Il est bordé à l'ouest sur 800 km par l'océan Atlantique, au nord par le Río Muni (Guinée Equatoriale) et le Cameroun, au sud et à l'est, par le Congo Brazzaville. La partie nord du Gabon présente un climat typiquement équatorial, caractérisé par un régime pluviométrique se répartissant entre deux saisons de pluies séparées par une grande saison sèche en Juillet – Août et une décroissance des pluies en Janvier – Février. La proximité du littoral et l'orographie influencent considérablement le total pluviométrique annuel dont les valeurs extrêmes sont de 1200 mm, à Tchibanga et de près de 3000 mm au nord de Libreville.

La forêt dense équatoriale couvre les trois quarts du Gabon. Caballé (1978) distingue trois types forestiers principaux, caractérisés par leur composition floristique: la forêt du bassin sédimentaire côtier à *Saccoglottis gabonensis*, la forêt centrale gabonaise à Irvingiaceae, Burseraceae et Caesalpiniaceae et la forêt du nord-est, caractérisée par l'absence d'*Aucoumea klaineana*.

Cet inventaire s'inscrit dans le cadre d'une étude de la diversité des Orchidaceae d'Afrique centrale atlantique qui couvre un transect de 800 km s'étendant des îles du Golfe de Guinée à la Réserve du Dja au sud du Cameroun. Les 23 sites inventoriés se trouvent donc principalement au nord Gabon, mais des inventaires ont été réalisés sur le littoral et dans le centre (Tableau 1, Fig. 1). Les 1024 échantillons d'Orchidaceae vivantes, récoltés sur le terrain à l'état stérile, ont été mis en culture dans des ombrières à Tchimbélé (Monts de Cristal), à Libreville et à La Lopé (centre). La liste des espèces présentes dans les 23 sites étudiés est basée sur la détermination au rang spécifique ou inférieur de 762 herbiers conservés à WAG, BRLU et LBV. Ces échantillons proviennent de la littérature mentionnée ci-dessus et des récoltes effectuées directement sur le terrain ou dans les ombrières tout au long des floraisons.

La détermination des Orchidaceae a été effectuée sur base de la littérature existante et par comparaison avec des herbiers de K et de BM.

TABLEAU 1. Caractéristiques des 23 sites inventoriés.

	Sites	**Nombre d'échantillons collectés (n)**	**Richesse spécifique (RS)**	**RS/n**	**Distance par rapport à l'océan (km)**	**Précipitation (mm/an)**
1	Tchimbélé	171	67	0,39	90	2000–3000
2	Libreville	58	38	0,66	0	2000–3000
3	Gamba et région de Rabi	46	36	0,78	45	2000–3000
4	Monts Doudou	36	35	0,97	72	1500–2000
5	Mont Koum (inselberg)	57	28	0,49	211	1500–2000
6	Région de Makokou et de Bélinga	32	28	0,88	360	1500–2000
7	Assep Bengong (inselberg)	28	21	0,75	200	1500–2000
8	Région de la Lopé et Mont Iboundji	20	19	0,95	250	1500–2000
9	Mont Mbilan (sommet du)	30	19	0,63	75	2000–3000
10	Mont Mbilan (bas du)	46	19	0,41	75	2000–3000
11	Kinguélé	23	17	0,74	75	2000–3000
12	Région de Oyem	24	17	0,71	200	1500–2000
13	De Kinguélé à Tchimbélé	23	16	0,70	80	2000–3000
14	Région de Mbé	20	15	0,75	100	2000–3000
15	Andok Foula	34	14	0,41	70	2000–3000
16	De Assok à Tchimbélé	17	14	0,82	80	2000–3000
17	Mont Miwa (inselberg)	19	13	0,68	200	1500–2000
18	Région de Ndjolé	13	13	1,00	160	1500–2000
19	Ossap Anda (inselberg)	16	12	0,75	205	1500–2000
20	Song (Monts de Cristal)	16	12	0,75	73	2000–3000
21	Région de Medouneu	14	11	0,79	135	2000–3000
22	Salem (inselberg)	12	10	0,83	210	2000–3000
23	Ntan (inselberg)	7	6	0,86	180	2000–3000

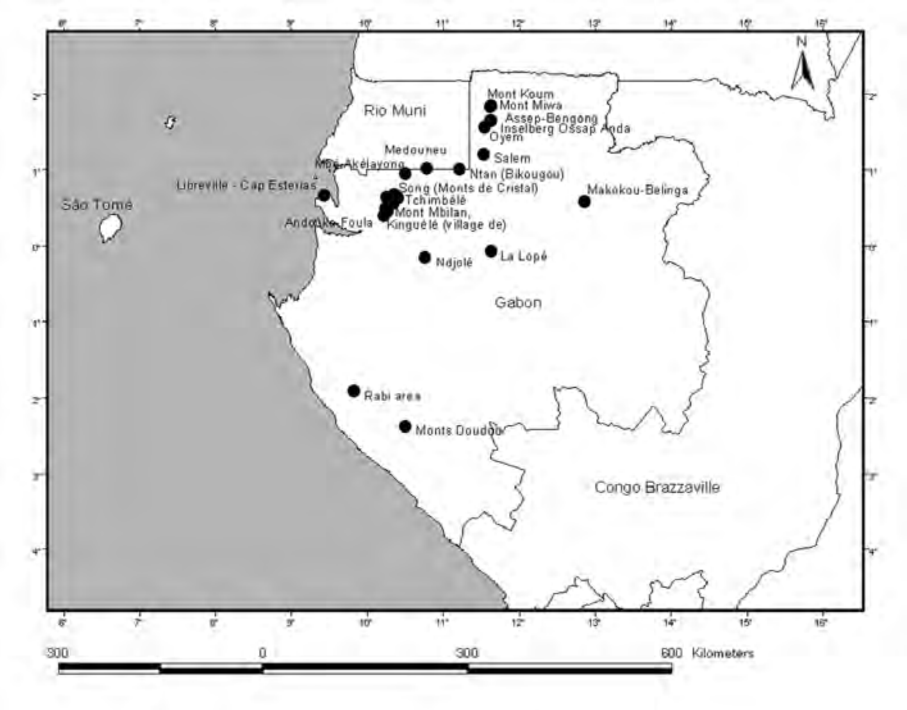

FIG. 1. Localisation au Gabon des 23 sites inventoriés.

2.2 Analyse phytogéographique

L'ordination a été réalisée en présence/absence sur base des listes floristiques des 23 sites par Detrented Canonical Analysis (DCA) à l'aide du logiciel CANOCO (ter Braak & Smilauer, 1998). A une échelle régionale (0–100 km), le paramètre qui explique le mieux les variations de richesse spécifique en Orchidaceae épiphytes est l'humidité atmosphérique (Sanford, 1969). Ainsi, la plus forte diversité en épiphytes par surface se rencontre dans les milieux humides ou montagnards (Gentry & Dodson, 1987; Hietz & Hietz-Seifert, 1995). Par ailleurs, à plus petite échelle le macroclimat et les précipitations semblent être les facteurs expliquant le mieux la distribution des épiphytes. Toutefois, il n'existe à ce jour que peu d'études à cette échelle. Afin de mesurer l'influence de la continentalité sur la richesse spécifique en Orchidaceae, nous avons testé la corrélation entre cette dernière et la distance par rapport à l'océan. Nous avons aussi testé le rapport richesse spécifique/nombre d'échantillons collectés et la distance par rapport à l'océan, et ce pour supprimer le biais apporté par l'échantillonnage. Dans les deux cas, nous avons utilisé les coefficients de corrélation de Spearmann et de Pearson (Sokal & Rohlf, 1995).

3 Résultats

3.1 Flore

Notre connaissance de la flore des Orchidaceae du Gabon reste assez limitée mais une estimation raisonnable fait état de 400 à 500 taxons. Cette estimation est basée sur

- la littérature (Geerinck, 1984, 1992; Summerhayes, 1968; Szlachetko & Olszewski, 1998b, 2001a, 2001b)
- nos nouvelles additions à la flore du pays
- les espèces présentes dans les pays limitrophes et dont l'écologie et la distribution rendent fort probable leur présence au Gabon.

La publication prochaine de la Flore des Orchidaceae du Gabon (Szlachetko & Olszewski, en préparation), devrait permettre d'évaluer avec plus de précisions cette richesse en Orchidaceae. Au final, elle devrait être comparable à celle du Cameroun et largement supérieure à celles des trois autres pays cités (Tableau 2).

L'effort d'échantillonnage très variable entre sites rend la comparaison de leur richesse spécifique peu pertinente. On peut néanmoins constater que la diversité en Orchidaceae est plus importante dans les régions montagneuses ou à fortes précipitations.

Le tableau 1 montre que les deux sites situés le long de l'océan (Libreville, ainsi que la région de Rabi et Gamba) possèdent une richesse spécifique supérieure à 30. Ces deux sites reçoivent de fortes précipitations. La forte richesse spécifique de Tchimbélé s'explique par un effort d'échantillonnage important (Tableau 1: 171 herbiers, rapport RS/n de 0,39) mais surtout parce que cette région montagneuse offre des conditions d'humidité très favorables aux épiphytes et a joué un rôle de refuge forestier durant les périodes glaciaires (Ngok Banak, 2002; Sosef, 1994).

Parmi les sites les plus pauvres, on retrouve un grand nombre de sites continentaux. La forte diversité du Mont Koum s'explique par l'échantillonnage important et celle de la région Bélinga/Makokou par sa superficie très vaste.

Toutefois, nous n'avons pas trouvé de corrélation entre la richesse spécifique et la distance par rapport à la mer ($P > 0,25$). De même, la corrélation entre le rapport richesse spécifique (RS)/nombre d'échantillons collectés (n) et la distance par rapport à la mer ne s'est pas montrée significative ($P = 0,13$). La continentalité et les quantités de précipitations ne semblent donc pas être des paramètres significatifs pour expliquer les variations de richesse spécifique au Gabon. Le paramètre qui expliquerait le mieux la diversité en Orchidaceae au Gabon serait donc la présence d'une chaîne de montagnes s'étalant des Monts de Cristal au Massif du Chaillu.

Parmi les 212 taxons répertoriés dans notre étude, 51 sont nouveaux pour le Gabon (Tableau 3).

TABLEAU 2. Richesse spécifique en Orchidaceae de quelques pays d'Afrique (Stévart, 2003).

	São Tomé et Príncipe	**Guinée Equatoriale**	**Gabon**	**Cameroun**	**Côte d'Ivoire**
Nombre de taxons	132	258	212 (400–500)	489	240
Superficie (km^2)	950	28,050	257,670	465,400	322,464
Altitude max. (m)	2024	3007	1020	4070	1750

TABLEAU 3. Orchidaceae nouvellement recensées au Gabon.

	Noms	**Echantillons de référence**
1	*Aerangis calantha* (Schltr.) Schltr.	Biteau & Stévart 27, BRLU
2	*Ancistrorhynchus metteniae* (Kraenzl.) Summerh.	Stévart 1372, BRLU
3	*Ancistrorhynchus ovatus* Summerh.	Stévart & Biteau 1299, BRLU
4	*Ancistrorhynchus schumannii* (Kraenzl.) Summerh.	Biteau & Stévart 4, BRLU
5	*Ancistrorhynchus* sp. nov.	Stévart 1664, BRLU
6	*Ancistrorhynchus tenuicaulis* Summerh.	Wilks 3645, BRLU
7	*Angraecum affine* Schltr.	Stévart 1792, BRLU
8	*Angraecum* aff. *aporoides* sp. nov.	Stévart & Biteau 1292, BRLU
9	*Angraecum pungens* Schltr.	de Wilde (WALKB-series) & Arends ; Louis ; Karper; Bouman 230, WAG
10	*Angraecum* sect. *Dolabrifolia* sp. nov.	Stévart & Biteau 1300, BRLU
11	*Angraecum subulatum* Lindl.	de Wilde (WALKB-series) & Arends ; Louis ; Karper; Bouman 228, WAG
12	*Bolusiella iridifolia* (Rolfe) Schltr. subsp. *iridifolia*	Stévart 1318, BRLU
13	*Bolusiella talbotii* (Rendle) Summerh.	Stévart 1770, BRLU
14	*Bulbophyllum acutibracteatum* De Wild. var. *rubrobrunneopapillosum* (De Wild.) J.J.Verm.	Wieringa 677, WAG
15	*Bulbophyllum minutifolium* Stévart sp. nov.	Stévart, Ngok & Mendu 1094, BRLU
16	*Bulbophyllum resupinatum* Ridl. var. *resupinatum*	Stévart & Pauwels 1876, BRLU
17	*Chamaeangis* sp. nov.	Parmentier et Nguema 504, BRLU
18	*Cynorkis debilis* (Hook.f.) Summerh.	Reitsma & Reitsma 1953, WAG
19	*Cyrtorchis hamata* (Rolfe) Schltr.	Biteau & Stévart 30, BRLU
20	*Cyrtorchis henriquesiana* (Ridl.) Schltr.	Stévart 1847, BRLU
21	*Cyrtorchis injoloensis* (De Wild.) Schltr.	de Wilde & de Wilde-Bakhuizen 11378, WAG
22	*Cyrtorchis letouzeyi* Szlach. & Olsz.	Biteau & Stévart 29, BRLU
23	*Cyrtorchis ringens* (Rchb.f.) Summerh.	Biteau & Stévart 71, BRLU
24	*Cyrtorchis seretii* (De Wild.) Schltr.	Stévart 1669, BRLU
25	*Diaphananthe sarcorhynchoides* J.B.Hall	Biteau & Stévart 28, BRLU
26	*Diaphananthe* aff. *laticalcar* sp. nov.	Stévart 1745, BRLU
27	*Diaphananthe* sp. nov. de Bikurga, Mt. de Cristal et Rabi	Stévart 877, BRLU
28	*Eulophia magnicristata* Szlach. & Olsz.	Wieringa 928, WAG
29	*Habenaria stenochila* Lindl.	de Wilde & Arends ; de Bruijn 9100, BR, C, K, LBV, MA, MBG, MO, P, PRE, SRGH, WAG
30	*Liparis caillei* Finet	Stévart 854, BRLU
31	*Liparis gracilenta* Dandy	Stévart, Ngok & Mendu 1103, BRLU
32	*Liparis tridens* Kraenzl.	de Wilde & Arends ; de Bruijn 9052, WAG
33	*Microcoelia microglossa* Summerh.	Reitsma & Reitsma 1688, WAG
34	*Microcoelia* sp. nov.	Biteau & Stévart 55, BRLU
35	*Platycoryne buchananiana* (Kraenzl.) Rolfe	Reitsma & Reitsma 2760, WAG
36	*Polystachya bipoda* Stévart	Stévart 1795, BRLU
37	*Polystachya lejolyana* Stévart	Stévart, Mounoumoulossi & Kombila 1704, BRLU
38	*Polystachya modesta* Rchb.f.	Stévart & Biteau 1362, BRLU
39	*Polystachya moniquetiana* Stévart & Geerinck	Stévart, Mounoumoulossi & Kombila 1621, BRLU
40	*Polystachya mystacioides* De Wild.	Biteau & Stévart 63, BRLU
41	*Polystachya obanensis* Rendle	de Wilde (WALKB-series) & Arends ; Louis; Karper; Bouman 536, BR, K, LBV, MO, WAG
42	*Polystachya pobeguinii* (Finet) Rolfe	Wieringa 521, WAG
43	*Polystachya* sect. *Cultriforme* aff. kubale	Stévart, Mounoumoulossi & Kombila 1644, BRLU
44	*Rangaeris longicaudata* (Rolfe) Summerh.	Biteau & Stévart 31, BRLU
45	*Rangaeris rhipsalisocia* (Rchb.f.) Summerh.	Parmentier & Nguema 1116, BRLU
46	*Stenoglottis fimbriata* Lindl.	Louis 2805, LBV, MO
47	*Stolzia elaidum* (Lindl.) Summerh.	Stévart 1660, BRLU
48	*Summerhayesia laurentii* (De Wild.) P.J.Cribb	Arends, de Wilde & Louis 613, WAG
49	*Tridactyle lagosensis* (Rolfe) Schltr.	Biteau & Stévart 8, BRLU
50	*Tridactyle laurentii* (De Wild.) Schltr. var. *laurentii*	de Wilde & Arends ; Louis ; Wieringa 9718, WAG
51	*Tridactyle scottellii* (Rendle) Schltr. var. *scottellii*	Biteau & Stévart 53, BRLU.

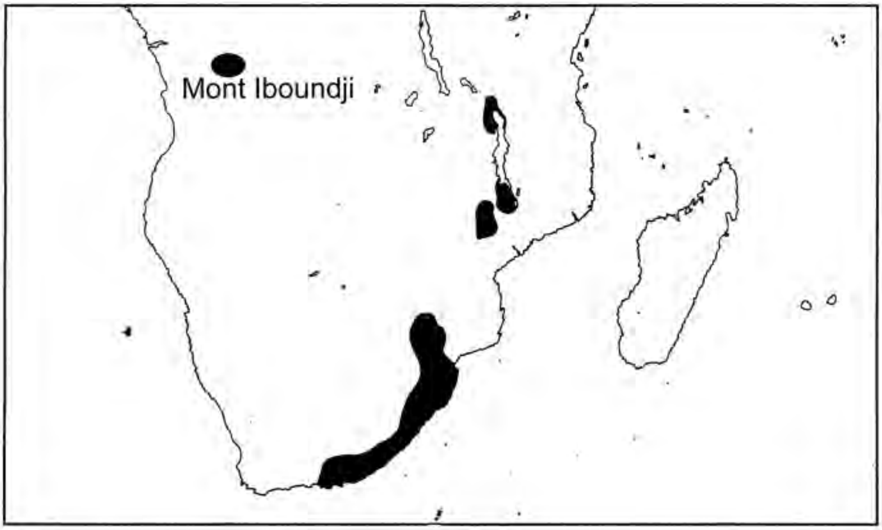

FIG. 2. Distribution du genre *Stenoglottis* en Afrique (modifié de Pridgeon *et al.*, 2001). Mont Iboundji = première signalisation de ce genre au Gabon.

Parmi ces taxons nouvellement signalés, on notera la présence de *Stenoglottis fimbriata* dont l'aire de distribution était limitée à l'Afrique de l'Est et à l'Afrique Australe (Fig. 2) et qui constitue la première mention du genre au Gabon. De même, *Liparis gracilenta* était considéré comme endémique de São Tomé et Príncipe, et *Cyrtorchis injoloensis* était considéré comme endémique de l'Afrique de l'Est.

3.2 Les Orchidaceae endémiques du Gabon

Le Tableau 4 présente les 25 taxons d'Orchidaceae qui sont actuellement considérés comme endémiques du Gabon. Parmi ceux-ci figurent *Veyretella hetaerioides* et *Renzorchis pseudoplatycoryne*, deux genres monospécifiques. Le taux d'endémisme au sein de notre inventaire est d'environ 12% (25/212). Si on considère notre estimation de la flore des Orchidaceae du Gabon, il est d'environ 6% (25/400). C'est un pourcentage minimum qui ne préjuge pas de nouvelles découvertes avec l'augmentation de l'effort de collecte.

Huit taxons, considérés dans la littérature comme endémiques du Gabon, ont récemment été découverts au Río Muni, à Príncipe et à São Tomé: *Ancistrorhynchus crystalensis* au Río Muni et à Príncipe, *Polystachya testuana* au Río Muni, *Polystachya odorata* subsp. *gabonensis* au Río Muni (Fig. 4), *Cynorkis gabonensis* à São Tomé et à Príncipe, *Vanilla chalotii* au Río Muni et probablement à Príncipe, *Tridactyle latifolia* à Príncipe et *Bulbophyllum coriscense* au Río Muni. Ces découvertes montrent que la connaissance des aires de distribution des espèces est loin d'être complète (et donc le niveau d'endémisme des Orchidaceae dans les pays concernés), et confirme que les forêts de ces régions possèdent de fortes affinités floristiques.

3.3 Distribution des Orchidaceae au Gabon

L'ordination selon les axes 1 et 3 met en évidence un gradient s'étalant des sites situés dans les Monts de Cristal aux sites de la région d'Oyem (Fig. 3). Les sites côtiers sont intermédiaires à ces deux extrêmes. L'axe 1 explique seulement 7,8 % de la variabilité des données. Il peut en partie s'interpréter comme un gradient d'humidité:

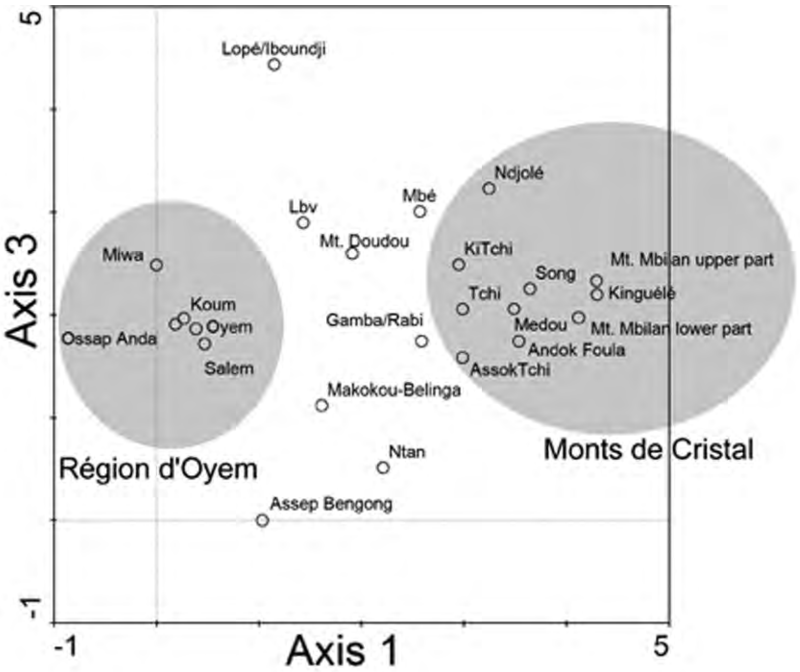

FIG. 3. Diagramme d'ordination (DCA, Axes 1 et 3) des 23 localités inventoriées (Tchi = Tchimbélé, Lbv = Libreville, Gamba/Rabi = Gamba et région de Rabi, La Lopé= Région de la Lopé et Mont Iboundji, Ki/Tchi = De Kinguélé à Tchimbélé, Assok/Tchi = De Assok à Tchimbélé, Medou = Région de Medouneu).

moyenne à la côte, plus forte dans la zone montagneuse et très faible derrière celle-ci. L'ordination selon les axes 1 et 2 (non représentée ici) individualise le sommet du Mont Mbilan qui est caractérisé par un endémisme propre et par un type de végétation typique des crêtes d'altitude à affinité submontagnarde. La présence de ce type de végétation à moyenne altitude s'explique par un effet de foehn qui a pour conséquence de maintenir un couvert nuageux permanent sur les crêtes.

4 Discussion

4.1 Flore

D'après notre estimation, le Gabon compte autant d'Orchidaceae que le Cameroun, alors que ce pays est plus vaste et que la superficie couverte par les zones de végétation montagnarde riches en épiphytes est bien supérieure. Cette estimation a été confirmée par Stévart (2003). Cet auteur a montré que la richesse spécifique en Orchidaceae de différentes régions situées en Afrique centrale atlantique (Cameroun, Guinée, Monts de Cristal, Rio Muni, îles du Golfe de Guinée, etc.) suivait parfaitement la loi d'Arrhenius. De part la diversité en habitats qui en résulte, l'altitude est probablement le meilleur paramètre pour expliquer la richesse spécifique en Orchidaceae d'une région car les épiphytes sont généralement très nombreux dans les formations végétales submontagnardes. Ainsi, ce paramètre pourrait expliquer la richesse spécifique de São Tomé et Príncipe dont la superficie est très faible.

TABLEAU 4. Orchidaceae endémiques du Gabon.

	Espèces	**Commentaires**
1	*Ancistrorhynchus* sp. nov.,	À décrire
2	*Angraecopsis hallei* Szlach. & Olsz.	
3	*Angraecum* aff. *aporoides* sp. nov.	À décrire
4	*Angraecum cribbianum* Szlach. & Olsz.	
5	*Angraecum* sect. *Dolabrifolia* sp. nov.	À décrire
6	*Bulbophyllum pandanetorum* Summerh.	
7	*Chamaeangis gabonensis* Summerh.	
8	*Diaphananthe* aff. *laticalcar* sp. nov.	À décrire
9	*Liparis hallei* Szlach.	Probablement *L. platyglossa*
10	*Microcoelia* sp. nov.	À décrire
11	*Nephrangis bertauxiana* Szlach. & Olsz.	
12	*Polystachya bipoda* Stévart sp. nov.	
13	*Polystachya cussetei* Szlach. & Olsz.	Probablement *P. polychaete*
14	*Polystachya kubalae* Szlach. & Olsz.	
15	*Polystachya lejolyana* Stévart	
16	*Polystachya moniquetiana* Stévart & Geerinck	
17	*Polystachya* Sect. *cultriforme* aff. kubale sp. nov.	À décrire
18	*Renzorchis pseudoplatycoryne* Szlach. & Olsz.	Genre monospécifique endémique du Gabon
19	*Rhipidoglossum magnicalcar* Szlach. & Olsz.	= *Diaphananthe magnicalcarata*
20	*Tridactyle brevicalcarata* Summerh.	Pourrait être présent au Cameroun et au Nigeria (flore du Cameroun)
21	*Tridactyle* sp. nov. du Gabon	À décrire
22	*Tridactyle truncatiloba* Summerh.	
23	*Vanilla hallei* Szlach. & Olsz.	
24	*Vanilla heterolopha* Summerh.	
25	*Veyretella hetaerioides* (Summerh.) Szlach. & Olsz.	Genre monospécifique endémique du Gabon

Les variations de richesse spécifique observées entre les différents sites (Tableau 1) pourraient s'expliquer par un gradient d'humidité mais aussi par la diversité en habitat des différents sites et par le taux d'échantillonnage.

4.2 Phytogéographie

Sur les 24 Orchidaceae considérées comme endémiques du Gabon, 10 ont été décrites récemment et 7 doivent encore être décrites. Il est vraisemblable qu'une part importante de ces espèces soit aussi présente dans les pays limitrophes mais qu'elles n'aient pas encore été collectées ou qu'elles ne soient pas encore identifiées. En outre, deux taxons décrits comme endémiques du Gabon, sont probablement conspécifiques d'autres espèces (Tableau 3). Enfin, d'après Szlachetko & Olszewski (2001b), *Tridactyle brevicalcarata* pourrait être présent au Nigeria et au Cameroun.

Le faible taux d'endémisme des Orchidaceae du Gabon (6%) n'empêche pas l'existence d'un endémisme prononcé pour cette famille au sein du domaine bas-guinéen. Ce faible taux s'explique donc par la présence d'un grand nombre d'espèces présentes au Gabon et dans les régions mitoyennes. Il semble probable que durant les dernières glaciations une zone refuge s'étendait de manière discontinue le long de l'océan, depuis le sud du Cameroun jusqu'au sud du Gabon. La taille de cette zone refuge a dû varier en fonction des précipitations et surtout de la topographie de la chaîne de montagne de moyenne altitude qui la délimite à l'est. Sa forte diversité peut

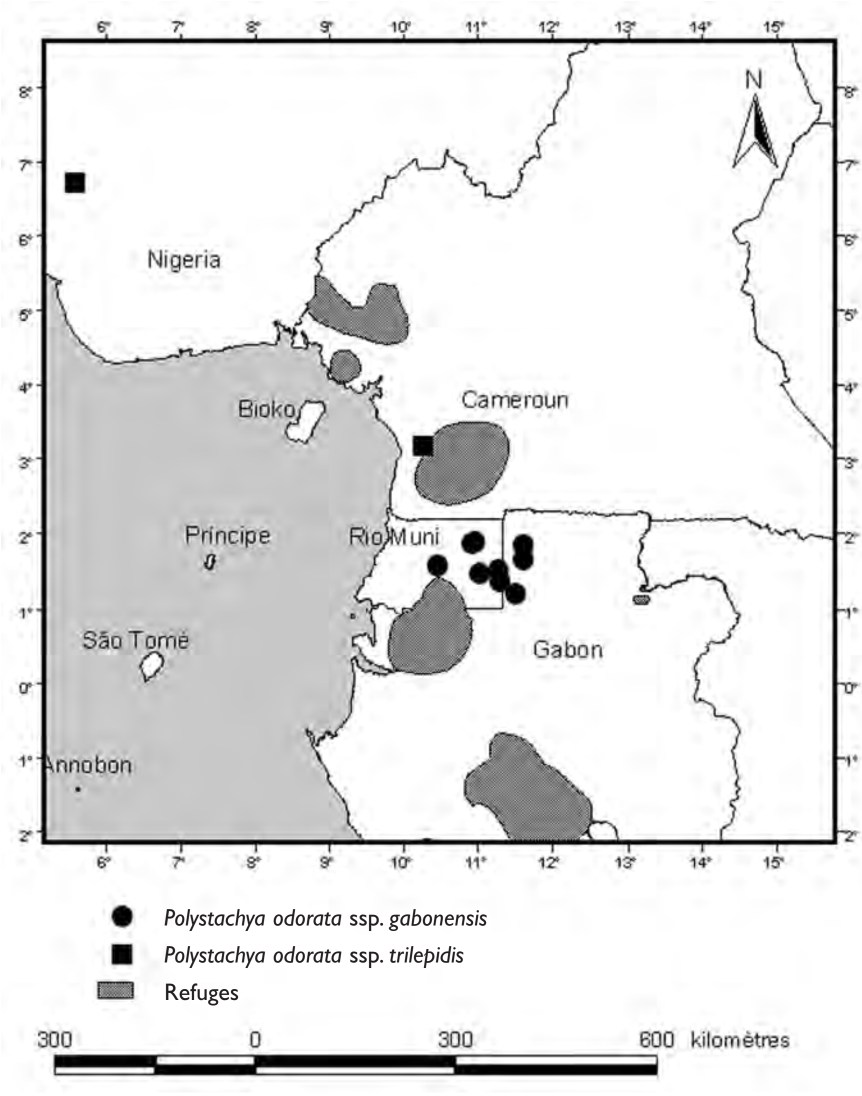

FIG. 4. Distribution de *Polystachya odorata* subsp. *gabonensis* et *Polystachya odorata* subsp. *trilepidis* en Afrique centrale atlantique; localisation des refuges forestiers d'après Sosef (1994, 1996).

être expliquée, d'une part par un endémisme important résultant de l'isolation de cette région pendant les périodes glaciaires et d'autre part par une juxtaposition sur une superficie limitée de deux types de végétation très distincts, submontagnard et planitiaire. On peut aussi supposer la présence entre ces deux types de végétation, d'une zone de transition possédant des éléments montagnards, reliques des dernières glaciations ainsi que des éléments planitiaires en expansion.

Dans les Monts de Cristal, la zone de végétation à affinité submontagnarde de moyenne altitude et disposant d'un endémisme propre en Orchidaceae, représente vraisemblablement la partie montagnarde de la zone de refuge localisée dans cette région. D'autres traces de végétation submontagnarde ont été signalées au Gabon: un peuplement de *Podocarpus latifolius*, une espèce afromontagnarde, à été signalé au partie congolaise du Massif du Chaillu (Maley *et al.*, 1990); un type de végétation ouvert, caractérisé par l'abondance d'épiphytes, assez proche de la végétation du Mont Mbilan, a été signalé à Itsiba de Chaillu par Olivier Pauwels (comm. pers.) et dans les Monts Doudou par Sosef *et al.* (2004). Enfin, les Monts de Bélinga abriteraient des formations végétales très riches en épiphytes. Le caractère submontagnard de ces formations est prouvé par la présence de *Cynorkis debilis* à 600 m d'altitude dans les Monts Doudou. Cette Orchidaceae est considérée comme afromontagnarde et se rencontre au Cameroun et à São Tomé entre 1450–1900 m d'altitude.

Par ailleurs, la flore des Orchidaceae du Gabon abrite un grand nombre de taxons pouvant être considérés comme des éléments de liaison et des éléments disjoints. Parmi ces derniers figure *Stenoglottis fimbriata*, signalée au sommet du Mont Iboundji (Fig. 1). Cette espèce présente une aire de distribution limitée aux régions montagneuses d'Afrique orientale et de l'Afrique australe. Cette disjonction renforce l'hypothèse de White (1993) et de Maley *et al.* (1990), supposant la présence d'une voie de migration sud qui aurait permis des échanges entre les flores montagnardes d'Afrique orientale et de l'Afrique centrale.

La distribution de la végétation au Gabon semble s'expliquer par un effet de continentalité, par l'influence des montagnes sur les précipitations et par la présence d'une zone refuge. Le parallélisme entre la distribution des Orchidaceae et la carte de végétation du Gabon de Caballé (1978), nous amène à penser que ces paramètres définissent aussi la distribution des Orchidaceae. Cette relation entre la végétation et la distribution des Orchidaceae épiphytes a déjà été observée au Nigeria (Sanford, 1974).

Les Orchidaceae sont théoriquement capables de dispersion à très longue distance. Elles produisent un grand nombre de diaspores facilement dispersées par le vent et ne devraient donc pas constituer un bon marqueur pour localiser les zones refuges. Leur distribution devrait, dès lors, s'expliquer principalement par les paramètres environnementaux et historiques. Pourtant, la nécessité d'un champignon symbiotique pour leur germination et l'existence d'agents pollinisateurs spécifiques limitent cette capacité de dissémination et expliquent la présence de microendémiques. En fin de compte, on constate qu'à petite échelle, les aires de distribution des Orchidaceae en Afrique centrale correspondent aux territoires phytogéographiques et aux éléments définis par White (1979), reflétant une histoire commune.

Par ailleurs, les Orchidaceae épiphytes sont capables de résister à des conditions microclimatiques extrêmes. Dans certains cas, elles présentent un mode de vie terrestre ou lithophyte et sont appelées épiphytes facultatives (Benzing, 1990). Ces plantes épiphytes facultatives forment une part importante de la flore des affleurements rocheux, tels que les inselbergs, les carrières ou les coulées de lave, mais aussi les cuirasses latéritiques des bords de route. On peut citer le cas de la Réserve de La Lopé qui constitue une zone théoriquement très défavorable pour les épiphytes à cause des faibles précipitations résultant d'un effet de foehn au niveau des Monts du Chaillu. Un inventaire réalisé sur l'affleurement rocheux du Mont Mbigou (au sud de la Réserve de la Lopé ou les précipitations sont plus élevées) a mis en évidence la présence de 14 taxons d'Orchidaceae lithophytes et épiphytes, soit presque autant que l'inventaire des Orchidaceae du reste de la Réserve. Ces Ochidaceae épiphytes sont bien adaptées à la grande variabilité d'éclairement et aux variations de sécheresse et d'humidité rapides. En effet, elles peuvent valoriser sur le long terme, au cours de l'année, des rosées et brouillards; et ce soit dans la canopée ou sur inselbergs. Les adaptations morphologiques les plus caractéristiques qui résultent de ces conditions extrêmes sont la présence de tiges transformées en organes de réserve (pseudobulbes), de feuilles coriaces ou crassulantes, de la microphyllie ou des adaptions permettant de réduire la surface foliaires exposée au soleil, ainsi qu'un système racinaire spécialisé dans l'absorption d'eau sous forme de brouillard.

Si les conditions microclimatiques le permettent, les Orchidaceae se maintiendront, même quand la végétation arbustive ou arborescente aura disparu. On peut dès lors supposer que durant les dernières glaciations, des Orchidaceae épiphytes ont pu se maintenir dans des zones dominées par des prairies et des affleurements rocheux. Ce changement de mode de vie a dû servir de moteur de spéciation.

C'est vraisemblablement le cas du *Polystachya odorata* subsp. *gabonensis*, un taxon endémique des prairies à *Afrotrilepis pilosa* des inselbergs du Río Muni et du Gabon. Ce taxon est apparenté à la sous-espèce *odorata*, un taxon généralement épiphyte et largement répandu en Afrique, mais qui présente occasionnellement un mode de vie terrestre. De plus, la sous-espèce *gabonensis* est fortement apparentée à la sous-espèce *trilepidis*, endémique des inselbergs du Nigeria et de l'ouest du Cameroun (Fig. 4). On peut supposer que ces deux taxons sont en cours de spéciation et que la forêt située au sud-ouest du Cameroun forme actuellement une barrière entre les inselbergs du Nigeria et ceux du Gabon et du Río Muni. La faible différenciation de ces taxons implique des contacts récents entre ces populations. Il est probable que le refuge forestier localisé dans l'ouest du Cameroun (région de Bipindi - Akom II - Campo) a du être partiellement perméable durant des périodes de glaciation, ou qu'un processus de dissémination à longue distance ait pu se produire à cette époque alors que les prairies couvraient une plus grande superficie. Plus récemment, le processus de dissémination paraît peu probable tant la surface couverte par son habitat est faible.

5 Conclusions

Le Gabon possède une flore très riche en Orchidaceae. Cette richesse pourrait s'expliquer par la diversité en habitats liés à un gradient d'humidité et par le maintien de la forêt dans des refuges durant les dernières glaciations. Nous confirmons l'hypothèse de Sosef (1992, 1994), selon laquelle les refuges reconnus au Gabon sont composés de deux zones distinctes: l'une planitiaire et l'autre montagnarde. Nous supposons que ces refuges s'étendent d'avantage vers le nord jusqu'à Monte Alén (Río Muni) et vers le sud jusqu'au partie congolaise du Massif de Chaillu. Cette hypothèse repose sur l'existence d'une végétation à affinité montagnarde dans les Monts de Cristal et à Monte Alén présentant un endémisme propre en Orchidaceae, ainsi que sur la présence d'une population relictuelle de *Podocarpus* au sud du Gabon. Des nouveaux inventaires sont nécessaires pour localiser précisément les refuges montagnards. Nous proposons d'inventorier en priorité la zone d'Itsiba de Chaillu et les crêtes des Monts Doudou qui abritent une végétation identique à celle du Mont Mbilan et qui présente une abondance en épiphytes.

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ANALYSE FLORISTIQUE DE LA FORÊT DE NGOTTO (RÉPUBLIQUE CENTRAFRICAINE)

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Abstract

Following investigations carried out in the forest of Ngotto, 989 specimens were collected; 89 families, 315 kinds and 441 species were determined. Euphorbiaceae and Rubiaceaeae dominate the forest and characterize especially the species of undergrowth. The species of the canopy are characterized by Sapotaceae and Meliaceae. Among the 441 determined species, 366, i.e. 83%, are phanerophytes; the proportions of the hemicryptophytes, the geophytes, the therophytes, the epiphytes and the chamephytes vary between 1,1% to 5,4%. The arborescent species account for 61,7%, the lianas, the shrubs, the sub-shrubs and the grasses account for 38,3% of the total. The majority of the species have small fleshy fruits whose dissemination is ensured by the animals. A considerable number of the species have fruits equipped with appendices allowing their dissemination by the wind. The examination of the ecological groups to which the various species belong show that the forest of Ngotto mainly consists of elements of primary forest with a rather notable proportion of the species with affinity for secondary forests and forest edges.

Résumé

Suite aux investigations de terrain réalisées dans la forêt de Ngotto, 989 spécimens d'herbiers ont été collectés; 89 familles, 315 genres et 441 espèces ont été déterminés. Les Euphorbiaceae et les Rubiaceaeae dominent dans l'ensemble et caractérisent surtout les espèces de sous-bois. Les espèces de la voûte sont plutôt caractérisées par les Sapotaceae et les Meliaceae. Parmi les 441 espèces déterminées, 366, soit 83%, sont des phanérophytes; les proportions des hémicryptophytes, des géophytes, des thérophytes, des épiphytes et des chaméphytes sont comprises entre 1,1% à 5,4%. Les espèces arborescentes représentent 61,7%, les lianes, les arbustes, les arbrisseaux, les sous-arbrisseaux et les herbes représentent 38,3% du cortège. La plupart des espèces possèdent des petits fruits charnus dont la dissémination est assurée par les animaux. Une part non négligeable des espèces possèdent des fruits pourvus d'appendices permettant leur dissémination par le vent. L'examen des groupes écologiques auxquels appartiennent les différentes espèces identifiées a montré que le fond floristique de la forêt de Ngotto est constitué par les éléments de forêt primaire de terre ferme avec cependant une proportion assez notable des espèces à affinité pour les forêts secondaires et les lisières.

Key words: Central African Republic, floristic composition, forest.

1 Introduction

La République Centrafricaine est mal pourvue en matière d'ouvrages floristiques. Les rares ouvrages floristiques contemporains relèvent des auteurs tels que Aké Assi (1978, 1980), Boulvert (1977) (*in* Lebrun & Stork, 1991), Tisserant (1950), Vivien & Faure (1985) et Souane (1989). Les explorations dans la région étudiée sont assez récentes. En 1962, quelques prospections et inventaires forestiers ont été réalisés par le service des eaux et forêts de Bangui dans la forêt de Ngotto (Boulvert, 1986). En 1965, le CTFT (Centre Technique Forestier Tropical) est intervenu dans la zone de Bambio (Bastin, 1996). Avant la mise en exploitation de la forêt de Ngotto, l'IFB (Industrie Forestière de Batalimo) a procédé à des inventaires de prospection, probablement entre 1987 et 1988. SECA-AGRER, en 1989, a effectué quelques inventaires dans la zone d'influence de la route du quatrième parallèle (Bastin, 1996). Boulvert (1986), pour la réalisation de la carte phytogéographique de la République Centrafricaine, a effectué des inventaires dans la région de Ngotto et de Bambio. De 1992 à 1993, l'ensemble de la région a fait l'objet d'inventaires par le projet PARN (Projet d'Aménagement des Ressources Naturelles) (Bastin, 1996).

À partir de 1993, des travaux botaniques un peu plus approfondis sur la forêt de Ngotto ont été réalisés dans le cadre du programme ECOFAC-Composante R.C.A. (Conservation et utilisation rationnelle des écosystèmes forestiers en Afrique centrale). Ces travaux concernent surtout les espèces arborescentes dont le dbh (diamètre à hauteur de poitrine) est d'au moins 10 cm. Environ 200 espèces d'arbres et d'arbustes ont été ainsi inventoriées (Lejoly, 1996a).

Malgré ces travaux antérieurs, notre dition reste peu connue sur le plan botanique. Pour apporter notre contribution à une meilleure connaissance de la composition floristique de la forêt de Ngotto et à la constitution de l'herbarium national, nous nous sommes attelée à faire un inventaire plus global allant des herbes aux arbres. Pour mieux connaître la flore de la forêt de Ngotto et comprendre le tempérament des espèces rencontrées, c'est-à-dire leur comportement, nous rassemblons des données concernant leurs types biologiques, leurs types morphologiques, leurs diaspores et leur écologie. Ces données proviennent d'une part de nos observations sur le terrain, mais surtout de la littérature.

2 Méthodologie

2.1 Présentation du site

La forêt de Ngotto est située dans le sud-ouest de la République Centrafricaine entre 3°30'–4°25'N et 16°20'–17°43'E, à une altitude de 500 à 600 m. D'après White (1986), elle appartient au domaine de la forêt dense ombrophile semi-sempervirente humide mélangée et relève du Centre régional d'endémisme guinéo-congolais. Le régime pluviométrique de la forêt de Ngotto est de type tropical avec deux pics de précipitations en mai et en août et une seule saison sèche d'une durée de trois mois allant de décembre à février. Les précipitations atteignent en moyenne 1 692 mm par an.

2.2 Inventaire

De novembre 1998 à Février 2001, nous avons parcouru régulièrement la forêt de Ngotto. Nous avons effectué plusieurs inventaires selon la méthode des transects (Lejoly, 1995). Des inventaires systématiques ont été aussi réalisés lorsque les plantes repérées sont en fleurs ou fruits ou lorsqu'elles sont facilement identifiables à partir de caractères végétatifs très remarquables. D'autres inventaires proviennent des relevés phytosociologiques exécutés selon les principes de la phytosociologie synusiale (Gillet *et al.*, 1991).

Des récoltes d'échantillons botaniques accompagnent ces inventaires. Les échantillons sont récoltés si possible en trois exemplaires, dont deux sont destinés à l'Herbier national. Un troisième exemplaire est déposé au Laboratoire de Botanique systématique de l'Université Libre de Bruxelles.

La nomenclature botanique utilisée pour les Phanérogames est celle adoptée par Lebrun et Stork (1991, 1992, 1995, 1997). Pour les Ptéridophytes, les familles sont précisées selon la nomenclature suivie par Mabberley (1997); les noms des espèces proviennent des flores du Gabon, du Cameroun et de l'Afrique de l'Ouest.

2.3 Types biologiques

Les principaux types biologiques ont été considérés en accord avec la classification de Raunkiaer (*in* de Foucault, 1986):

- phanérophytes (Ph): arbres, arbustes et arbrisseaux, lianes;
- chaméphytes (Ch): sous-arbrisseaux;
- hémicryptophytes (Hc): herbacées pérennes;
- géophytes (G): plantes à tubercules, rhizomes ou bulbes;
- thérophytes (Th): plantes annuelles;
- épiphytes (Epi).

Pour nous permettre de comparer nos résultats à ceux d'autres auteurs (Lejoly & Mandango, 1982; Sonké, 1998; Kouka, 2000, etc.), nous avons subdivisé les phanérophytes comme ci-après:

- Mégaphanérophytes (Mg-Ph): grands arbres et lianes d'au moins 30 m;
- Mésophanérophytes (Ms-Ph): arbres moyens et lianes de hauteur d'au moins 15 m et inférieure à 30 m;
- Microphanérophytes (Mi-Ph): petits arbres et lianes de hauteur d'au moins 7 m et inférieure à 15 m;
- Nanophanérophytes (N-Ph): arbustes et lianes d'au moins 2 m et inférieurs à 7 m.

2.4 Types morphologiques

Pour chaque espèce, nous indiquons son port. La silhouette des espèces peut varier suivant les habitats; ainsi, lorsqu'une espèce est décrite, par exemple, comme un arbuste et un petit arbre, nous optons pour le niveau supérieur, c'est-à-dire pour le petit arbre. Nous retenons les symboles suivants pour les différents types considérés:

- A_1: grands arbres ou mégaphanérophytes;
- A_2: arbres moyens ou mésophanérophytes;
- A_3: petits arbres ou microphanérophytes;
- a_1: arbustes ou nanophanérophytes;
- a_2: arbrisseaux et sous-arbrisseaux;
- H: grandes herbes (> 1 m);
- h: petites herbes (1 m);
- Lia: lianes.

2.5 Types de diaspores

Les types de diaspores retenus répondent aux catégories définies par Dansereau et Lems (1957) et Lebrun (1960) (*in* Lejoly & Mandango, 1982), Évrard (1968):

- ballochores (Ballo): diaspores sèches ou charnues déhiscentes;
- barochores (Baro): diaspores lourdes, sèches ou charnues, indéhiscentes de dimensions (diamètre, hauteur) supérieures à 5 cm;
- desmochores (Desmo): diaspores accrochantes ou adhésives pouvant être déhiscentes ou non;
- pogonochores (Pogo): diaspores à appendice plumeux ou soyeux;
- ptérochores (Ptéro): diaspores munies d'appendices aliformes;
- sarcochores (Sarco): diaspores totalement ou partiellement charnues, indéhiscentes, de dimensions (diamètre, hauteur) inférieures à 5 cm.
- sclérochores (Scléro): diaspores sèches, légères

2.6 Groupes écologiques

Comme de nombreux auteurs (Lebrun & Gilbert, 1954; Duvigneaud, 1955; Évrard, 1968; Lubini & Mandango, 1981; Mosango, 1990; Sonké, 1998), nous utilisons le critère «habitat» pour définir les groupes écologiques. En nous basant sur des données essentiellement bibliographiques rassemblées sur les différents habitats auxquels est inféodée chaque espèce, nous avons considéré les catégories suivantes:

- Fp: espèces de forêts primaires sempervirentes ou semi-décidues de terre ferme;
- Fs: espèces de forêts secondaires, recrûs forestiers et jachères forestières;
- Fsh: espèces de forêts sur sols hydromorphes, forêts riveraines, ripicoles, marécageuses;
- F: espèces se rencontrant dans tous les types forestiers, tant de terre ferme que sur sols hydromorphes;
- Lis: espèces se rencontrant dans les lisières forestières;
- S: espèces de savane;
- H: espèces se rencontrant dans les habitats humains, terrains vagues, bords de piste, champs, espèces plantées;
- U: espèces ubiquistes, rencontrées en forêt, savane, dans les lisières, dans les formations secondaires et les habitats humains.

Les symboles précités peuvent être réunis par des traits d'union lorsqu'une espèce est rencontrée dans au moins deux habitats différents (exemple: Fp-Fs-Lis, espèces se rencontrant en forêt primaire, secondaire et dans les lisières).

3 Résultats

3.1 Richesse floristique

Suite à nos travaux, 989 spécimens ont été collectés. 441 espèces (on a pris en compte également les données des travaux antérieurs effectués sur notre site d'étude), 315 genres et 89 familles ont été déterminés. On retiendra que certains échantillons ont pu être déterminés seulement jusqu'au niveau de la famille ou du genre. Ces 441 espèces sont réparties entre 294 genres et 84 familles. Parmi les genres, 11 comportent au moins 5 espèces et constituent à eux seuls 22,4% de l'effectif des genres (avec 66 espèces); il s'agit par ordre d'importance de: *Diospyros* (7 espèces), *Drypetes* (7 espèces), *Ficus* (7 espèces), *Celtis* (6 espèces), *Chrysophyllum* (6 espèces), *Macaranga* (6 espèces), *Rinorea* (6 espèces), *Trichilia* (6 espèces), *Albizia* (5 espèces), *Cola* (5 espèces), *Garcinia* (5 espèces). Onze des 84 familles comportent au moins 11 espèces; ce sont respectivement les Euphorbiaceae (42 espèces, soit 9,5%), les Rubiaceae (38 espèces, soit 8,6%), les Caesalpiniaceae (18 espèces, soit 4,1%), les Sapotaceae (17 espèces, soit 3,9%), les Apocynaceae et les Moraceae à égale proportion (16 espèces, soit 3,6%), les Meliaceae (15 espèces, 3,4%), les Sterculiaceae (13 espèces, soit 3%), les Mimosaceae (12 espèces, soit 2,7%), les Annonaceae et les Sapindaceae à contribution égale (11 espèces, soit 2,5%). Ces onze familles représentent 13,1% de l'effectif des familles et 47,4% (avec 209 espèces) du cortège spécifique.

3.2 Structure biologique

Le spectre biologique des 441 espèces inventoriées met en évidence une nette dominance des phanérophytes, soit 83% (366 espèces) du total des espèces (Fig. 1). Viennent ensuite les hémicryptophytes avec 5,4% (24 espèces) et les géophytes avec 4,5% (20 espèces). Les thérophytes, les épiphytes et les chaméphytes présentent respectivement des pourcentages de 2,9% (13 espèces), 2,7% (12 espèces) et 1,1% (5 espèces) de l'effectif total. Le type biologique d'une espèce est indéterminé, ce qui représente 0,2% de l'effectif.

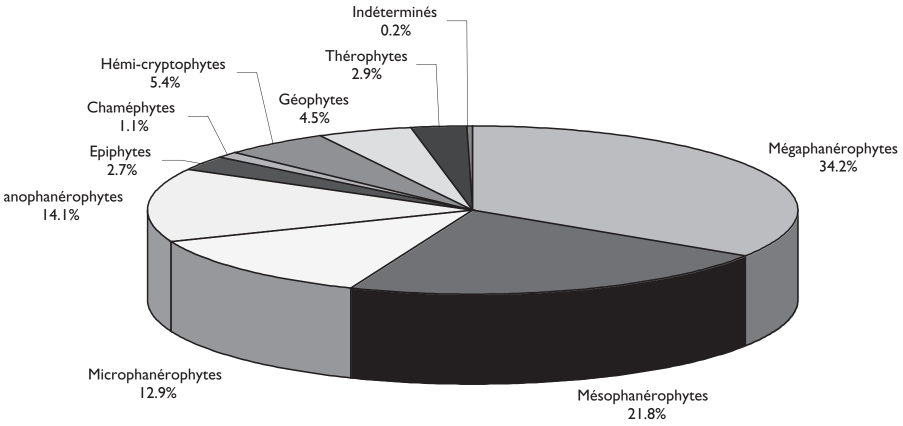

FIG. 1. Spectre biologique des espèces de la forêt de Ngotto

3.3 Structure morphologique

366 espèces déterminées, soit 61,7% de l'effectif total, sont des arbres (Fig. 2); les lianes, les arbustes, les arbrisseaux, les sous-arbrisseaux et les herbes représentent 38,3% du cortège. Parmi les arbres, 133 espèces (30,2%) sont des grands arbres d'au moins 30 mètres, 90 espèces (20,4%) sont des arbres moyens et 49 espèces (11,1%) sont des petits arbres. Les lianes, les arbustes, les petites herbes, les grandes herbes et les arbrisseaux ont des pourcentages respectifs de 12,2% (54 espèces), 10,7% (47 espèces), 10% (44 espèces), 4,5% (20 espèces) et 0,9% (4 espèces).

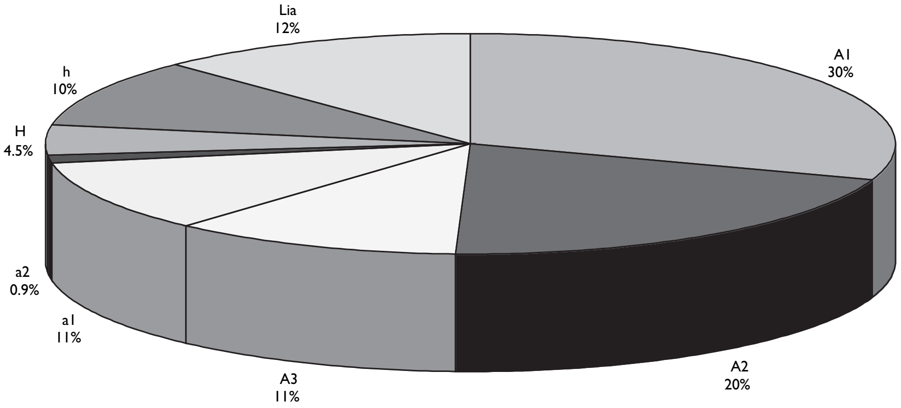

FIG. 2. Spectre morphologique des espèces de la forêt de Ngotto. A1: grands arbres; A2: arbres moyens; A3: petits arbres; a1: arbustes; a2: arbrisseaux; H: grandes herbes; h: petites herbes; Lia: lianes.

3.4 Spectre des types de diaspores

Avec 42,9% (189 espèces) de l'effectif total viennent en tête les espèces sarcochores, suivies des espèces ballochores avec 28,1% (124 espèces) (Fig. 3). Les autres espèces se répartissent selon les types de diaspores suivants: barochores (43 espèces, soit 9,8%), ptérochores (36 espèces, soit 8,2%), sclérochores (31 espèces, soit 7%), desmochores (9 espèces, soit 2%), pogonochores (6 espèces, soit 1,4%). Les espèces aux types de diaspores non encore définis représentent 0,7% (3 espèces) de l'effectif total.

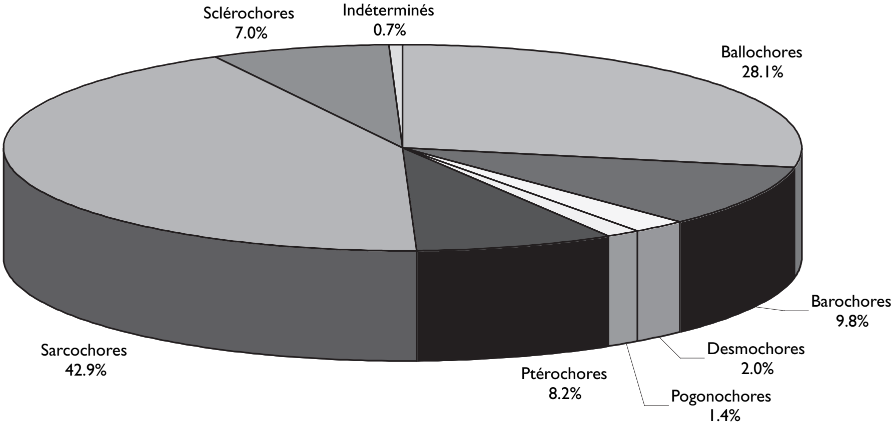

FIG. 3. Spectre des types de diapores des espèces de la forêt de Ngotto.

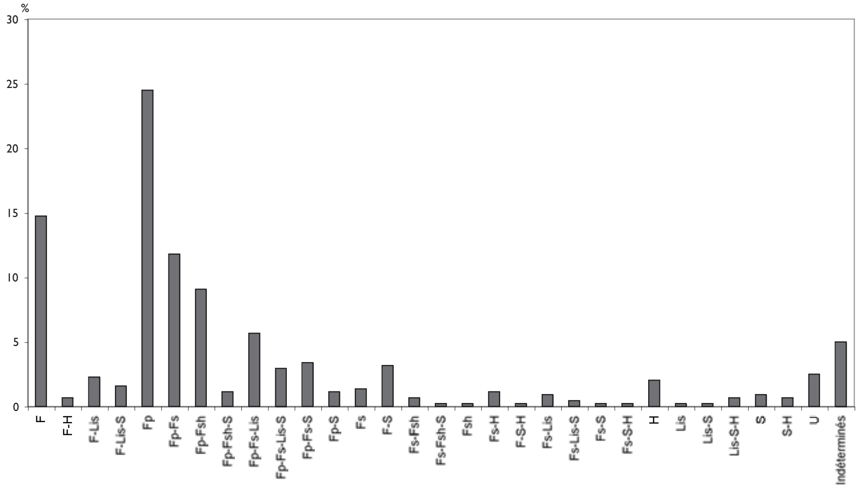

FIG. 4. Spectre des groupes écologiques des espèces de la forêt de Ngotto.

3.5 Structure écologique

Nous avons identifié sur l'ensemble des 441 espèces déterminées 30 groupes écologiques. Ces groupes et leurs proportions sont illustrés à la Fig. 4. On note une dominance du groupe Fp d'espèces de forêt primaire sempervirente ou semi-sempervirente de terre ferme; 108 espèces relèvent en effet du groupe Fp, elles représentent 24,5% de l'effectif total; ce sont notamment *Ochna calodendron*, *Anonidium mannii*, *Beilschmiedia congolana*, *Autranella congolensis*, *Entandrophragma cylindricum*, *Staudtia kamerunensis*, *Uvariodendron mirabile*, *Belonophora coriacea*. En deuxième position, vient le groupe F d'espèces se rencontrant indifféremment dans tous les types forestiers aussi bien en forêts primaires et secondaires de terre ferme que sur sols hydromorphes; on en compte 65, soit 14,7% de l'effectif total; il s'agit d'espèces telles que *Canarium schweinfurthii*, *Chytranthus macrobotrys*, *Cleistopholis glauca*, *Aidia micrantha*, *Penianthus longifolius*, *Rourea obliquifoliolata*, etc. En troisième position arrive le groupe Fp-Fs d'espèces qui se retrouvent en forêt primaire dans des zones perturbées mais affectionnent préférentiellement les forêts secondaires; elles sont au nombre de 52, soit 11,8%; on peut citer notamment *Musanga cecropioides*, *Macaranga paxii*, *Tetrorchidium didymostemon*. Le groupe Fp-Fsh représenté par des espèces qui se retrouvent aussi bien en forêts primaires de terre ferme que sur sols humides arrive en quatrième position avec 40 espèces, soit 9,1%; au nombre de ces espèces, on peut mentionner *Calamus deërratus*, *Copaifera mildbraedii*, *Samanea leptophylla*, *Treculia africana*, *Uapaca heudelotii*, *Xylopia staudtii*. Le groupe Fp-Fs-Lis d'espèces à forte affinité pour les forêts secondaires et les lisières arrive en quatrième position avec 25 espèces, soit 5,7%; il s'agit entre autres de *Aframomum melegueta*, *Costus afer*, *Trema orientalis*, *Hugonia platysepala*, *Whitfieldia elongata*, *Klainedoxa gabonensis*, *Margaritaria discoidea*. Les proportions individuelles des autres catégories sont plus faibles, on compte tout au plus 15 espèces dans chacune d'elles avec des pourcentages n'atteignant pas 4%. Les espèces qui relèvent de ces dernières catégories se rencontrent dans divers types forestiers, dans les lisières, dans la savane ou dans les milieux anthropisés (terrains vagues, bords de piste, etc.). Il s'agit d’espèces telles que *Milicia excelsa*, *Maranthes kerstingii*, *Hexalobus monopetalus*, *Xylopia aethiopica*, *Drypetes floribunda*, *Aoranthe cladantha*, *Bridelia atroviridis*, *Adenia lobata*, *Phytolacca dodecandra*, *Chromolaena odorata*. L’écologie de 22 espèces n’est pas connue faute d’information, ce qui représente 5% de l’effectif total.

4 Discussion

4.1 Richesse floristique

Dans les travaux antérieurement réalisés dans la forêt de Ngotto, 210 espèces arborescentes à diamètre à hauteur de poitrine supérieur à 10 cm avaient été inventoriées (Lejoly, 1995). Sur l’ensemble de 441 espèces identifiées dans nos travaux, 366 espèces sont arborescentes, 156 espèces de plus sont connues actuellement. Dans l’état actuel des connaissances publiées, les résultats obtenus dans la forêt de Ngotto sont du même ordre de grandeur que ceux obtenus dans quelques forêts d’Afrique centrale. Dans la forêt de Monte Alen en Guinée équatoriale, 306 espèces arborescentes ont été inventoriées (Lejoly, 1996b). Sonké (1998) a recensé 372 espèces arborescentes dans la Réserve de Dja au Cameroun. Kouka (2000) a dénombré 238 espèces arborescentes dans le Parc National d’Odzala au Congo-Brazzaville. Signalons aussi que les inventaires réalisés par ces auteurs ont concerné surtout les individus à diamètre à hauteur de poitrine supérieur à 10 cm. Ces résultats bien que préliminaires confirment la grande richesse des forêts denses humides d’Afrique centrale.

Dans la forêt de Ngotto, le pourcentage des genres représentés par une espèce est très élevé, il est égal à 72,8%. Il est plus élevé que la plupart de ceux observés dans d’autres forêts d’Afrique centrale: 52,3% dans la Cuvette centrale en ex-Zaïre (Évrard, 1968), 67,2% dans la région de Kikwit en ex-Zaïre (Masens, 1997), 68% dans la Réserve de faune de Dja au Cameroun (Sonké, 1998). La proportion obtenue par Kouka (2000) est par contre plus élevée que la nôtre: elle atteint, en effet, 77,3% dans le Parc national d’Odzala au Congo-Brazzaville. Plusieurs des genres les plus diversifiés dans la forêt de Ngotto sont aussi bien représentés dans d’autres forêts; le rapprochement est surtout assez fort pour la Réserve de Dja: ce sont notamment *Diospyros*, *Drypetes*, *Entandrophragma*, *Trichilia*, *Albizia*, *Cola*. Le genre *Diospyros* arrive en tête aussi bien en forêt de Ngotto (7 espèces) qu’à Odzala (8 espèces). Dans la réserve de Dja, il se place en seconde position avec 5 espèces.

Le classement des dix familles les plus importantes du point de vue spécifique est quasi similaire à celui qui est observé pour la flore forestière de la Réserve de faune du Dja au Cameroun (Sonké, 1998). En effet, dans la Réserve de faune du Dja, sur un ensemble de 372 espèces réparties entre 55 familles, 12 familles comptant au moins 10 espèces y ont été recensées avec le classement suivant: Euphorbiaceae > Rubiaceae > Caesalpiniaceae > Sapotaceae > Annonaceae > Meliaceae > Sterculiaceae > Mimosaceae > Flacourtiaceae > Apocynaceae > Olacaceae > Sapindaceae. Dans la forêt de Ngotto, les Annonaceae (9 espèces) arrivent en onzième position devant les Ulmaceae (8 espèces) et les Olacaceae (7 espèces).

4.2 Biologie des espèces

Le fort pourcentage des phanérophytes dans la forêt de Ngotto n’est guère étonnant. Les valeurs enregistrées sont du même ordre que celles de la plupart des forêts denses.

4.3 Morphologie des espèces

La forêt est dominée par les espèces arborescentes. Les espèces de la voûte hautes d'au moins 30 mètres sont plus nombreuses que les représentants de la strate basse. Ce constat est assez général en Afrique centrale (Lebrun & Gilbert, 1954; Évrard, 1968). Bien que dans le cadre de ce travail, seules les espèces de lianes déterminables aient été recensées, on a enregistré 54 espèces avec un pourcentage de 12,2% de l'effectif total; la forêt de Ngotto est particulièrement riche en lianes, celles-ci sont surtout favorisées par l'abondance des chablis. L'importance des lianes dans les forêts semi-sempervirentes a été aussi soulignée par Lebrun et Gilbert (1954) ainsi que par Évrard (1968). Comme dans toutes les forêts denses humides de la sous-région, les arbrisseaux sont rares en forêt de Ngotto; dans la synusie herbacée basse, ce sont surtout les plantules d'arbres et d'arbustes qui sont fréquentes. Les espèces herbacées généralement héliophiles supportent mal l'ambiance ombragée du sous-bois, ce qui limite leurs installation et prolifération. Les herbes forestières sont très rares, on en compte à peine une dizaine (Letouzey, 1983). Les proportions assez notables (petites herbes: 44 espèces, soit 10%; grandes herbes: 20 espèces, soit 4,5%) observées sont dues à la présence des espèces à forte affinité pour les forêts secondaires qui trouvent des conditions favorables dans les zones perturbées, notamment dans les trouées, les pistes ouvertes à l'intérieur de la forêt. La proximité des savanes favorise également l'installation des herbes.

4.4 Types de diaspores et modes de dissémination

La dominance de la sarcochorie est signalée dans la plupart des travaux en Afrique centrale avec des proportions très généralement supérieures à 50% (Sonké, 1998; Kouka, 2000; Mosango, 1990; Lubini & Kusehuluka, 1991). L'examen du Tableau 1 montre que le pourcentage des sarcochores observé dans la forêt de Ngotto est un peu moins élevé, il est égal à 42,9%. Les espèces ballochores ont une contribution non négligeable avec un pourcentage de 28,1%. L'importance des ballochores dans la forêt de Ngotto est due surtout à l'abondance des espèces des Mimosaceae, Caesalpiniaceae, Meliaceae, Sterculiaceae qui possèdent des fruits secs déhiscents.

La correspondance des types de diaspores avec la classification plus usuelle d'après Molinier & Müller (1938) adaptée par Van der Pijl (1972) (*in* de Foucault, 1995) donne une idée sur les modes de dissémination:

- sarcochores, desmochores (zoochores), 44,9%: diaspores dispersées par les animaux;
- ptérochores, pogonochores, sclérochores (anémochores), 16,6%: diaspores dispersées par le vent;
- ballochores (autochores), 28,1%: diaspores dispersées par la plante elle-même;
- barochores, 9,8%: diaspores à dispersion passive par simple gravité.

La proportion des espèces zoochores souligne l'importance du rôle des animaux dans la dissémination des diaspores. Dans nos milieux, cette dissémination concerne surtout les oiseaux et quelques vertébrés frugivores, notamment les antilopes, les singes (Lebrun & Gilbert, 1954; Évrard, 1968; Gauthier-Hion *et al.*, 1985; Colyn, 1993; Wilson *et al.*, 1989 *in* Kouka, 1994). Vu la proportion des anémochores, le rôle du vent est aussi non négligeable dans la dispersion des diaspores dans la forêt de Ngotto; les espèces concernées sont essentiellement des représentants de la voûte, dont *Entandrophragma cylindricum*, *Entadrophragma angolense*, *Entandrophrama candollei*, *Terminalia superba*, *Pteleopsis hylodendron*, *Alstonia boonei*. La proportion des espèces barochores à dispersion passive est surtout le fait des espèces de la famille des Sapotaceae qui possèdent de grosses baies.

TABLEAU 1. Comparaison des spectres des types de diapores des espèces de quelques forêts d'Afrique centrale.
Ballo: ballochores, Baro: barochores, Desmo: desmochores, Pogo: pogonochores, Ptéro: ptérochores, Sarco: sarcochores, Scléro: sclérochores.

	Spectres bruts des types de diaspores (%)						
	Ballo	**Baro**	**Desmo**	**Pogo**	**Ptéro**	**Sarco**	**Scléro**
Forêt de Ngotto, Centrafique (Présente étude)	28,1	9,8	2	1,4	8,2	42,9	7
Forêt Marantaceae de Tombi 1, Congo-Brazzabille (Kouka, 2000)*	12,3	6,2	–	1,5	9,2	70,8	–
Forêt primaire de l'île Kongolo, ex-Zaïre (Mosango, 1990)	10,2	1,9	1	1,6	3,5	72,8	9
Forêt hétérogène typique de Dja, Cameroun (Sonké, 1998)*	4	4	–	2	5	83	2
Forêt à Celtis mildbraedii de Kikwit, ex-Zaïre (Lubani & Kusehuluka, 1991)	10,3	3,3	0,5	0,5	6,6	75,6	3,3

*: les études dans ces sites ne concernent que les espèces ligneuses

4.5 Écologie des espèces

L'analyse des groupes écologiques a montré que la grande majorité des espèces considérées relèvent de la forêt avec des transgressions assez notables dans les lisières, les savanes et les endroits anthropisés. Les espèces qui relèvent exclusivement de la savane (groupe S: 4 espèces, 0,9%) et des habitats anthropiques (groupe H: 9 espèces, 2%) sont faiblement représentées; leur présence est favorisée surtout par l'ouverture des pistes au travers de la forêt et la proximité des savanes; elles sont en effet essentiellement cantonnées aux bords des pistes et ne se retrouvent que très rarement en pleine forêt. Le groupe Fp des espèces de forêts primaires de terre ferme dominent mais avec une proportion peu importante (soit 24,5%); par ailleurs, l'importance que revêtent les espèces de forêts secondaires, lisières, de savane et de milieux anthropisés (groupes Fp-Fs et Fp-Fs-Lis, Fp-Fs-Lis-S, Lis-S-H, etc.) s'explique par des perturbations aussi bien naturelles qu'anthropiques. La présence de ces dernières est vraisemblablement favorisée par le caractère hygrophile beaucoup moins accusé lors des saisons sèches prolongées. La structure écologique de la forêt de Ngotto présente un caractère hétérogène et remanié. La comparaison de la proportion des espèces de forêt primaire de terre ferme (groupe Fp: 24,5%) à celle obtenue ailleurs pour les mêmes types de forêts montre que la forêt de Ngotto est moins stabilisée. Dans la forêt semi-caducifoliée de Kisangani, en ex-Zaïre, Mosango et Lejoly (1990) ont enregistré 52% des espèces de forêts primaires. Á Kikwit, toujours en ex-Zaïre, les espèces de forêts primaires recensées représentent 49,7% (Lubini & Kusehuluka, 1991).

5 Conclusion

En conclusion, dans l'état actuel des connaissances, nos résultats ont montré que la forêt de Ngotto est tout aussi riche floristiquement que d'autres forêts denses humides d'Afrique centrale. Les résultats obtenus, loin d'être exhaustifs, ne constituent qu'une première étape pour une meilleure connaissance de la forêt de Ngotto en particulier et des écosystèmes forestiers centrafricains en général. De nombreuses espèces demeurent encore non identifiées; des inventaires floristiques doivent être encouragés en mettant l'accent surtout sur les espèces de sous-bois, les lianes et les fougères. Il serait intéressant d'étudier avec plus de détails les espèces des genres *Rinorea*, *Drypetes*, *Cola*, *Ficus*, *Trichilia*, *Landolphia*, *Salacia* qui sont bien représentées physionomiquement et numériquement dans la forêt. Un accent devrait être mis sur les deux familles les plus importantes du point de vue spécifique, Euphorbiaceae et Rubiaceae. Des observations sur les relations plantes-animaux permettront de préciser le rôle spécifique des animaux dans la dissémination et indirectement dans la régénération.

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THE GENUS *DISCOPODIUM* HOCHST. (SOLANACEAE) IN AFRICA

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Abstract

The genus *Discopodium* Hochst., one of the two Solanaceae genera endemic to Africa, has long been considered as monospecific. It is shown here that the two species *D. penninervium* Hochst. and *D. eremanthum* Chiov. can be separated on a number of characters, and that the latter is often restricted to higher altitudes of isolated mountain forests. The two species are illustrated, a key to their delimitation and full species descriptions are given, and their distribution is mapped.

Résumé

Le genre *Discopodium* Hochst. (Solanaceae) en Afrique. Le genre *Discopodium* Hochst., un des deux genres de Solanaceae endémiques d'Afrique, a longtemps été considéré comme monospécifique. Nous montrons ici que les deux espèces *D. penninervium* Hochst. and *D. eremanthum* Chiov. peuvent être séparées sur base de différents caractères et que la seconde est souvent limitée aux altitudes les plus élevées des forêts montagneuses isolées. Les deux espèces sont illustrées, une clé permettant de les différencier, et des descriptions complètes sont données ainsi qu'une cartographie de leurs distributions.

Key words: *Discopodium*, Solanaceae, taxonomic revision, Flora of Tropical East Africa.

1 Introduction

Discopodium Hochst. is one of only two genera belonging to the Solanaceae which are thought to be truly endemic to Africa (D'Arcy, 1991). Symon (1991) suggested that *Discopodium* together with *Withania* Pauquy, with which it shows affinity, and *Mellissia* Hook.f., an endemic monospecific critically endangered genus found on St. Helena (Cronk, 2000), form a phytogeographically coherent suite representing a distinctive African element of the family Solanaceae. He further proposed that these three genera constitute a Gondwanan element.

Although generally considered to be monospecific, various collectors have suggested that *Discopodium* is represented by two distinct species (Edmonds, 2005). During the revision of this genus for the Flora of Tropical East Africa, critical examination of all African specimens of the genus housed in the herbaria of the Royal Botanic Gardens, Kew (K) and the Natural History Museum, London (BM) confirmed previous field observations by various collectors, and demonstrated that there are indeed two species which can be delimited by a number of morphological characters. The more common species *D. penninervium* Hochst. is frequently found at high elevations in mountain forests of east, west and central tropical Africa, while *D. eremanthum* Chiov. is restricted to even higher altitudes of East Africa and Ethiopia.

The family Solanaceae Juss. has been the subject of innumerable classificatory studies, and these were reviewed by D'Arcy (1979). Belonging to the subfamily Solanoideae Kostel [1834], *Discopodium* was placed in the tribe Jaboroseae Miers [1849] by D'Arcy (1991). He had previously suggested that *Discopodium* was possibly congeneric with *Acnistus* Schott and *Withania* (D'Arcy, 1973), while stressing the desirability of a comparative study of these three genera. Hunziker (2001) later dismissed D'Arcy's suggestion, postulating that *Discopodium* was clearly but not closely related to both *Acnistus* and *Witheringia* L'Hér. He also considered D'Arcy's placement of *Discopodium* in the tribe Jaboroseae to be "an irrelevant decision". Olmstead *et al.* (1999) subsequently placed the genus in the tribe Solaneae Dumort. [1829], largely on morphological criteria since it was not included in their chloroplast DNA variation analyses. From their results, Olmstead *et al.* (1999) suggested a more narrowly defined tribe than that of previous authors, which includes *Solanum* L. (with *Cyphomandra* Mart. ex Sendtn. and *Lycopersicon* Mill.), *Jaltomata* Schltdl. and a few genera, like *Discopodium,* of uncertain relationship to *Solanum.* Hunziker (2001) too placed this genus in the tribe Solaneae, though he included *Discopodium* in the subtribe Witheringinae (Miers) Hunz. [2001] together with eight other genera including *Witheringia* and *Acnistus.* He thought the latter were related to *Discopodium,* though not closely. Clearly more molecular analyses augmented by continued morphological work is necessary to clarify the generic relationships within the tribes and subtribes of this complex family, and to determine the correct placement of *Discopodium* itself.

The suprageneric authorities used here are largely taken from the *Indices Nominum Supragenericorum Plantarum Vascularium* website compiled by James L. Reveal (www.life.umd.edu/emeritus/reveal/PBIO/WWW/supragen.html); the dates of their publication are given in square brackets.

2 Taxonomic treatment

Discopodium Hochst. in Flora, 27: 22 (1844); Dunal in DC., Prodr. 13(1): 478 (1852); Bentham & Hooker, Gen. Plant., 2: 893 (1876); Wettstein in Engler & Prantl, Nat. Pflanzenfam.: 14 (1895); Wright in Fl. Trop. Africa, 4: 253 (1906); Heine in Hutchinson & Dalziel, Fl. West Trop. Africa, 2, 2nd ed.: 328 (1963); Troupin in Fl. Pl. ligneuses Rwanda, in Musée Royal L'Afrique Central-Tervuren, Belg. Ann., Ser. 8(2): 651 (1982) & Fl. Rwanda, Sperm., 3: 366 (1985); Hunziker, Genera Solanacearum: 186 (2001); Gonçalves in Fl. Zambesiaca (in press).

Bush, shrub or small tree. Stems woody. Leaves solitary, usually alternate, petiolate, prominently penninervate, often with long, simple, eglandular, multicellular hairs. Inflorescences solitary flowers or 2–many-flowered axillary fascicles, epedunculate, pedicels slender. Flowers 5-merous, sometimes aromatic; buds obovoid and often densely pubescent and ochraceous. Calyx broadly cupulate, with scattered hairs internally, glabrous to pilose/villous externally; sepals broadly triangular. Corolla campanulate-urceolate, tube broadly cylindrical, densely pubescent with short appressed hairs above calyx externally, glabrous internally apart from pilose band between filament bases, lobes narrowly triangular, usually recurved when anthers often exposed, occasionally spreading, densely pubescent with short hairs on both surfaces, apices acute. Stamens included, usually equal; filaments filiform, broader at the base, adnate to middle of corolla tube, alternating with petal lobes, free parts glabrous; anthers usually all fertile, bithecate. Ovary globose to conical, bilocular, ovules numerous, placentation axile; style included; stigma discoid/capitate/peltoid with central depression, occasionally bilobed; disc annular, glabrous, orange, fleshy and sulcate below ovary. Fruit a berry, globose to ovoid, yellow, orange, red or blackish. Seeds orbicular or reniform with vesciculate testa.

Key to the species

Mature leaves large, usually 10–24 cm long × 5–14.5 cm wide; flowers usually in many-flowered fascicles, corollas usually 5–7(rarely –8) mm long; styles usually pilose or villous, rarely glabrous; berries globose or broadly ovoid; seeds 10–34 per berry, 2.5–3.5 mm long, orbicular, pale brown . . . . 1. **D. penninervium**

Mature leaves small, usually <8 cm long and <5 cm wide; flowers solitary, rarely in fascicles of 2(–4); corollas (7–)10–13 mm long; styles usually glabrous, occasionally pilose; berries usually longitudinally ovoid; seeds 1–5 per berry, 5–6 mm long, reniform, dark brown . . . . 2. **D. eremanthum**

1. **D. penninervium** Hochst. in Flora, 27: 22 (1844); Dunal in DC., Prodr., 13(1): 478 (1852); Engler, Hochgebirgsfl. Trop. Afr.: 374 (1892); Wettstein in Engler & Prantl, Nat. Pflanzenfam.: 15 (1895); Wright in Fl. Trop. Africa, 4: 253 (1906); Dammer in Wissenschaft. ergebnisse Deutsch. Zentral- Afrika Exped., 2 (1910–1914): 282 (1914); Battiscombe, Trees & Shrubs of Kenya Col.: 158 (1936); Eggeling, Indigenous Trees of Uganda Protectorate: 233 (1940), rev. ed.: 413 (1952); Robyns, Fl. Sperm. Parc National Albert Congo Belge, 2: 203 (1947); Brenan & Greenway, Check-Lists Forest Trees & Shrubs of Brit. Empire, Pt. 2: 574 (1949); Dale & Greenway, Kenya Trees & Shrubs: 537 (1961); Cufodontis, Enum. Plant. Aethiop., Sperm., 2: 856 (1963); Heine in Hutchinson & Dalziel, Fl. West Trop. Africa, 2, 2nd ed.: 328 (1963); Agnew, Upland Kenya Wild Flowers: 528 (1974); Troupin in Fl. Pl. ligneuses Rwanda, in Musée Royal L'Afrique Central-Tervuren, Belg. Ann., Ser. 8(2): 651 (1982) & Fl. Rwanda, Sperm., 3: 368 (1985); Beentje, Kenya Trees, Shrubs & Lianas: 578 (1994); Gonçalves in Fl. Zambesiaca (in press).

Type: Ethiopia, mountains around Bahara in Haramat, Tigre, *Schimper* 917 (TUB, ?holo.; BM!, CGE!, K!, MPU, OXF!, iso.). Fig. 1.

Synonyms:

Solanum cosmeticum Delile in Rochet, Sec. Voy. Choa: 340 (1846), *nomen nudum.* Type: Ethiopia, Choa, *Rochet d'Hericourt* 10 (MPU-Delile, holo.; P, iso.) *fide* Lester, pers. comm.

Withania holstii Dammer in Engler, Pflanzenwelt Ost.-Afrika & Nachbargebiete, 50: 351 (1895), *fide* Bitter in Engler, Bot. Jahrb. 57: 15–16 (1920). Type: Tanzania, Usambara, Magama, *Holst* 3843 (?B†, ?holo.).

Discopodium penninervium Hochst. var. *holstii* (Dammer) Bitter in Engler, Bot. Jahrb. 57: 16 (1920); Brenan & Greenway, Check-Lists Forest Trees & Shrubs of Brit. Empire, Pt. 2: 574 (1949). Type: Tanzania, Lushoto Distr., Usambara, *Holst* 3843 (B†, syn.); Kwai, *Albers* 143, 381 (B†, syn.).

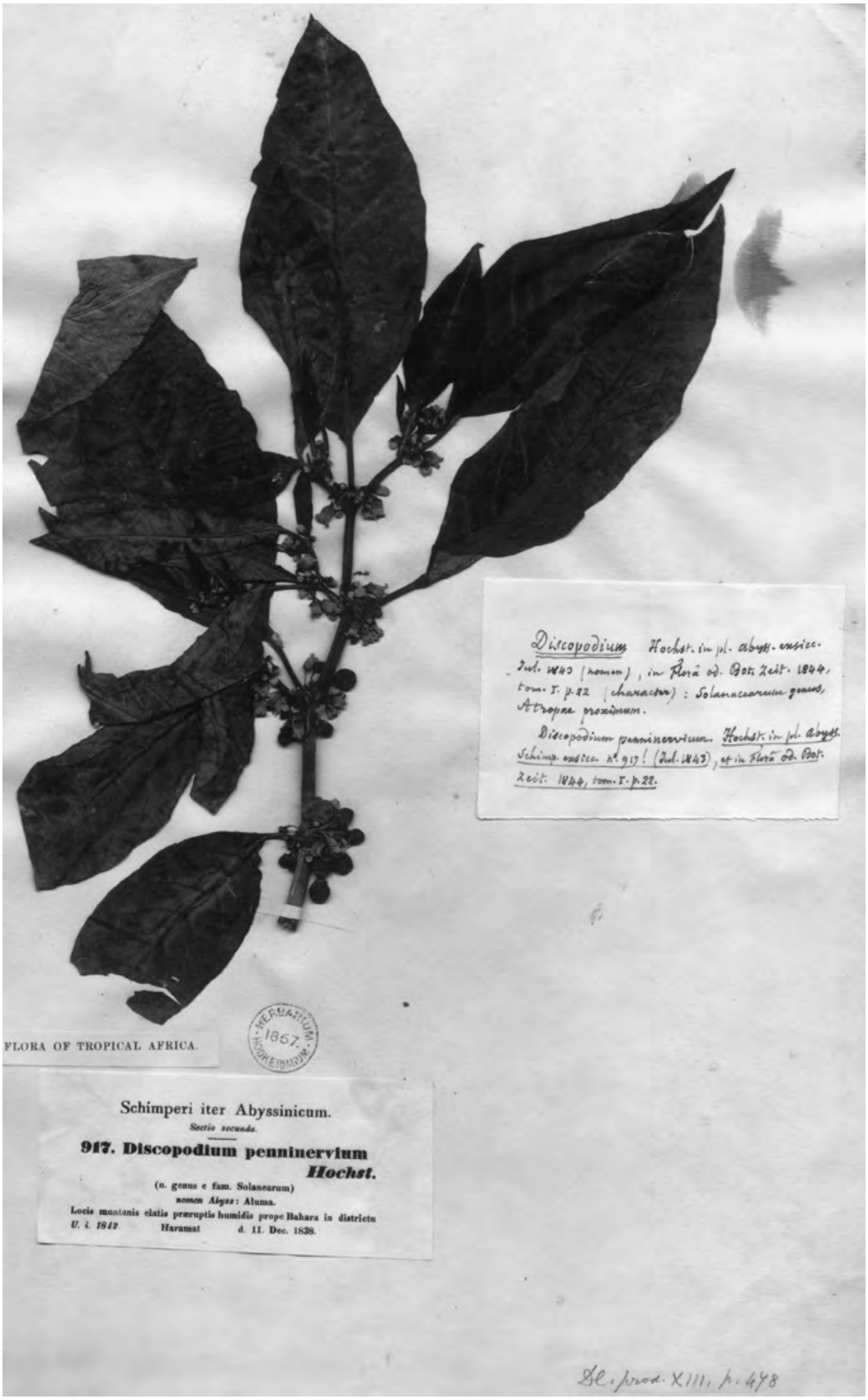

FIG. 1. Isotype of *D. penninervium* (*Schimper* 917, K)

D. paucinervium Engl. in Engler & Drude, Veget. der Erde, IX, Pflanzenwelt Afrikas, 1(1): 381 (1910), *nomen nudum*; Brenan & Greenway, Check-Lists Forest Trees & Shrubs of Brit. Empire, Pt. 2: 574 (1949).

D. penninervium Hochst. var. *nervisequum* Bitter in Engler, Bot. Jahrb. 57: 17 (1920). Type: Uganda, Toro Distr., Ruwenzori, *Scott Elliot* 7714 (B†, holo.; BM!, lecto.).

D. penninervium Hochst. var. *intermedium* Bitter in Engler, Bot. Jahrb. 57: 17 (1920); Brenan & Greenway, Check-Lists Forest Trees & Shrubs of Brit. Empire, Pt. 2: 574 (1949). Type: Tanzania, Lushoto Distr., Usambara, *Braun*, B.L. Institut Amani 2738 (B†, holo.).

D. penninervium Hochst. var. *sparsearaneosum* Bitter in Engler, Bot. Jahrb. 57: 17 (1920). Type: Cameroon, Manenguba mountains near Bare, *Schäfer* 100 (B†, holo.)

D. penninervium Hochst. var. *magnifolium* Chiov. in Nuovo Giorn. Botan. Italiano, 36: 367 (1929). Type: Ethiopia, Arussi, Mount Galamo, *Cosimo Basile* 68 (TO, ?holo.)

Note: The synonymy of most of the varieties given above is based largely on their protologues and the morphological variability exhibited by the species. Vegetative pubescence, especially that associated with the leaves, is particularly variable in this genus, and the minor differences in leaf pubescence used by Bitter to differentiate several varieties are considered to be within the limits acceptable in this species. The holotypes of most of these varieties were located in Berlin and presumably have been destroyed. Duplicate specimens have not yet been traced, with the exception of *Scott Elliott* 7714. A specimen of this collection located at the BM, has been designated the lectotype of *D. penninervium* var. *nervisequum.*

Tall shrub, slender bush or small tree, usually 1.5–5 m, occasionally to 10 m high. Stems soft and somewhat succulent to woody, green, yellow or brownish, glabrous, pilose, villous or densely flocculose, often varying from villous/flocculose to glabrescent as they mature. Leaves usually membraneous, ovate to ovate-lanceolate, margins usually entire to sinuate, occasionally sinuate-dentate with 1–6 acute antrorse lobes, (8.8–)12–24 cm long, 5–14.5 cm wide, upper surfaces often glabrous apart from midribs and primary veins which sparsely to moderately pilose, lower surfaces sparsely pilose, tomentose or villous/flocculose; petioles 1–6(–11) cm long, glabrous, pilose or villous. Inflorescences (3–)6–30-flowered fascicles, flowering pedicels 5–12(–15) mm long, usually erect, varying from densely pilose/villous to glabrous. Calyx broadly cupulate, 1–2(–4) mm long, glabrous to densely pilose or villous externally; sepals broadly triangular or ovate, 0.75–2 mm long, 1.5–2.5 mm wide, with or without a ciliate fringe which can appear tufted. Corolla white, cream, yellow or greenish, occasionally purplish or yellowish-red, 5–7(–8.5) mm long; tube 2.5–5 mm long, petals narrowly triangular, 2–3.5(rarely –6) mm long, 0.5–2(rarely –3) mm wide. Stamens with filaments free for 0.5–2.5 mm; anthers yellow to brown, 1–2 mm long and 0.6–1.25 mm wide. Ovary 1–2(–3.5) mm diameter; style green, usually pilose throughout, rarely villous, occasionally glabrous (**T** 2 and Ethiopia), usually filiform, sometimes clavate, 1–2.5 mm long, 0.3 mm wide; stigma green, capitate, 0.8–1.5 mm diameter; disc orange or brown, 2–3.5 mm diameter. Fruit globose to broadly ovoid, orange, orange-yellow or red, 5–8(–11) mm diameter; fruiting calyx cupulate with broadly triangular or ovate sepals 1–2.5 mm long and 2–3 mm wide whose apices are usually semi-reflexed; fruiting pedicels erect or spreading, 8–20 mm long, densely villous, pilose or glabrous, often becoming woody. Seeds many, 10–34 per berry, usually orbicular, 2.5–3.5(–4) mm long, 2.25–3(–3.6) mm wide, light brown. Figs. 2 a–j; 3 a–c; 4.

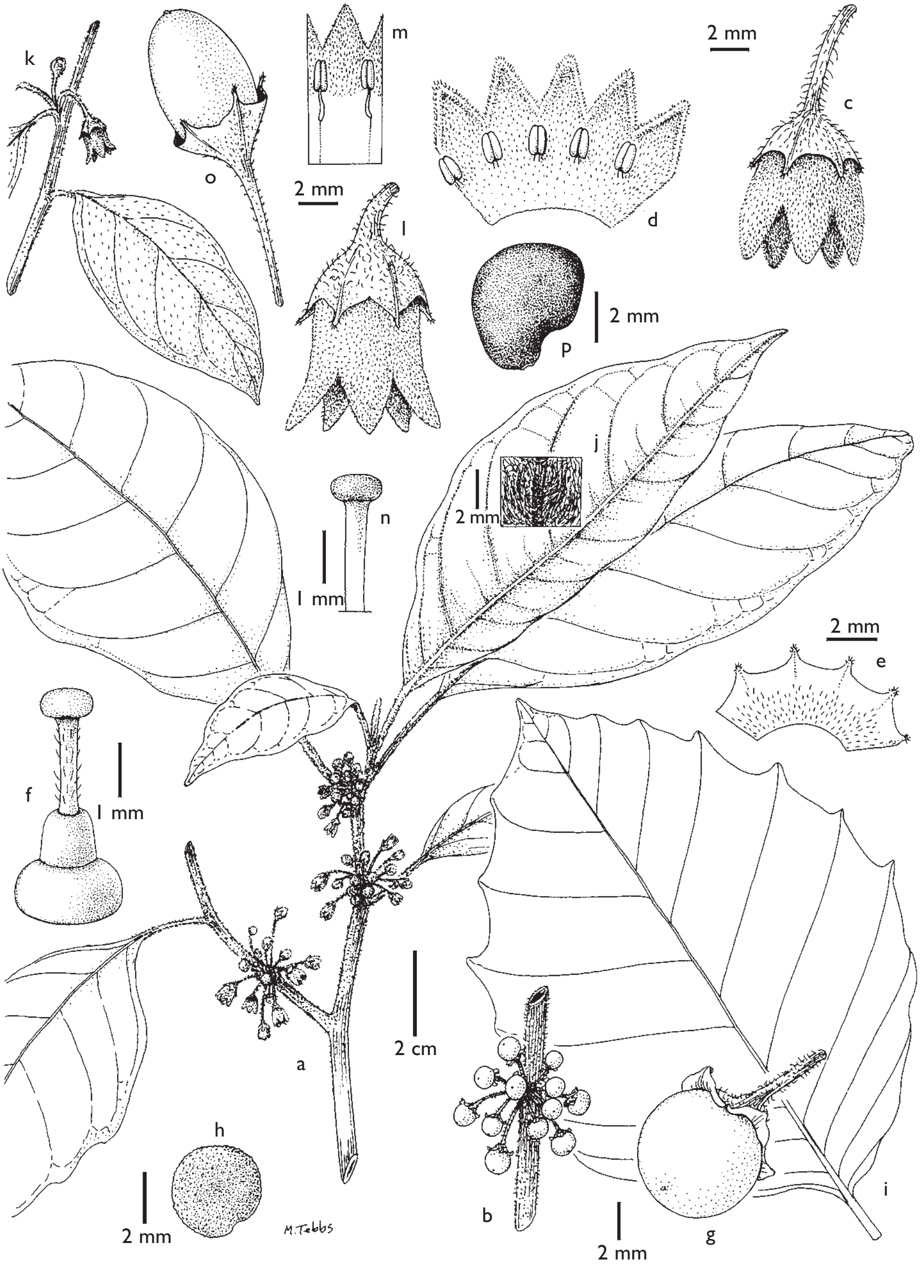

FIG. 2. a–j – *D. penninervium*: a. habit and inflorescences; b. infructescence; c. flower; d. open flower; e. calyx; f. disc, ovary, style and stigma; g. fruit with reflexed sepal lobes; h. seed; i. leaf with sinuate-dentate margins; j. leaf pubescence (a, c–e, f & j – *Geesteranus* 5622; b, g & h – *Lucas & Polhill* 83; i – *Eggeling* 1625). k–p – *D. eremanthum*: k. inflorescence; l. flower; m. part of open flower; n. style and stigma; o. fruit with adherent calyx lobes; p. seed (k–n – *Katende* 466; o & p – *Hedberg* 1994).

FIG. 3. a–c. *D. penninervium*: a & b – shrubby habit (Kenya (**K** 4): Kiambu Distr., Tigoni near Limuru, 2150 m; *Luke* s.n.), c. small roadside tree (Ethiopia, Bale Mountain National Park (BA), Harenna Forest side of Rira on southern side of Sanetti Plateau, 2800 m; *Friis & Edmonds* 11412); d. *D. eremanthum*: shrub in wet *Erica/Hagenia* woodland (Ethiopia, Bale Mountain National Park (BA), southern slopes of Sanetti Plateau, 3300 m; *Friis & Edmonds* 11411).

FIG. 4. *D. penninervium*: inflorescences showing prominent discs beneath ovaries which are orange (Uganda (**U** 2): Kabarole Distr., Kibale Nat. Park near Kanyawara, 1400–1500 m; *Knapp* 9808 (copyright NHM)).

Distribution

Often restricted to higher elevations of isolated mountain forests in west and east tropical areas; Bioco (Equatorial Guinea), Nigeria and Cameroon but more common in the eastern tropics, especially in Ethiopia, Rwanda, Burundi, Uganda (**U** 1–4), Kenya (**K** 3–5), Tanzania (**T** 2, 3, 6 & 7) from where it extends to southern Sudan, and southwards to eastern Zaire and Malawi. Within eastern Africa, this species seems to have a fairly restricted distribution in Kenya, though it is often common in habitats in which it is found. It is more widely distributed in Uganda and Tanzania and particularly well-distributed in Ethiopia, where the leaves are reputedly used as 'tobacco'. (*cf.* Fig. 5).

Habitat

Upland or montane rain-, bamboo- or scrub-forest, including edges, paths, stream- and river-sides, dampish copses, and Bamboo-*Dracaena* thickets; also in scrub, grass-swamp and -bushland, on mountain sides and as a roadside ruderal. 1400–2500(–3000) m.

2. **D. eremanthum** Chiov. in Racc. Bot. Miss. Consol. Kenya: 89 (1935); Dale & Greenway, Kenya Trees & Shrubs: 537 (1961) (as *Discopodium* sp.); Agnew, Upland Kenya Wild Flowers: 528 (1974); Beentje, Kenya Trees Shrubs & Lianas: 577 (1994).

Type: Kenya, Mt. Aberdare E., Kinangop-Toeine forest, *Balbo* 121 (TOM deposited at FT, holo., photo!). Fig. 6.

Synonyms:

D. grandiflorum Cufod. in Senck. Biol., 46 (Illustr. Suppl. 14): 90 (1965). Type: Ethiopia, Gamu-Gofa, Dita-Berg, *Kuls* 773 (FR!, holo.). Fig. 7.

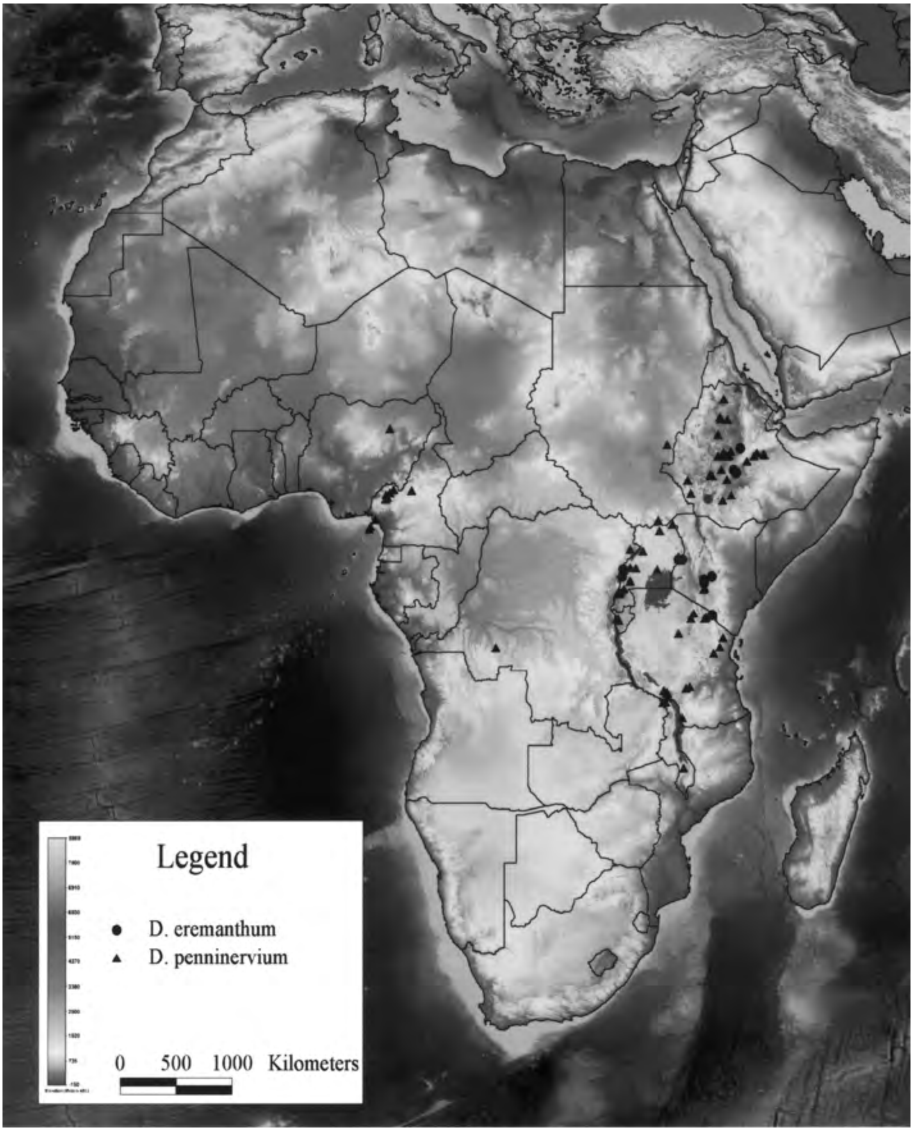

FIG. 5. Distribution of *Discopodium* species based on specimens at K and BM.

Shrub or small often much-branched tree, 1–3(–5) m high; branches ascending with terminal foliage. Stems woody, angular, often almost glabrous when mature though young stems can be fuscous and densely flocculose/villous. Leaves usually coriaceous, elliptic, ovate, ovate-lanceolate or lanceolate, margins entire or sinuate, 4–7.8(rarely –17) cm long and 1.4–5(rarely –7.6) cm wide, upper surfaces varying from glabrous to pilose especially on midribs and primary veins, lower surfaces glabrous, tomentose or villous/flocculose, often appearing fuscous; petioles 4–15(–30) mm long, glabrous, pilose or villous. Flowers usually solitary, occasionally in 2–3(–4)-flowered fascicles,

FIG. 6. Holotype of *D. eremanthum* (*Balbo* 121, FT).

Expedition des Frobenius-Instituts
der Universität Frankfurt a. M. nach Süd-Aethiopien, 1954/56.

Fam.: Solanaceae

Gatt. und Art: Discopodium grandiflorum Cuf., /n. sp.

Tag und Fundort: Gamu-Gofa: Dita-Berg, 2900-3100 m häufig, 22.8.55.-2-3 m hohes Holzgewächs, Blüten grün-gelb, Beerenfrucht.-Amhara[redacted]: amararo, Galla:[redacted] maío.

Sammler: Dr. W. Kuls Det.: Cufodontis 1964

Sammelnummer: 773 Herb. Senckenb. Nr.:

FIG. 7. Holotype of *D. grandiflorum* (= *D. eremanthum*) (*Kuls* 773, FR).

often aromatic; pedicels 7–14 mm long, often pendulous, sparsely pilose to glabrous. Calyx green to purplish, (2.5–)3–5 mm long; sepals shallow, 2–5 mm wide and 1.25–3.5 mm long, sparsely hairy to pilose externally usually with distinct ciliate fringe often appearing as tufts on protruding apices. Corolla pale green, yellow or pale purple, (7–)10–13 mm long, tube (5–)6–8 mm long, petals triangular, (2.5–)4–5 mm long and (1.5–)2.5–4 mm wide. Stamens with filaments free for 1–3 mm; anthers greenish, yellow or brown, (1.25–)1.75–2.25 mm long and 0.75–1 mm wide. Ovary green, 1.5–2.5 mm diameter; style green, usually glabrous, occasionally pilose, (1.1–)2–4 mm long and 0.25–0.75 mm wide, filiform; stigma green, discoid/capitate, often bilobed, 0.75–1.5(–1.9) mm diameter; disc orange or yellow, 3–4 mm diameter. Fruit yellowish-orange, orange or red, usually longitudinally ovoid, rarely globose, 6–15 mm long and (4.5–)6–10 mm wide; fruiting calyx cupulate with shallow sparsely pilose sepal lobes 2–5 mm wide and 1.3–3.5 mm long, adherent to base of berry; fruiting pedicels 10–22 mm, erect. Seeds solitary or few, 1–5 per berry, usually reniform, (4–)5–6 mm long and (2.5–)4–4.5 mm wide, dark brown. Figs. 2 k–p; 3 d.

Distribution

Confined to high altitudes in Ethiopia, Uganda (**U** 2/Zaire; **U** 3), Kenya (**K** 3, 4 & ?5) and Tanzania (**T** 2) (Fig. 5).

Habitat

Moorlands, old lava, mountain slopes in high montane scrub, *Podocarpus-, Rapanea-Hagenia-, Erica-* or bamboo- forests in glades, edges, clearings, or on tracks through degraded *Arundinaria* forest; often in damp or boggy conditions. (2100–)3000–3500 m.

One of the characters often used in distinguishing the two species is the stylar pubescence. The styles of *D. penninervium* are typically pilose, while those of *D. eremanthum* are usually glabrous. A number of specimens, however, exhibit intermediate stages, especially in Tanzania (**T** 2) and Ethiopia, while the styles of the various isotypes of *D. penninervium* itself (*Schimper* 917) also vary from being glabrous to sparsely pilose. The density and type of stylar pubescence may reflect the considerable variability of this character found in the vegetative parts of these species, and this character should therefore only be used in association with the more definitive floral and fruiting characters to differentiate the two species.

During the post-Congress AETFAT tour to the Bale Mountain National Park (BA), the recognition of two distinct species in this genus, distinguishable by the characters given above, was verified. The rarer *D. eremanthum* with solitary or few-flowered inflorescences composed of large flowers which are succeeded by longitudinally ovoid berries with only a few large reniform, dark brown seeds occurred as scattered shrubs in an extremely wet *Erica arborea/Hagenia* mixed woodland on the southern slopes of the Sanetti plateau at an altitutude of 3300 m (6°47'N, 39°44'E). In contrast the more common *D. penninervium* with smaller flowers borne in many-flowered fascicles followed by spherical or broadly ovoid berries containing numerous small, orbicular, light brown seeds was found as a small roadside tree, bordering open grassland which had probably been cleared, at the lower altitude of 2800 m (6°44'N, 39°42'E) on the Haranna forest side of Rira. The berries of both species were bright orange. It seems that within the berries of *D. eremanthum*, only one or at best a few seeds develop to maturity, the majority of ovules remaining white, apparently inviable and somewhat vestigeal, and that while the inflorescences may be up to 4- or 5-flowered initially, the mature infructescences are only one- or two-berried. A study of the relative fertility of these two species and their potential ability to hybridise would clearly be of considerable interest. Voucher specimens of both species have been deposited in the herbarium at Addis Ababa (*Friis & Edmonds* 11411 & 11412, ETH).

Finally, new and interesting withanolides have recently been isolated from the leaves and roots of these species, with phytochemical analyses also revealing cytotoxic and immunosuppressive activities to be associated with this genus (*cf.* Hunziker, 2001). In Ethiopia, the leaves are said to be used as a form of 'tobacco'.

Acknowledgments

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AFRICAN SAPROPHYTES: NEW DISCOVERIES

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Abstract

An overview is given of new saprophytes discovered since 1997. New species have been described in *Afrothismia* (4 species), *Kupea* (1 species), and the new monospecific genus *Kihansia.*

Résumé

Saprophytes africaines: de nouvelles découvertes. Un aperçu est donné de nouvelles saprophytes découvertes depuis 1997. De nouvelles espèces ont été décrites dans les genres *Afrothismia* (quatre espèces), Kupea (une espèce) ainsi que le nouveau genre monospécifique *Kihansia.*

Key words: Africa, saprophytes, mycotrophs

1 Introduction

At the AETFAT Congress in 1997, in Zimbabwe, I presented a review of African saprophytes, that is, achlorophyllous mycotrophs (Cheek & Williams, 1999). These plants lack chlorophyll entirely, and derive their nourishment from fungal mycorrhizae. The fungi in turn feed either on tree roots, or from organic matter. African saprophytes occur in undisturbed evergreen forest, with the exception of *Schwartzkopfia* (Orchidaceae), a genus of two savanna species.

At the heart of the 1997 review I gave a table detailing the species of saprophyte, and the African countries in which they occur. In this paper that matrix is updated with new taxa and new country records that have come to light since 1997. The text that follows gives more details on these new records.

2 New taxa

The most interesting saprophyte discoveries since 1997 were sent to me directly as a result of the AETFAT presentation, from Tanzania by Jon Lovett. In 1995 in Cameroon we had found a new genus of Triuridaceae, *Kupea* (Cheek *et al.*, 2003). Lovett had found a site of a few square metres in Tanzania, with three species of saprophytes. One was an *Afrothismia* (Burmanniaceae), the other two were Triuridaceae. Of these Triuridaceae, one turned out to be a second species of the Cameroonian genus *Kupea,* and the other needed a new generic name, *Kihansia.* The two genera required the establishment of a new tribe, *Kupeaeae,* so far endemic to Africa (Cheek, 2003a).

TABLE 1. Distribution by country of saprophyte species in Africa. New discoveries in bold.

Species	S.Africa	Angola	Botswana	Zimbabwe	Zambia	Malawi	Mozam.	Tanzania	Kenya	Ethiopia	Sudan	Uganda	Congo	D.R.C.	Annob.	Eq. Guinea	Gabon	C.A.R.	Cameroon	Nigeria	Benin	Togo	Ghana	C. Ivoire	Liberia	S. Leone	G. Bissau	G. Conakry	Total
Burmannia hexaptera																			x	x									2
Burmannia congesta		x												x			x	x	x				x		x			x	8
(Burmannia densiflora)																			x										1
**Oxygyne trandra*																			x										1
**Oxygyne sp. nov.*																			x										1
Afrothismia winkleri																			x	x									2
**Afrothismia pachyantha*																			x										1
**Afrothismia insignis*								x																					1
**Afrothismia 'amietii'*																			x										1
**Afrothismia sp. nov.*					x	x																							2
****Afrothismia baerae***									**x**																				**1**
****Afrothismia mhoroana***								**x**																					**1**
****Afrothismia gesneroides***																			**x**										**1**
****Afrothismia salingei***																			**x**										**1**
Gymnosiphon bekensis																	x	x	x										3
Gymnosiphon longistylus														x			x		x	x			x		x	x			7
Gymnosiphon usambaricus				?	x	x		x	x																				4
Gymnosiphon danguyanus								x																					1
**Gymnosiphon sp. nov.*				?		x																							1
Voyria primuloides																	x			x			x		x				4
Sebaea oligantha										x	x	x		x			x	x	x	x				x			x		10
Sciaphila ledermanii																			x	x									2
Sciaphila africana																							x	x					2
**Seychellaria africana*								x																					1

TABLE 1. continued

Species	S.Africa	Angola	Botswana	Zimbabwe	Zambia	Malawi	Mozam.	Tanzania	Kenya	Ethiopia	Sudan	Uganda	Congo	D.R.C.	Annob.	Eq. Guinea	Gabon	C.A.R.	Cameroon	Nigeria	Benin	Togo	Ghana	C. Ivoire	Liberia	S. Leone	G. Bissau	G. Conakry	Total
**Kupea martinetugei*																			x										1
Kupea jonii								**x**																					**1**
Kihansia lovettii								**x**																					**1**
Auxopus macranthus												x		x					x	x			x	x					6
Auxopus kamerunensis																			x	x			x	x	x				5
Epipogium roseum						x			x		x	x		x	x	x			x	x			x						10
Didymoplexis africanum				x		x	x	x															?						4
**Didymoplexis pallens*		x																											1
Didymoplexis verrucosa	**x**																												**1**
Eulophia galeiodes								x	x		x			x						x									5
**Eulophia epiphanoides*								x																					1
Eulophia richardsiae					x																								1
**Eulophia gastroides*							x																						1
Gastrodia africana																			**x**										**1**
Gastrodia sesamoides	**x**																												**1**
Schwartzkopffia lastii		x		x	x	x	x	x						x															7
Schwartzkopffia pumilio																				x		x		x		x			4
Totals 1997	0	3	0	2	4	6	3	8	3	0	3	3	0	7	1	1	4	3	16	11	0	1	7	5	4	2	1	1	
Totals 2003 (if different)	**2**							**11**	**4**	1							**5**		**19**										

Note: *denotes only known from one collection or locality

Source: Compiled from Flora accounts, herbarium records (K, YA, SRGH), personal observations and literature cited in this paper

So, for Truridaceae, Africa goes from having just 3 species in two genera, to six species in four genera, and to having an endemic tribe, only the third in the family.

The next round of discoveries occurred in the genus *Afrothismia*, beginning in September 2002, when Henk Beentje referred to me a photo from Quentin Luke in Kenya. This was the first record of the genus from Kenya, and the taxon is morphologically isolated in the genus. It is known only from a few square metres in the Shimba Hills, where it was collected by Sabine Baer, after whom it is named (Cheek, 2003b).

Shortly after this paper had been submitted, Phil Cribb notified me of an *Afrothismia* that he had received from Tanzania as ?Orchidaceae, collected by Jannerup and Mhoro. This has been submitted for publication as *Afrothismia mhoroana,* closely related to *A. insignis* Cowley (Cheek & Jannerup, in press).

A few months before this congress, Hiltje Maas told me that she had a new species from Cameroon collected by de Winter in Cameroon. This proved to be another new species (Maas, 2004), related to *A. pachyantha* Schltr.

Finally, the week before this congress I was sent another paper to review, purporting to be a new species from Mt Kupe in Cameroon. Since I and my colleagues have spent months over several years studying saprophytes on Mt Kupe, this seemed most unlikely. Amazingly, it proved to be the most morphologically bizarre, and largest, species of *Afrothismia* yet known (Franke, 2004).

3 Range extensions

I am grateful to Mike Gilbert for the first record of an obligate saprophyte from Ethiopia. This appears, from study at ETH, to be the only record of the species for the country. It is remarkable that it is from a grassland habitat, not forest:

Sebaea oligantha (Gilg) Schinz. Ethiopia, Wollega Region, E slopes of Didessa R. valley, 1300 m, 09°03' N, 36°11' E. In deep shade under tall grass often with *Anthoceros, Gilbert & Thulin* 709 (ETH!).

Numerous recent records of a spectacular gentian, *Voyria primuloides*, were seen for Gabon at LBV in 2002 (pers. obs.), mostly made by collectors from WAG. I am grateful to Bonaventure Sonké for bringing to my attention the only known record of the same species from Cameroon: *Stevart & Droissart* V.2102, Akom II (Est de Kribi). Sommet 2 (1005 m), 7/3/2004 (BRLU).

4 The saprophyte table

The updated table (Table 1) shows a considerable increase in the number of species and genera compared with its predecessor. From 32 species in 14 genera, the number has climbed to 42 species in 17 genera. Apart from the increase in Triuridaceae, referred to above, four new *Afrothismia* and three extra Orchidaceae (two added as a note in proof to the text of the 1999 paper) account for the rise. *Epipogium roseum* (Orchidaceae) remains the most widely distributed and common (on a country occurrence basis) saprophyte, and is closely followed by *Sebaea oligantha* (Gentianaceae).

The spate of discoveries in recent years shows that it is likely that there are still many more saprophytic species waiting to be discovered. *Gymnosiphon* (Burmanniaceae) is the genus that most needs further taxonomic analysis, and for this more alcohol preserved specimens are necessary.

So, all those working in evergreen forest, please keep looking at the ground for strange small plants, especially near the end of the wet season. If you find a saprophyte, put it in a little bottle or jar in 70% alcohol, make good notes, and send it for identification please.

Note: Since the above was written, two further species of *Afrothismia* from Cameroon have been published: *A. foertheriana* (Blumea 49: 451–456, 2004) and *A. hydra* (Nordic J. Bot. 23: 299–303, 2005).

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CENTENARY OF THE EAST AFRICAN HERBARIUM, NAIROBI: 1902–2002

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Abstract

The East African herbarium (EA), Nairobi, marked its centenary in August 2002. A brief history of EA is highlighted from its origin at Amani in the East Usambara Mts, Tanzania, as a department of a German Biological-Agricultural Research Institute in 1902 to its current status as the main regional herbarium. EA is the largest and oldest herbarium in tropical Africa with about 1 million specimens comprising mostly vascular plants with a few bryological and mycological collections. Among the collections are about 4000 types and several classical collections such as those of Ehrenberg from Eritrea, Schimper from Ethiopia, Kotschy from Ethiopia, Peters from Mozambique, Stuhlmann from Central and East Africa, Busse from German East Africa and Warnecke from Togo. The achievements and role of EA in the taxonomic study and conservation of the East African flora, training of botanists and conservationists, and its current research capacity in terms of personnel and facilities are briefly discussed.

Résumé

Centenaire de l'‘East African Herbarium’, Nairobi: 1902–2002. L'‘East African Herbarium’ (EA) de Nairobi, a fêté son centenaire en août 2002. Un bref historique de EA est brossé, de ses origines en 1902 à Amani dans les Mts Usambara en Tanzanie, en tant que département du ‘Biological-Agricultural Research Institute’ allemand jusqu'à son statut actuel de principal herbier de la région. EA est le plus grand et le plus ancien herbier d'Afrique tropicale avec environ 1 million de spécimens, principalement de plantes vasculaires mais aussi quelques collections bryologiques et mycologiques. Parmi ces collections, 4000 types et plusieurs collections historiques comme celles de Ehrenberg pour l'Erythrée, Schimper pour l'Ethiopie, Kotschy pour l'Ethiopie, Peters pour le Mozambique, Stuhlmann pour l'Afrique centrale et orientale, Busse pour l'Afrique de l'est allemande et Warnecke pour le Togo. Les réalisations et le rôle de EA dans l'étude taxonomique et la conservation de la flore d'Afrique de l'Est, la formation des botanistes et conservationnistes et son potentiel de recherche actuel en terme de personnel et de moyens sont brièvement discutés.

Key words: Amani, Coryndon Museum, East African Herbarium, Kenya

1 The beginning in Amani

On 9th August 1902, the Imperial Governor of German East Africa, Count (Graf) Gustav Adolf von Götzen, issued a Gazette notice that established the Biologisch-Landwirtschaftlichen Institut (Biological-Agricultural Institute), here abbreviated as BL, at Amani near Tanga in the East Usambara Mountains, Tanzania (von Goetzen, 1903). Among the mandates of BL were to study the flora and fauna of German East Africa. Prof. Dr. Albrecht Zimmerman became the deputy director and botanist of BL and was the overall head of the Institute for about three years. A building to house a zoological and botanical laboratory including the herbarium was among the first to be built and was ready for occupation in April 1903. This also marked the beginning of the Amani Institute Herbarium that later became known as the East African Herbarium (EA). From the early BL annual reports for the years 1902 to 1906 (Zimmermann, 1903, 1905, 1906; Stuhlmann, 1906), we learn a lot about the beginnings of BL. Subsequent annual reports up to 1914 were published in the journal, *Der Pflanzer,* produced in Dar es Salaam. Even though Dr Franz Stuhlmann, a zoologist from Hamburg was appointed Director in April 1903, he did not take up the post until May 1905. Stuhlmann only stayed at Amani up to January 1908 and had to return to Hamburg due to poor health. Thereafter, Zimmermann became the Director from 1911 up to the end of the First World War (1914–1918). Administrative duties were taking up a lot of Zimmermann's time in the absence of Stuhlmann and therefore Dr Karl Braun was employed in October 1904 to be his botanical assistant. In subsequent years other botanists were employed and they included Dr F. Kränzlin in 1908 and Dr A. Eichinger in 1910. Most of the botanists were occupied with research on economic crops such as coffee, tea, cotton, rubber trees, cinchona, sisal, and pasture, plant pathology, and in providing advice and information to other stations in German East Africa and thus had little time for collecting and studying the native flora.

A guest house was built at Amani by the end of 1902 through a lottery grant, to cater for government officials and other scientific visitors that came to BL or were in transit to other places. The first prominent botanists who visited and left important specimens in the herbarium were Prof. Dr. Adolf Engler, the Director of the Botanical Garden Berlin, in 1902 and 1905, and Dr W. Busse and Dr J. Holtz, both in 1905. Later visiting botanists included Prof. A. Peter from the University of Göttingen, Dr. C. Holst, and Dr. G. Volkens. Reciprocal plant specimen exchange and loan started quite early. Notable duplicate material sent from Berlin to Amani are collections made by W. Busse and C. Uhlig, including many isotypes now particularly important since the holotypes were mostly destroyed (1943) at the Berlin Herbarium during the Second World War (Verdcourt, 2003). Zimmermann was largely responsible for the establishment of the herbarium. Mr. Raden Soleman from Java was the BL illustrator for the first few years. Africans were only employed as labourers and most of them were from the Nyamwezi and Sukuma tribes (Stuhlmann, 1906; Zimmerman, 1914). The foremen and other semi-skilled jobs were given to Indian and Javanese workers. Probably the Shambaa who reside in East Usambara were not interested in working as labourers on German farms. The BL library developed fast and by 1905 it had about 1921 books and 222 journals and periodicals that were either purchased or received in exchange for the BL publications.

During the first months of the First World War, BL become a production centre for commodities such as food and medicine that were needed by German troops and civilians in German East Africa. Among the products that were produced on site were chocolate, toothpaste, whisky and quinine (Zimmermann, 1924; Greenway, 1952;

Verdcourt, 2003). Zimmerman (1914, 1924) summarises the establishment of BL in the annual report of 1913/14 and in a paper presented at a symposium in 1924. After the First World War, significant changes in global politics and economy resulted in the British taking over German East Africa as a Protectorate after the defeat of the Germans, and renaming it Tanganyika. The British were however very reluctant to maintain Amani Institute and subsequent years were marked by neglect from the British Government. They appointed a director, Mr. A. Leechman who took charge in 1920 but resigned in 1923 leaving Mr. F.M. Rogers in charge. No further appointments of staff were made and moves were even made to close the Institute. It was not until 1927 that plans were made to reopen Amani through the efforts of the Kew Director, Lt. Col. Sir David Prain, who had known about the good reputation of BL from his days as Director of Calcutta Botanic Garden (Verdcourt, 2003). Dr. Peter J. Greenway was appointed botanist of Amani and arrived at the station in April 1928. Greenway took charge of the herbarium by assessing the state of the collections, which was found to be good, thanks to the mercuric chloride poisoning of the time, and thereafter embarked on a job of a herbarium curator until his retirement in 1958. Greenway also assessed the state of the vast plantations at Amani and prepared an inventory of all the living collections (Verdcourt, 1981).

The political administration and research were reorganised in British East Africa and Amani Herbarium became part of the East African Agricultural Research Station in 1928. In 1944 there was again a reorganisation and Amani became part of the East African Agricultural Research Institute. After the Second World War (1939–1945), there was another major reorganisation of research in British East Africa and Amani became part of the East African Agriculture and Forestry Research Organisation (EAAFRO). Muguga near Nairobi was made the headquarters of EAAFRO and almost all the departments at Amani were moved there. With the focus on Nairobi, Amani was virtually abandoned and all the vast plantations of economic, ornamental and exotic plants that had been set up by the Germans went into irreversible decline (Verdcourt, 1981). Nairobi was chosen because it was more central, commodious and had a good infrastructure and also because of its cool climate (Greenway *et al.*, 1950; Verdcourt, pers. comm.). Over the years the herbarium had grown enormously and its services especially of naming plant specimens were very much in demand by other departments in British East Africa and beyond. Greenway was overworked and the need to employ an assistant was long overdue. Dr. Bernard Verdcourt was employed in October 1948 and arrived in Amani in December 1949 after a one year stint at Kew (Verdcourt, 2003). The rich history of BL and its botanical activities has been documented by other writers including Zimmermann (1914, 1924), Schlieben (1940), Timler and Zepernick (1987), Iversen (1991), and Schulman *et al.* (1998).

2 Relocation and amalgamation in Nairobi

The BL Herbarium was moved from Amani to Nairobi in August 1950 and the Amani collection were amalgamated with the botanical collections of the Coryndon Memorial Museum (now National Museums of Kenya) at Ainsworth Hill (now Museum Hill) to form the East African Herbarium. The Coryndon Museum was opened in 1929 but most of its early collections emanated from the East Africa and Uganda Natural History Society which was founded in 1910. The curator of the Society's collections was Dr. V.G.L. van Someren. The herbarium started in 1930 through donations of specimens and collecting by members of the Society. The Hon. Mrs. Evelyn Molony was employed as the Coryndon Museum botanist from 1930 to 1934 and thus laid the foundation for the Coryndon Museum Herbarium (Milne-Redhead, 1952; Bally, 1953). After the departure of Mrs. Molony, it was not until 1938 that a new botanist, Peter R.O. Bally, was employed. Head botanists before and after the merger of the Amani and Coryndon herbaria are listed in section 5.

The Herbarium remained under EAAFRO even after the three East African countries became independent. The East African Community (EAC) which was created in 1967 administered the common services for East Africa including scientific research. When the EAC collapsed in 1977 due to ideological and political disagreements, all the common services collapsed. The Kenya Agricultural Research Institute (KARI) and the Kenya Forestry Department took up most of the botanical functions of EAAFRO. The Herbarium was administered by KARI despite the fact that it was located next to Nairobi Museum on the premises of the National Museums of Kenya (NMK). The break-up of the EAC was a turbulent time for EA, with the funding from the EAC ceasing and staff being demotivated. The future of the Ugandans and Tanzanians working at EA became uncertain. In addition, there were wrangles over the ownership of EA by the former partner countries of the EAC. Later on there were also wrangles between KARI and NMK over the ownership of the Herbarium. The Herbarium was finally taken over by NMK in 1982, following recommendations by a Committee formed by the then Minister for Constitutional Affairs and National Heritage, Mr. Charles Mugane Njonjo.

3 Infrastructure and local capacity

From a single room at Amani, the herbarium moved into a spacious, purposely designed, two-storey building at Museum Hill, Nairobi in 1950 (Greenway, 1952). The amalgamation of the Amani and Coryndon Museum collections and the expanding new accessions soon filled the building and a new extension was built and was ready for occupation in 1965. By early 1980's, it was clear that the herbarium was filling up quite fast and a new extension was needed. A grant was obtained from the European Union (EU) for a four-storey extension with a basement and other botanical laboratories (Palynology and Phytochemistry). The building was completed in 1989. The collections are currently in need of more space but this is because a considerable proportion of the EU extension is used for non-Herbarium related activities.

Amani Institute was like other similar establishments in the colonies founded for German economic interests (Timler & Zepernick, 1987; Schulman *et al.*, 1998). Although the German botanists were quite thorough in their research as can be seen in the many achievements including publications at Amani, there is no evidence that any deliberate efforts were made to train Africans to do any notable tasks in the Herbarium or any other departments of Amani Institute. The situation was more or less similar with the British, except for a few individuals such as Greenway who took personal interest in training support staff who usually had very low formal education. Greenway was probably fairly successful in training local staff because he could speak good Swahili and hence could communicate effectively. Among the notable early Africans who gained good field knowledge and became quite good in naming East African plants are Mr. George R. Sangai (alias George Williams), Samuel Kibuwa (alias Samuel Paul), Francis Magogo (alias Frank Charles), all Shambaa from Lushoto, Tanzania, and Mr. Peter Kirrika Kayu, a Kikuyu from Kiambu, Kenya. Jan Gillett also made efforts to train technical and scientific staff in post-colonial Kenya. Technical staff that benefited from the expertise of Greenway and Gillett and also from the early generation of technical staff were Mr. Simon G. Mathenge, Onesmus Mwangangi, Francis Gachathi, and Geoffrey Mungai. Kokwaro (1994) features several technical and support staff in the list of some of the most prolific collectors in East Africa. They have thus contributed to the knowledge and study of the East African flora through their collections.

In the colonial era, all scientific staff were foreigners from Europe. Capacity building in the sense of training local people was non-existent, and this was a major handicap that still afflicts taxonomic botany in East Africa today. For example, a major project such as the *Flora of Tropical East Africa* (FTEA), which is now over 50 years old, has been and still is largely written by non-East Africans. The FTEA fascicles published so far by East Africans are Sonneratiaceae and Lecythidaceae (Sangai, 1968, 1971), Rutaceae, Anacardiaceae, Valerianacae and Geraniaceae (Kokwaro, 1968, 1971, 1982, 1986), Oxalidaceae (Kabuye, 1971), Gentianaceae (Sileshi, 2002) and Apocynaceae part 1 (Omino, 2002). Although in the recent years since the mid 1990s, a number of East Africans, especially Kenyans, have had professional training and acquired masters and doctorate degrees, local constraints ranging from poor working terms and conditions, lack of motivation and declining economies have hampered scientific production.

4 Role of the East African Herbarium in systematics and conservation

The mission statement of the EA is *'To collect, preserve, research and disseminate botanical information on Kenya and the East African region for conservation and utilisation'*. A herbarium is traditionally a collection of preserved plants built up over a long period of time. The collections are used for the following primary purposes:

- as reference material;
- as a means for identification and arbitration of correct names;
- and as a comprehensive databank (Bridson & Forman, 1998; Kokwaro, 1994).

EA collections constitute mainly a representation of the East African flora. The collections are consulted by a very broad variety of people ranging from taxonomists to forensic experts, pharmaceutical prospectors, plant breeders, horticulturists, conservationists, ecologists, fossil specialists and veterinarians. The oldest classical collections in EA include those of C.G. Ehrenberg from Eritrea (1825); W.P. Schimper from Ethiopia (1837–1863); T. Kotschy from Ethiopia (1837–1838); W.C.H. Peters from Mozambique (1842–1848); F. Stuhlmann from Central and East Africa (1888–1901); W. Busse from German East Africa (1900–1904); and O. Warnecke from Togo (1900–1901).

To meet the challenges of the day, a number of peripheral units which complement the core roles have been established. These are the Plant Conservation Programme, Nairobi Botanic Garden and Mycology. Databasing is crucial in ensuring that the vast amount of data on the collections themselves and the associated literature is well documented in a comprehensive and easily retrievable way. A number of databasing projects have been implemented by EA since the early 1990s in the quest to improve access and delivery of plant information to researchers and the general public both locally and internationally (Bytebier *et al.*, 1996; Knox & Vanden Berghe, 1996; Pearce *et al.*, 1996; Pearce & Bytebier, 2002). The herbarium is involved in many national and international projects on plant taxonomy, biodiversity, plant genetic resources and conservation (cf. Maunder *et al.*, 2002). The following are some of the key roles of EA (Kabuye, 1994; Masinde, 2002).

- As a repository for close to a million plant specimens from eastern Africa and beyond, it is an invaluable reference collection for any field of study that touches on plants;
- the authentically named plant specimens and a taxonomic library unmatched in the region make it possible to provide a reliable plant identification service by providing correct scientific names;
- the collections are principally used in taxonomic studies and revisions. Among the botanical authoritative works that EA has supported or continues to support in production include the *Flora of Tropical East Africa* (since 1952 to present), *A Manual of Kenya Grasses, Kenya Trees Shrubs and Lianas, Upland Kenya Wild Flowers* and *Traditional Food Plants of Kenya*;
- the collections are the basis for Kenya's plant biodiversity inventories and assessments of their conservation status (cf. Pearce, 1998);
- the East African Herbarium has informally trained several scientists and technicians over the years through internships or affiliations;
- and since 1994, it offers periodically two formal courses at certificate level: in Herbarium Techniques and in Plant Conservation. Most of the courses have been regional in nature and have been attended by participants from Uganda and Tanzania.

As part of activities to mark the EA centenary, an inaugural botanical art exhibition with the theme, *'botanical expressions... plants through art'*, was staged at Nairobi Museum from 29 Jun.–27 Aug. 2002 (Masinde & Ngugi, 2002). Participants included school-going children, and both amateur and professional artists. Some of the aims of the exhibition were to encourage botanical art among artists and the youth and enhance knowledge and appreciation of the diversity of the native flora. It is hoped that through regular similar exhibitions, the general public will learn more about plants and the work of EA. One of us (PSM) was also involved in organising a botanical illustration course that partly overlapped with the art exhibition and had participants from Ethiopia, Kenya, Uganda, Tanzania, Zambia and Zimbabwe.

5 Head botanists of EA from 1902 to present

Amani Herbarium

1902–1918	Prof. Dr. Albrecht Zimmermann (1860–1931). Head botanist at Amani; laid the foundation of Amani Herbarium.
1928–1950	Dr. Peter J. Greenway (1897–1980). Botanist in Charge of Amani Herbarium (see below as well).

Coryndon Memorial Museum Herbarium

1930–1934	Hon. Mrs Evelyn Molony (1902–1952). Better known to botanists as Miss E.R. Napier. First botanist in charge of the Coryndon Memorial Museum Herbarium, and laid its foundation.
1938–1950	Dr. Peter Rene Oscar Bally (1895–1980). Botanist in Charge. A Swiss and second husband of the world-renowned naturalist and botanical artist, Joy Adamson.

East African Herbarium

1950–1958	Dr. Peter J. Greenway (1897–1980). First Botanist in Charge of EA. A prolific collector with over 10,000 specimens. Better known in Kenya for his monumental book, *Kenya Trees and Shrubs* (1961), co-authored with I.R. Dale.
1958–1964	Dr. Bernard Verdcourt (1925–). Currently based at Kew, UK. A prolific author on the East African flora and a foremost taxonomist on East African snails.
1964–1971	Mr. Jan B. Gillett (1911–1995). The largest single collector in East Africa with over 25,000 specimens, with an interest in many subjects, including *Commiphora*.
1971–1994	Miss Christine H. Sophie Kabuye. (1938–). The first African (Ugandan) Botanist in Charge. Specialised in grasses.
1996–2004	Dr. Beatrice N. Khayota (1959–). The first Kenyan EA head. Interests in Orchid taxonomy and conservation.
2004–	Dr. P. Siro Masinde (1964–). Interests in taxonomy and systematics mainly of Apocynaceae-Asclepiadoideae, bioinformatics, medicinal plants and plant conservation

Among other EA staff that are actively engaged in taxonomic herbarium research are the authors of this paper (Drs Masinde and Muasya), Mr. Geoffrey Mwachala and Mr Itambo Malombe. Among systematic botanists that had stints ranging from one to ten years as EA staff are Miss Diana M. Napper (deceased), Prof. Gren Gl Lucas, Dr. Roger Polhill, Prof. John O. Kokwaro, Dr. Robert Faden, Mr. Mike G. Gilbert, Dr. Henk J. Beentje and Prof. Eric B. Knox.

6 Future prospects

The large collection, relatively good facilities and a critical number of trained scientific and technical staff are of advantage to EA. The East African Herbarium is currently the second largest herbarium in Africa with about 1 million specimens, after Pretoria in South Africa, and one of the top ten largest herbaria in the southern hemisphere. Its holdings are an important natural heritage to East Africa and the world at large. The main challenges are maintenance of the collections in a good physical state, curation, and motivation of the current staff so that they can remain devoted to their herbarium work. The various links with other institutions such as the Royal Botanic Gardens, Kew, need to be strengthened with formal agreements to enhance collaboration and capacity building.

The first 100 years of EA can be said to be a success especially in a region of Africa that has undergone various difficulties of colonization, wars, and increasing poverty. There are thus few institutions in tropical Africa that have had a steady uninterrupted growth for a century. The many past staff members, people and institutions from around the world that have supported EA have bequeathed us with a herbarium that we shall be proud of forever. It is hoped that the lessons learnt in the past and current strengths will help to guide the future growth of EA.

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TAXONOMIC BIOLOGY AND GLOBALIZATION

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Abstract

The science of taxonomy, by its nature, requires unhindered access to all organisms. Globalization has caused biodiversity to become an economic resource; this has resulted in national and international law regulating access to biodiversity – which hampers taxonomy. The granting of private intellectual property rights to living organisms is becoming commonplace. Seed breeders' rights laws have now become similar to patenting, and this has caused the patenting of living things to become accepted. This is not only an injustice, with Northern companies patenting Southern resources, but it is also a restraint to science. Much of the information in genetic engineering is protected as 'undisclosed information', and by this process much of the scientific research has become protected and secret. This might be the beginning of the end of objective science. The Convention on Biological Diversity requires information generated by research on genetic resources to be repatriated to the host country of that resource – but industrialized countries have refused to accept an international law on benefit-sharing to this effect. This results in developing countries having very little power of enforcement in these matters.

Résumé

Taxonomie et Globalisation. Par nature, la science de la taxonomie demande un accès sans contraintes á tous les organismes. La mondialisation a eut pour conséquence de transformer la biodiversité en une ressource économique. Ceci a résulté á la création de lois nationales et internationales de régulation á l'accès á la biodiversité, gênant la pratique de la taxonomie. L'obtention du droit intellectuel de propriété sur les organismes est devenue monnaie courante. 'Plant breeder rights' PBR sont devenus similaires au brevetage et ainsi ce même brevetage des organismes vivants est devenu acceptable. Ceci n'est pas seulement une injustice produite par les industries de l'hémisphère Nord brevetant les ressources de l'hémisphère Sud mais cela restreint aussi la recherche scientifique. La plupart des informations du génie génétique sont protégées et par ce procédé la plupart de cette recherche est devenue elle aussi protégée et secrète. Ceci pourrai être la fin des sciences 'objectives'. La convention sur la diversité biologique exige des informations générées par la recherche génétique d'être rapatriées dans le pays d'ou la ressource est originaire. – Mais les pays industrialisés ont refusés d'accepter une loi internationale du partage des intérêts. Les pays en voie de développement ayant peu de moyens pour faire respecter ceci.

Key words: data, globalization, patenting, repatriation, taxonomy

1 Introduction

This paper is largely based on previous papers I wrote (Egziabher, 1999, 2002, 2003, 2004) on issues related to my present topic. But globalization is changing its faces fast, and I have had to add new information even since 5 September 2003!

Taxonomic biology is based on the comparison of many individual organisms within a group across their distribution. Therefore, by its nature, it requires an unhindered global access to all organisms.

Human societies make use of all the economic resources in their respective ecosystems. They use these resources for themselves or for trade, or make goods out of them for use or trade. Therefore, they become possessive of their economic resources and develop laws and administrative procedures to protect them.

In the past, only biomass was an economic resource and biodiversity could be accessed freely. That was the age of golden opportunity for taxonomic biologists.

But, with the advent of globalization and the development of intellectual property rights protection systems to govern private but not community innovations involving biological resources, not only biomass but also biodiversity has become an economic resource. National and international laws and administrative procedures have, therefore, been and are continuing to be put in place to regulate access to biodiversity. The fact that biodiversity is seen as the raw material for modern biotechnology, and the fact that modern biotechnology is largely out of the public sector is a complicating factor in all considerations of benefit-sharing and hence also on access to the whole diversity of organisms for taxonomic study. This is compromising the integrity of scientific investigation, making people view it as an instrument of fraud, and the taxonomic biologist, who is at its interface with the public, especially that of the South, as a charlatan.

This problem is exacerbated in the South by the injustice displayed by Northern patent offices that have been granting private intellectual property rights to Northern individuals and organizations on technologies and the uses of biological resources developed by Southern local communities. In the context of injustice, the patenting of living things and traditional medicines are being seen as prominent; and in the context of the erosion of scientific objectivity, the protection of scientific information, especially in molecular biology and genetic engineering, as confidential or “undisclosed information” for use by corporations, but by definition, without being subjected to peer review, is being seen as unsound.

1.1 The norms of access to knowledge, technologies and biodiversity in local and indigenous communities

The creative individual in a local or indigenous community has complete and free access to all the knowledge and technologies as well as biodiversity in the community. To the extent that she/he can physically make it, access to the knowledge, technologies and biodiversity of other local or indigenous communities is also unrestricted.

Therefore, based on collective generation, modification, conservation and exchange across generations and communities, knowledge, technologies and biodiversity become generated, owned and managed by the community, and use by any one who wants them is free, though reciprocation in kind is a necessary element of the system. The exception to a totally free access is for medicinal plants that can be dangerous and thus require specialized handling.

Patents and other Intellectual Property Rights (IPRs) are a means of commercializing access. The main weakness of the commercialization of knowledge, technologies and biodiversity is that benefits accruing from commercialization are not necessarily readily diversified, and this creates opportunity for unscrupulous privatization by the most selfish both within and outside the community. This is because the prevalent commercial system is totally based on private control; even cooperatives function under the individual norms of the North as single legal persons.

Intellectual Property Pights (IPRs) are now a means of privatizing knowledge and technologies for commercialization. This became an issue for the first time during the negotiations for the Convention on Biological Diversity (CBD). It will be recalled that this convention was adopted in 1992. The debate, intensified with the patenting of living things in the United States of America, has now spread to Europe. It motivated me to read about, think, and relate it in writing to my experience in my traditional farming local community, where I was born and grew up.

The communal approach of my local community and all other local communities to discoveries and inventions is strengthened by social values which see communal action (that subsumes individual initiative) as essential for individual survival.

The individual centred culture of the industrialised North, which sees survival inside a local community as a denial of self-expression and a curtailment of liberty, has now been imposed as the dominant global culture. Therefore, the individuals of the North, even when professing communal allegiances, behave as loners interacting with the state, and those of the South, even when professing capitalist individualism, are largely communal in their social relations with other individuals.

Nevertheless, the elite of the South satisfy their personal material desires through individualistic grabbing for personal gain while depending on what is left of their waning urban local community for satisfying their social needs. That is why they usually use communal channels to acquire personal wealth at the expense of other members of the community. When seen through this light, petty corruption becomes understandable though not the less insidious, and thus remains even more unacceptable. The fear of the state without any local community shield to protect her/him makes the Northern individual afraid of, and thus less prone to, petty corruption but more predisposed to the unrestrained personal gambling in large scale abuse, including corruption.

The community management system has always allowed reward for labour input. Any charge for the biomass embodying the biodiversity on a per weight or volume basis, or any charge for the technology on a per piece of hardware (an implement or a prescription) basis fits in well with the community system. But charging for the community's intellectual achievement is fraught with difficulties and it has never been tried. The difficulties include, among others:

- The problems of identifying the beneficiaries:
  - should the benefit go only to members of rural communities alone, or should it go to the whole population of a country or indeed of the world?
- If the community is to be the beneficiary, it becomes difficult to ensure that:
  - all communities which have contributed, whatever their country, benefit
  - all individuals who are entitled to the benefits are included within the community
  - The community has the organizational and the technical capabilities and capacity for this additional task of claiming and apportioning benefits

If the community is granted a patent protection and is expected to act as a single legal person in direct competition with Northern individual and corporate entities, the problems include:

- Raising in hard currency the money required to register patents. (This is estimated in the USA to be about 10 to 20 thousand dollars (Gaia Foundation, undated) for application. In addition, it requires annual payments)
- Deploying the personnel and managing the global industrial espionage system that would be required to prevent infringements, and affording this financially in hard currency. (It should perhaps be noted that IPRs are now used in the North to control markets, and maintaining a patent usually costs more than the royalties can fetch. It is estimated that, on average, maintaining a patent for its lifetime in the US costs about US$ 250,000) (Gaia Foundation, undated)
- Dealing with the quick emergence of private patents on roughly the same technology and/or biodiversity which modify the community technology only a little (e.g. substituting extraction with water, which is most likely the case in a community technology, with extraction by ethyl alcohol, or even with a chemical totally unknown by the community, e.g. chloroform).

These and many other problems arise because, when we patent community knowledge and technologies, we would be trying to force one system, the communal, to run entirely under the norms of another, the private. If we want both systems to continue giving us the services which we are now taking for granted, we must consciously interrelate them, in such a way as to make both systems viable and co-operative, not the individual predatory on the communal.

1.2 The dynamics of the global status quo

The South's values are largely those of its local communities, and the North's are largely those of its individuals. It is, therefore, hardly surprising that the North is now predatory upon the South.

The history of the development of the South's position of disadvantage, and how institutions from the past perpetuate this position of disadvantage, is linked to European expansion (Egziabher, 1999, 1998).

The South is now in the post-colonial era, but it still finds more of its resources and fruits of labour flowing Northwards than fair exchange or trade would lead one to expect (Hancock, 1991). As a result, the South gets poorer and the North gets richer at an ever-increasing rate. This is because the voice of conscience for helping the decolonized countries build capacity has become harnessed by preparing that capacity to become an effective pump taking Southern resources and fruits of labour Northwards. The Southern elite, who have been acculturated to focus at personal gain à la North, have been easy to coopt into being the operators of this pump.

The international institutions and their traditions, which control the world now (e.g. the United Nations system, the Bretton Woods Institutions) were put in place in the colonial era and thus still function with the dynamics of that era. Southern countries achieved independence one by one, and joined the United Nations system one by one, and have made no impact that can contribute towards changes in its workings. For example, it is still largely the colonial masters that have veto power in the Security Council of the United Nations Organization. As for the Bretton Woods Institutions, they are openly and unabashedly controlled by those very old slave and colonial masters who, through evil punctuated by the dictates of conscience, accumulated the massive wealth they now use.

1.3 Impacts of the agreements of the World Trade Organization on taxonomic biology

The idea of creating a world body to regulate trade so that it becomes rule-based, predictable and as free as possible, was born at the end of the Second World War. In 1947, the United Nations Conference on Trade and Employment was convened in Havana, Cuba. It came up with the Havana Charter. But the United States and the United Kingdom failed to ratify it and the charter lost momentum. Twenty-three countries, however, decided to adopt the part of the Havana Charter that dealt with trade in goods and the General Agreement on Tariffs and Trade (GATT) was thus created.

The agreement that created GATT at the end of the 2nd World War, now often referred to as GATT 1947, is still a core of the WTO, but the new agreements added have strengthened it. Article XI of the Marrakesh Agreement establishing the WTO gave a special role to the "original members" (i.e. the Members that had joined GATT 1947 and a few more since 1947), which include all Western countries, the then colonial masters, and only some developing countries. This role was the institutionalization of the new WTO. It is, therefore, not surprising that the WTO was largely shaped to suit them, and it is the poorest countries of the South, especially those of Africa, that are finding it most harmful. That is why it is not surprising that the Ministerial Meeting of the WTO, which was convened in Cancun, collapsed on 14 September 2003, because the poorest countries of the South, especially those of Africa, refused to consider new issues before these injustices are corrected.

The Agreement on the Application of Sanitary and Phytosanitary Measures (SPS), which is a component of the Multilateral Agreement on Trade in Goods, deals with one of the main interfaces between environment and trade. Article 2.1 in combination with paragraph 1 of Annex A of SPS delimits the basic rights and obligations of Members. The rights it gives to Members include those to protect: (a) animals, plants and humans from pests and diseases, (b) humans and animals from risks posed by additives, contaminants, toxins, or disease causing agents in food or drink, (c) humans from diseases caused by animals, plants, or their products, and (d) agriculture and environment from pests.

The worry of the developing countries is that these rights would be used unfairly for arbitrarily restricting market access to their products. It is to reduce this fear that Article 2.2 stipulates that concerns regarding the risks to human, animal or plant life and health have to be scientifically valid, and Article 2.3 stipulates that SPS measures shall not constitute a disguised restriction of international trade. However, the determination of the scientific basis for a risk is not as objective as it may at first sound. This is because, as shown in the hormone treated beef dispute between the United State of America and the European Union, it is possible for two sides to claim to be scientifically correct and yet to differ. The likelihood of such a divergence of opinions is higher when the dispute is between a developing and a developed country. This is because their environments are dissimilar. But it is more so because the developed countries, on the whole, take the scientific capacity of the developing countries to be inferior and thus their science defective.

The Agreement on Technical Barriers to Trade (TBT) component of the Multilateral Agreement on Trade in Goods covers the standardization of the preparation, adoption and application of (a) technical regulations by governmental and government authorized non-governmental bodies, and (b) standards by governmental or non-governmental bodies. It also provides to governments procedures for assessing conformity with technical regulation and standards.

The objective of a technical regulation may be, among other things, the fulfilling of "national security requirements; the prevention of deceptive practices; protection of human health or safety, animal or plant life or health, or the environment" (Article 2.2). A technical regulation is defined in Annex 1 as a "document which lays down product characteristics or their related processes and production methods, terminology, symbols, packing, marking or labelling requirements as they apply to a product, process or production method". According to Annex 1 and Articles 2 and 3, implementation of a technical regulation is mandatory. A standard is defined in Annex 1 similarly to a technical regulation; but the implementation of a standard is voluntary. It helps avoid confusion to note that the use of the term "standard" in the TBT is unusual, and that, when used by many other documents, compliance with a standard is legally mandatory, i.e. that a "standard" is the same as a "technical regulation."

Articles 5–9 of the TBT require that a conformity assessment procedure, defined as "any procedure used, directly or indirectly, to determine that relevant requirements in technical regulations or standards are fulfilled", be put in place.

Complex issues of importance in trade and environment that can be used to distort trade, which we cannot pursue now owing to shortage of time, emerge from these provisions of the TBT.

The Agreement on Trade-related Aspects of Intellectual Property Rights (TRIPs) of the WTO forces member states to provide legal protection for copyrights, trademarks, geographical indications, industrial designs, patents, integrated circuits, and undisclosed information (industrial secrets) and to grant all Members "Most Favoured Nation" and "National" treatments (Article 3 & 4). They cannot refuse to handle requests for the registration of any of the seven categories of intellectual property rights (see articles 1.1 and 1.2). These and many other provisions of TRIPs have serious negative implications for the South, which has only 2% of patents of domestic origin (Egziabher, 2001).

The IPR protection system (Patents, breeders' rights, copyrights, trademarks etc.) was developed in the industrialized countries of Europe and North America. It all started with the patenting of mechanical inventions. The idea behind patenting was that if a person invents a new mechanical innovation, she/he should monopolize the use of that invention for a set period (usually 1525 years depending on national legislation) so as to reward her/him. Others who want to use that machine would then pay royalties to the inventor. However, a discovery was considered not protectable by patenting. This system sounds fair.

But it is being distorted and it has become unfair.

It has come to be applied to living things, and yet nobody has yet learned to create a living thing (Egziabher, 2001). We have, so far, only managed to discover living things, not to invent even one. But now, the industrialized countries are patenting living things as if they have invented them. It all started with the British government wanting to ensure that seeds used for agricultural production were of high quality. At the end of the Second World War, it instituted a system for registering good quality seed. Logically seed companies were then required to sell only registered seed. Soon after that, the British Government thought to reward individuals who improved seed further, and it gave them the legal right (Breeders' Right) to levy royalties on the sale of the new seed varieties they bred (Clumies-Ross, 1996). This worked well for some years.

But soon, four distorting developments took place, all originating from the desire to control the market even further.

The royalties became insignificant compared to the expense in industrial espionage and in legal fees (Gaia Foundation, undated) so that only big companies which wanted to control the market rather than individual inventive minds became the beneficiaries.

Particularly in seed production and marketing, the seed companies, initially slowly but later on blatantly, dropped good seed that was not IPR protected and focused only on IPR protected seed, again in order to control the market. Of course, the companies promoted their own seed, or seed that was under royalty sharing arrangements with IPR holders. Seed production, therefore, moved from the hands of the farmer to the corporations.

Breeders' Rights laws became more and more restrictive until the 1991 version of UPOV became very similar to patenting.

Perhaps because the restrictive Breeders' Rights laws prepared the ground, the patenting of living things became accepted, first in the USA, and then in Europe. In fact the United States of America introduced domestically the patenting of hybrid varieties in 1956 and the patenting of genes in 1980. No other country patented any living thing or life processes until after the creation of the WTO in 1994. Doyle (1985) maintains that such patenting was deliberately created so that United States companies would have a head start on companies from other countries and dominate the world. It was when the world, especially the countries of the South, were unaware of this United States design that the recognition of patents in the CBD and TRIPs was sneaked in.

The multinational corporations of the industrialized world and thus also the governments of the industrialized world now see community knowledge, technologies and biodiversity as a raw material. It gives them traits which their modern biotechnology or genetic engineering and related recent biomolecular manipulation techniques can use in various combinations in microbial, plant or animal transgenic varieties, or even in *in vitro* enzyme systems. They expect that these transgenic varieties will produce commodities they want, including food, medicines and other bioactive molecules, and chemicals which have hitherto been made through the use of cumbersome industrial plants. Of course, developing countries also aspire, and some do indeed try modern biotechnology to varying degrees of success, to do the same.

However, patents have been granted even for non-genetically engineered living things.

The use of neem (*Azadirachta indica*), native to tropical Asia, traditionally used in the Indian subcontinent as a pesticide, has, for example, been patented in the USA, Germany and Japan without any use of modern biotechnology. The traditionally esteemed Basmati rice (*Oryza sativa*) of India has been patented in the USA. So have Endod (*Phytolacca dodecandra*) and coffee (*Coffea arabica*) from Ethiopia been patented in the USA, and teff (*Eragrostis tef*), taken from Ethiopia and grown in the USA only for one season in order to describe its morphology, has been given a breeders' right protection in the USA. Literally thousands of such cases of piracy have been recorded. The original producers of Basmati rice, the smallholder farmers of India and Pakistan, are already losing their market to the USA. And things seem to be set to get worse. Through Article 28.1 (a) of TRIPs, which prevents third parties, into which categories the farmers of Ethiopia, India and Pakistan have now been relegated, from "making, using, offering for sale, selling or importing" the IPR protected material, the US patent holders can use the WTO to completely stop the export of any rice from India and Pakistan under the name of "Basmati".

Perhaps the most damaging aspect of TRIPs is the control over agriculture that it gives to patent owners of genetically engineered crops through article 34 with its absurd reversal of the burden of proof of innocence in process patent infringement. When a farmer has her/his non-genetically engineered crop in the field contaminated by natural cross-pollination, she/he becomes an infringer of the patent. Each patented variety usually carries tens of patented genes. Negotiating with so many patent holders becomes internationally bureaucratic, and paying all the royalties becomes expensive. The South-North mistrust that this generates is exacerbated by the fact that much of the information in genetic engineering and other technological developments is kept as corporate secret through Article 39 of TRIPs, which forces countries to protect "Undisclosed Information", or to stand guard over information companies determine is confidential. It sounds absurd to protect what is "undisclosed", and hence unknown. In the past, trust was built in scientific research through peer reviewed publications. There can be neither peer reviewing nor publication of information that is thus guarded. And yet much of scientific research is nowadays funded by companies and its results increasingly guarded as "undisclosed information". Is this the way that science is becoming ritual protected and blending with mysticism? Is this the beginning of the end of objective science?

This ritual cannot be challenged unless the laws of the WTO change. The Understanding on Rules and Procedures Governing the Settlement of Disputed (DSU), which is an over-arching agreement, describes the dispute settlement mechanism which makes the WTO agreements very powerful instruments of international regulation. Dispute Settlement Panels (Articles 6–16) and the Appellate Body (Article 17) rule on disputes. What they rule is enforced through trade embargo (Article 22). A publication by the Centre for Science and Environment (Agarwal & Sharma, 1999) has summarized the eight cases on trade and environment which had been decided upon until 12 October 1998. The DSU is a formidable instrument when seen from the vantage point of developing countries.

1.4 Benefit-sharing and genetic resources

The Convention on Biological Diversity stipulates that when a state allows access to a sample of genetic resources, it is, in return, entitled to insist on a number of benefits. Research activities on the genetic resources it provides have to be done in its territory to help it build capacity. All the information generated by research on that genetic resource must be repatriated. Any biotechnology applied on the genetic resource must be made accessible to it. A fair and equitable share of benefits accruing from the use of the genetic resource, including from commercial gains, must also be given to it. But all this is conditional upon a mutually agreed contract. The industrialized countries know this, and many of them have been undertaking major expeditions to Africa to collect genetic resources before we do something to enforce our sovereign rights over these resources. As usual, we wake up after the thief has taken what he wants and has bolted. And as usual, in the World Summit on Sustainable Development in Johannesburg in August–September 2002, 10 years after they signed the CBD, the industrialized countries refused to agree to negotiate a legally binding benefit-sharing international law. It must be pointed out, however, that also in 2002, the Conference of the parties of the CBD in the Hague, the Netherlands, endorsed the voluntary Bonn Guidelines on Access and Benefit-sharing. The industrialized countries even agreed to accept to enforce any contract their citizens enter into in access and benefit-sharing. Of course this is weak. But it is because the South is weak.

The real benefit obtained depends on the legislation in each developing country and the trained human resource and infrastructure put in place to implement it. In most developing countries, including Ethiopia, neither the legislation, nor the systems of implementation, are comprehensively in place. The industrialized countries other than the Scandinavian and some of the smaller countries of the European Union, seem to want the situation to continue unchanged. For example, when the European Commission adopted a directive on patenting genetically engineered living things, it deleted the requirement for disclosing the country of origin of the living things used in the genetic engineering. This requirement had been introduced by the European

Parliament to help developing countries claim benefits from their genetic resources used by others. The European Union can get away with it because it feels strong. International law nowadays is strongly punctuated by specific actions of might.

1.5 Legal protection of the rights of local and indigenous communities

Taxonomists are at the interface where this might show itself to the South because they are the brokers of biotrade. When we consider biotrade, we are focussing on the interaction between communities and multinational corporations. Legislation is therefore essential in order to protect local and indigenous communities, which are, as already seen, at a total global and national disadvantage. Domestic legislation would protect them from their national weakness. International law is needed to partially protect them from their global disadvantage. Good will from the mighty of North America, Europe and Japan is needed to complete their global protection. The South can thus make the needed national laws, and both appeal to the generosity and exhibit the duplicity of the North through these national laws. The making of national law governing biotrade must, therefore, consider the conditions of access to the biodiversity, knowledge and technologies of communities, the benefits they will obtain from the trade, the rights they must have legally recognized in order to manage the giving of access and the receiving of benefits, and the technical support that the State must give them for all this to be possible.

The CBD recognizes that states have the sovereign right over their biological resources, and that granting or refusing access is their right (Article 3 & 15.1), but they shall endeavour to create conducive conditions for granting access (Article 15.2). The conditions of access are to be on mutually agreed terms (Article 15.4). However, the issues to be included in this mutual agreement have been specified.

The Organization of African Unity has developed and recommended for use by member states a “Model Law on Community Rights and on Access to Biological Resources”, which has taken consideration of all these issues. Many countries, including Ethiopia, are domesticating this law. But they are taking inordinately long. Perhaps it is because they realize that its real implementation would depend on the North’s good will. And this good will is not clearly visible, especially now that unilateralism seems to be on the upsurge.

The conditions of access which aim at ensuring a fair share of benefits, as given in the CBD and as provided for in the Model Legislation, are the following:

1. Research and development to be carried out in the country giving access (Article 4.1. of Model Law, c.f. Art. 15.6 of CBD)
2. Prior informed consent of both the State and the indigenous or local communities (Article 4.2 of Model Law, c.f. Article 15.5 & 8(j) of CBD)
3. A list of other conditions to agree to before a contract is signed (Article 4.3 of Model Law, c.f. Article 15.4 of CBD), including commitments for the conservation of biodiversity (Articles 4.3 (a), (g) & (h), Article 4.9 of the Model Law, c.f. Article 6.7, 8 (c), (d), (j), (k) & (l), 9(c) & (d), 10(a) & (b) of CBD)
4. Commitment to provide information and duplicate specimens to the country giving access (Articles 4.3 (b), (c) & (g) of Model Law, c.f. Article 15.7, 17.2 of CBD)
5. Commitment not to transfer to third parties without authorization (Article 4.3 (d) of Model Law, c.f. Article 15.5 of CBD)
6. Commitment not to patent or apply any other IPR (Article 4.3 (e) of Model Law, c.f. the fact that patenting biological materials is disallowed in the laws of most African countries, and also c.f. Article 16.2 of CBD, which though recognizing IPRs, does not specifically provide for the IPR protection of biological materials, showing that the choice of what to protect is left open)

7. Payment for the community labour that has gone into creating or knowing the specific characteristic of the biodiversity or for the knowledge or technology accessed and the work borne by the State in doing this (Art. 4.3 (f) of Model Law, c.f. common practice of hiring labour)
8. Commitment to abide by certain procedures aimed at ensuring the implementation of the mutually agreed terms (Articles 4.4, 4.5, 4.6, 4.7, 4.8, of Model Law, which are obvious and need no explanation, except for pointing out that in Article 4.7, a guarantor is required because, often, the person getting access will leave the country and there would then be no means of ensuring the observance by each party of the mutually agreed terms).

Article 5 of the Model Law creates Community Rights and provides for the implementation of those rights. It is largely based on Articles 8(j), 10(c) & (d), and 15.5 of the CBD, and on the decision on the implementation of Article 8(j) taken by the 5th Conference of Parties of the CBD in Bratislava in June 1998.

The remaining provisions of the model law, Article 6–10, are concerned with the implementation process. Their contents are self-evident and need no further comments.

2 Concluding remarks

The Multilateral Agreements on Environment have very little power of enforcement, consisting only of words of censure in conferences of parties. They are, therefore, usually disregarded (Wallach & Storza, 1999). Their harmonization with trade agreements is, therefore heavily skewed in favour of trade.

It seems, therefore, that we are allowing trade to destroy the environment. What will then be the point of trading? Is this one manifestation that shows that our species cannot help but be self-destructive? Or, are we prepared to genuinely harmonize trade and environmental agreements and provide them with equally forceful enforcement mechanisms, or perhaps even with a single forceful mechanism? The trade negotiations in Cancun failed on 14 September 2003. Subsequent moves at the weak United Nations Environment Programme (UNEP), will, therefore, most probably determine what happens. But I do not feel optimistic, be it in the context of equity or even survival.

In the meantime, it would be good to continue furthering scientific knowledge. I keep saying that from my vantage point as a scientist. But can I sound credible? Can the taxonomist really shed off the garb of the charlatan that the globalization that her/his very science has made possible has put on her/him? Can you? I wonder.

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CBD IMPLEMENTATION: EXPERIENCES AT KEW

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Abstract

Between 1997 and 2000 Kew co-ordinated a project, involving 28 botanical institutions from 21 countries, to develop CBD guidelines for botanical institutions. The resulting ‘Principles on Access to Genetic Resources and Benefit-sharing’ cover best practice in acquisition, curation, use and the supply of material, and associated benefit-sharing. The Principles have been endorsed by 21 botanical institutions worldwide, and form the basis of Kew’s current policy.

Kew uses several practical tools to implement the Principles internally. These include: an overseas fieldwork committee to ensure we work collaboratively, with appropriate permission, on mutually agreed terms, and share benefits; training and an intranet guide to assist staff in following new procedures; and standard model documents for acquisition and supply. In recent years Kew has placed emphasis on establishing longer partnerships with fewer countries. We use written agreements negotiated between partners to set out how we will work and what types of benefits will be shared, to ensure work is undertaken fairly and transparently and that everyone understands their roles and obligations.

We emphasise the importance of communication between biologists and policymakers. It is vital for individual biologists to understand and work with the CBD, and also to become more involved in explaining the relevance of their work, so that they can help support national implementation of the CBD.

Résumé

Mise en oeuvre de la CBD: experiences menées à Kew. De 1997 à 2000, Kew a coordonné un projet, impliquant 28 institutions botaniques dans 21 pays et dont l’objectif était de développer des directives CBD pour les institutions botaniques. ‘Principles on Access to Genetic Resources and Benefit-sharing’ en est le résultat et envisage les meilleures pratiques en matière d’acquisition, de gestion, d’utilisation et de fourniture de matériel et également le partage des bénéfices. Les principes ont été approuvés par 21 institutions botaniques de par le monde et forment la base de la politique actuelle de Kew en la matière. Kew utilise divers outils pratiques pour appliquer les principes en interne. Ceux-ci comprennent: un comité de missions de terrain outre-mer pour assurer que nous travaillons en collaboration et avec les autorisations appropriées, sur base de termes d’accord mutuel et que nous partageons les bénéfices; une formation et un guide intranet pour assister le personnel dans le suivi des nouvelles procédures; et des documents modèles standards pour l’acquisition et la fourniture. Ces dernières années, Kew a mis en avant l’établissement de partenariats plus durables avec un nombre moins élevé de pays. Nous utilisons des accords écrits négociés entre partenaires pour exposer comment nous travaillerons et quels types de bénéfices seront partagés, pour assurer que le travail sera entrepris d'une manière équitable et transparente et que chacun comprenne son rôle et ses obligations. Nous mettons en évidence l'importance de la communication entre biologistes et politiciens. Il est vital pour les biologistes de comprendre et de travailler avec la CBD mais également de consacrer de l'énergie à expliquer l'intérêt de leur travail de manière à soutenir la mise en application de la CBD au niveau national.

Key words: access, benefit-sharing, botanical institutions, CBD, implementation

1 Introduction

The Convention on Biological Diversity (or CBD) has effected significant changes to the political and practical world in which biologists work. In particular, its provisions on access to genetic resources and benefit-sharing (Article 15) have led to the development of new national policies and laws. Article 15 of the CBD focuses on access and benefit-sharing. It states that those wishing to get access to material must follow national provisions on access, that access must be with the prior informed consent of the Party providing the resource, and on mutually agreed terms. These terms should promote the fair and equitable sharing of benefits, such as the transfer of technology and the opportunity to participate in research, preferably in the country of origin. Over one hundred countries worldwide have introduced or are planning to introduce national or regional legislation to control access to their resources.

All stakeholders, including those working in botanic gardens and herbaria, have had to become more aware of their new roles and responsibilities. In this paper we aim to give a brief introduction to the development of access and benefit sharing policies by botanic gardens, then to give some practical examples of how the Royal Botanic Gardens Kew is implementing its own policy.

As people working in botanical institutions, we face common challenges. The original text of the CBD gave little guidance on practical implementation of access and benefit-sharing (ABS) and we are currently in a period of transition, with national laws developing and changing rapidly around us. We must ensure that we fulfil these new obligations, but continue to carry out our important scientific work. The recently-adopted 'Bonn Guidelines on Access to Genetic Resources and Fair and Equitable Sharing of the Benefits Arising out of their Utilization' (Secretariat of the CBD, 2002) now help providers and users of material understand what terms such as 'prior informed consent' and 'benefit-sharing' mean in practice, but in practice it can still be difficult to work out whose consent we should get, and how and what benefits we should share, or expect to be shared, and with whom. Botanic gardens and universities are often regarded as an initial source of biological material by commercial companies, and in the past they have acted as important clearing houses for material. We need to work together to make sure that we are not 'leaky', and to minimise the risk of being accused of biopiracy.

1.1 Principles on Access to Genetic Resources and Benefit-Sharing

Many botanical institutions, through regional and international networks (such as Botanic Gardens Conservation International) have already begun working together to find practical ways to implement the CBD. We will describe one project which helped establish a common approach for botanic gardens on access and benefit-sharing (Article 15 of the CBD).

Between 1997 and 2000, representatives of 28 botanic gardens and herbaria from 21 countries worked together in a project coordinated by the CBD Unit at Kew. The Pilot Project for Botanic Gardens group was chosen to be as representative as possible of the world's 2000 or so botanic gardens, and included both large well-established gardens and some smaller newly established ones. The participants from Africa were Aburi Botanic Gardens in Ghana, the National Herbarium in Ethiopia, Limbe Botanic Gardens in Cameroon, the Institute Agronomique in Rabat, Morocco, and NBI Kirstenbosch in South Africa. Other participants also present at this XVIIth AETFAT Congress included University of Bonn Botanic Gardens and Missouri Botanical Garden.

The work of botanic gardens and herbaria is dependent on the exchange and use of plant material, now governed by Article 15 of the CBD. So the group aimed to develop practical guidelines for botanic gardens and herbaria to be able to continue their work during these times of rapidly emerging national legislation. Institutions wanted the security of working with others facing the same problems, but also of knowing whatever policies they developed would be acceptable to their national authorities. The resulting 'Principles on Access to Genetic Resources and Benefit-sharing' (the 'Principles', see Box 1), and more detailed 'Common Policy Guidelines' (CPG), set out agreed best practice and give guidance to gardens and herbaria developing their individual policies (Latorre Garcia *et al.*, 2001; Williams, 2001). The Principles represent a voluntary commitment and to date have been endorsed by 21 botanical institutions worldwide. They form the basis of Kew's current policy.

The Principles aim to cover all aspects of botanical institutions' work in relation to getting access to material and sharing benefits arising from use of the material. They are wide-ranging and general in their approach, designed to be applicable to all botanical institutions, large and small, with both living and preserved collections. They give guidance on where to get prior informed consent for acquiring material from *in situ* conditions, and also from other *ex situ* collections, for instance through exchange with other institutions. They cover procedures necessary for the use, exchange and supply of material and recommend that institutions develop a transparent commercialization policy. They lay out obligations to share benefits from the use of material by an institution, and cover the importance of curation and tracking by an institution in order to comply with new obligations under the CBD and national law. Above all, the Principles were designed to form the basis of individual institutional policies on the CBD – which need to take into account the particular work that institution does, and the particular laws and regulations of its national government.

As one of the first practical examples of implementing the CBD's provisions on ABS, the Principles have turned out to be quite influential in shaping international policy and thinking on access and benefit-sharing. For example, the Principles strongly influenced the development of the Bonn Guidelines, which were adopted by the CBD Conference of the Parties in April 2002. The Indian Ministry of Environment and Forests considered the Principles and CPG in preparation of final drafting of the Indian Biodiversity Act 2003. In addition, the Australian Commonwealth Government's Environment Australia Department has used the Principles and CPG in the development of regulations regarding access to biodiversity on Commonwealth Lands: institutions that have signed up to the Principles may be granted facilitated access (personal communications with Helen Hewson & Geoff Burton, 2003).

Individual gardens involved in the project have actively begun implementing the Principles and using them as a model to guide their own institutional policies and the development of model agreements. Limbe Botanical and Zoological Gardens reviewed its policy on access to genetic resources and benefit-sharing, and developed a whole

BOX 1. Principles on Access to Genetic Resources and Benefit-Sharing for Participating Institutions

Participating Institutions endorse the following Principles on access to genetic resources and benefit-sharing:

Convention on Biological Diversity (CBD) and laws related to access to genetic resources and associated traditional knowledge and benefit-sharing

Honour the letter and spirit of the CBD, The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and laws relating to access and benefit-sharing, including those relating to traditional knowledge.

Acquisition of genetic resources

In order to obtain prior informed consent, provide a full explanation of how the genetic resources will be acquired and used.

When acquiring genetic resources from *in situ* conditions, obtain prior informed consent from the government of the country of origin and any other relevant Stakeholders, according to applicable law and best practice.

When acquiring genetic resources from *ex situ* collections (such as botanic gardens), obtain prior informed consent from the body governing the ex situ collection and any additional consents required by that body.

When acquiring genetic resources from *ex situ* sources, whether from *ex situ* collections, commercial sources or individuals, evaluate available documentation and, where necessary, take appropriate steps to ensure that the genetic resources were acquired in accordance with applicable law and best practice.

Use and supply of genetic resources

Use and supply genetic resources and their derivatives on terms and conditions consistent with those under which they were acquired.

Prepare a transparent policy on the commercialisation (including plant sales) of genetic resources acquired before and since the CBD entered into force and their derivatives, whether by the Participating Institution or a recipient third party.

Use of written agreements

Acquire genetic resources and supply genetic resources and derivatives using written agreements, where required by applicable law and best practice, setting out the terms and conditions under which the genetic resources may be acquired, used and supplied and resulting benefits shared.

Benefit-sharing

Share fairly and equitably with the country of origin and other Stakeholders, the benefits arising from the use of genetic resources and their derivatives including non-monetary, and, in the case of commercialisation, also monetary benefits.

Share benefits arising from the use of genetic resources acquired prior to the entry into force of the CBD, as far as possible, in the same manner as for those acquired thereafter.

Curation

In order to comply with these Principles, maintain records and mechanisms to:

- record the terms and conditions under which genetic resources are acquired;
- track the use in the Participating Institution and benefits arising from that use; and
- record supply to third parties, including the terms and conditions of supply.

Prepare a policy

Prepare, adopt and communicate an institutional policy setting out how the Participating Institution will implement these Principles.

This text is also available in French, Portuguese, Spanish, Russian, German and Chinese at www.kew.org/conservation

Institutions wishing to endorse the Principles should send a letter to the Director of Kew stating their endorsement.

suite of policy documents and model agreements to be used in their dealings with other scientific institutions and commercial organisations (Laird & Tonye Mahop, 2002; Laird & Wynberg, 2002). Rio de Janeiro Botanic Garden has established a cross-departmental staff team to monitor the collection's acquisition and supply, draft necessary documents and decide on policy (Pereira, 2000 and personal communication 2003). The National Botanical Institute (South Africa) (now South African National Biodiversity Institute) established a new interlinked gardens record database with fields for information on terms and conditions relating to the material, and have introduced new guidelines to staff on the procedure for the supply of material (personal communication with Maureen Wolfson, 2003).

1.2 Implementation of the Principles at Kew

Kew endorsed the Principles on Access to Genetic Resources and Benefit-sharing in March 2001. We are in the process of revising our own ABS policy so that it relates more directly to the Principles and in the light of more experience. As with any institution, we have had to design our policy so that it takes into account our particular circumstances. Kew is a complex institution, with four science and horticulture departments: the Herbarium, the Jodrell Laboratories (where work on sustainable use, genetics and plant morphology is conducted), Horticulture and Public Education (the living collections), and the Millennium Seed Bank's Seed Conservation Department.

When designing our implementation we have had to consider the range of activities at Kew, and the movement of material into and out of each department. Not all botanical institutions will face the same challenges. The CBD Unit was established to ensure Kew stays in compliance with the CBD and to handle CBD-related issues as they arise. We advise staff, helping them set up and keep track of agreements, get permits, deal with enquiries and requests from outside, and work out how to share benefits.

Kew places a heavier emphasis now on setting up and strengthening long-term partnerships with institutions. We negotiate written agreements with partners that set out clearly the terms of our collaborations, suggesting areas for joint work, clarifying what material will be collected and how any material going to Kew will be used at Kew, and setting out benefits that may arise and be shared.

For particularly sensitive germplasm such as living seeds, we develop detailed Access and Benefit-Sharing Agreements with partners that lay down mutual obligations and establish prior informed consent (Cheyne, 2003). These often have a government body as one of the partners, and may take years to put into place. In other cases, for example for most herbarium-led research, we generally develop a simpler Memorandum of Understanding between institutions. This sets out the obligation to obtain all necessary permissions, suggests probable areas for collaboration, depending on what funds are available, and also makes clear how we will use and handle any material that comes to Kew, and what benefits may be shared.

Kew has had an 'Overseas Fieldwork Committee' for some time, to disburse funds and equipment for Kew fieldwork, but now it is also one of our most successful tools for CBD implementation. Kew staff cannot get permission to travel for fieldwork without applying to this committee and getting a registration number. People fill in an OFC form and this is voted on by the committee. It is effectively a peer-review process, with all science departments represented on the committee. From the information on the form, we can see if we need to contact staff for more information or to advise them on how they can improve their proposed work. The OFC process ensures that staff are aware of Kew's CBD policy, looking ahead and considering how to work legally and fairly. It checks to see that people are working with local institutions and other partners, and that they are aware of who the relevant stakeholders are in the areas where they plan to work. It also checks that staff are aware of national procedures and what kind of prior informed consent they need – for collecting, import, CITES-listed species, and plant health, they need to have started the process of applying for them. The OFC also checks that staff are aware of the standard ways in which Kew uses material so that they can mutually agree terms with partners and permitting agencies that Kew can honour in practice, and that they have considered what benefits their work will generate and how they can share them. Staff file their permits, or any other records they have of the process of getting prior informed consent for their work, with the OFC upon their return.

Of course, not all new material comes from fieldwork. Like any herbarium or botanic garden, Kew also receives material through exchanges with other botanical institutions. Sometimes horticulturists or researchers buy plants from commercial sources. Occasionally Kew accepts donations of material. Material is then used in the science and horticulture departments, and sometimes plants (or their parts) may travel from one department to another. Kew may then supply material to other institutions. The main point to emphasise is that we are careful to check that the material we receive was acquired legally, with appropriate prior informed consent, and we check whatever terms come with the material. Then we need to make sure that these terms always stay associated with the material, and that we only use, exchange or supply the material as we are allowed to.

The CBD Unit has designed some standard documents for the stages in the cycle. A Use of Material letter sets out the standard ways in which material may be used at Kew, and staff may show this to authorities as part of the process of getting prior informed consent. We use a Donation Letter to ask potential donors if they have acquired the material legally, and to check that they agree to Kew's standard uses if we accept the material. Material Supply Agreements are used for all supply of plant material to others outside Kew. The terms vary depending on the material, but all have a non-commercialization clause.

It is vital to ensure that terms are recorded and are kept linked with material as it enters, moves around within and leaves Kew. Sometimes this means staff need to put this information into database fields, sometimes it means information also needs to be incorporated on specimen labels. Kew does not have one super-database that covers all the departments, but rather separate departmental ones, so we have had to ensure that each database has appropriate fields, and also that the information travels across by other means – i.e. via Kew staff. This means communication and training is very important. We have recently started to run training sessions for staff in each science department, for them to learn about the CBD and its relevance to work at Kew, about the procedures they need to know about, and their own responsibilities for getting prior informed consent, keeping track of terms, and sharing benefits. New staff receive information at induction, and the OFC process is a strong reminder for all fieldworkers. We have also developed an intranet guide so that staff have information at their fingertips.

Commercialization is probably the topic that attracts most attention and worry. The Principles set out the need for institutions to develop a clear commercialization policy, especially on how material collected before and after the CBD came into force on 29 December 1993 ('pre- and post-CBD') is treated. It is also important to decide how to define commercialization of genetic resources. Kew uses the definition from the Pilot Project for Botanic Gardens: applying for, obtaining or transferring intellectual property rights or other tangible or other intangible rights by sale or licence or in any other manner, commencement of product development, conducting market research, and seeking pre-market approval and/or the sale of any resulting product. Kew's policy is that it will not commercialize post-CBD material without the prior informed consent of the country of origin and appropriate stakeholders, and will ensure that any benefits are shared fairly and equitably. For pre-CBD material, Kew will share benefits as far as is possible with the country of origin and stakeholders.

Kew is a not-for-profit institution and carries out very little commercially-oriented work, though a small number of Kew sustainable use projects are conceived with the aim of discovering and developing marketable products. These projects are governed by specifically negotiated collaborative agreements with countries of origin and ensure fair and equitable benefit-sharing. In a break from Kew's past, we do not currently supply to the commercial horticulture sector. Horticultural development is not one of our current priorities and Kew does not have the staff resources it would need to conduct such work fully in the letter and spirit of the CBD, that is, with prior informed consent and involvement from the country of origin and with an appropriate commercial partner. If we are approached by a commercial company, we ask them to contact institutions and botanic gardens in the country of origin. We are developing an Intellectual Property Rights (IPR) policy at Kew. Currently, IPR terms in agreements are agreed with partners on a case-by-case basis.

One of the three main objectives of the CBD is 'the fair and equitable sharing of the benefits arising out of the utilization of genetic resources' (Article 1). It is up to the Parties involved to decide what is fair and equitable in the circumstances. Reflecting this, benefit-sharing at Kew can take many forms. We use a wide definition to include both benefits associated with particular projects and benefits arising from the general use of Kew's global historical collections. One of the key messages for staff is the importance of always thinking about what benefits one can share on an everyday basis, for example, the importance of communicating new determinations for old material, sending reprints to colleagues in countries of origin, citing the country of origin in publications and on gene sequences submitted to GENBANK, and so on. Benefit-sharing is really only limited by our imaginations.

The following are examples of some of the larger-scale benefits which Kew, and other institutions, may share:

- Joint fieldwork within country partners offers many mutual benefits, such as the opportunity to share knowledge and experience, a chance for students to learn from their colleagues and expand networks, and there are may be important benefits depending on the particular project, for example Kew is sometimes able to donate equipment.
- Working in partnership increases the chances to carry out joint research and produce co-authored papers, over the short term and the long term.
- Kew is actively working to open up its collections and to share historical specimen images and information with countries of origin and the international scientific community. We are also working on digitising the Floras and selected rare books to make them more accessible.

Training programmes form an important component of Kew's benefit-sharing strategy. Kew runs a suite of diploma courses for international specialists in Plant Conservation Techniques, Herbarium Techniques, Botanic Garden Management and Botanic Garden Education, with participants from over 90 countries. Places on these courses are often offered as part of a benefit-sharing package, for example in Millennium Seed Bank projects. There are also a number of project-based workshops held at Kew and in-country. Some projects involve staff exchanges, for training in particular technically-challenging areas such as orchid micropropagation. A number of Kew projects involve provision of higher education opportunities, with staff training and supervision of Masters and PhD students from partner institutions.

We have aimed to give fellow scientists an idea of how Kew is working in practical terms, and also the benefits of working together, sharing ideas, staying involved and taking opportunities to contribute to the CBD process. The more we can all show that we are working positively with the CBD's provisions, the more we can build trust between ourselves and with governments in how the taxonomic community is working. If you would like more information about the Principles and on how Kew is implementing them, or copies of our model documents, please contact us directly (cbdunit@kew.org) or check the Kew website (www.kew.org/conservation). In addition, we have recently developed a presentation pack, 'The CBD for Botanists', (Williams, Davis & Cheyne, 2003; see also www.kew.org/data/cbdbotanists.html). It is designed as a flexible training tool for people working with botanical collections, but can also be read for practical guidance on implementation.

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THE CBD AND THE LIMBE BOTANICAL AND ZOOLOGICAL GARDENS: POLICY ON ACCESS TO GENETIC RESOURCES AND BENEFIT-SHARING, COLLABORATIVE RESEARCH, DATA AND INFORMATION EXCHANGE

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Abstract

The Limbe Botanical and Zoological Gardens (LBZG) working to become the Mount Cameroon Biodiversity Conservation Centre (MCBCC) is involved in a wide range of activities and relationships with outside research institutions, government agencies, and local communities. Over the past year, a policy review and development process was undergone in order to implement, more effectively, provisions of the Convention on Biological Diversity (CBD) that impact LBZG/MCBCC's work, in particular those on 'access and benefit-sharing'. This has led to a series of internal meetings, consultations with various groups and individuals within and outside of Cameroon, and drafting a package of policy documents. In addition, particular agreements that reflect LBZG/MCBBC's need were developed to set terms for the supply and acquisition of biological materials and associated traditional knowledge.

Résumé – Les Jardins Botanique et Zoologigue de Limbé (JBZL) en voie de devenir le Centre de Conservation de la Biodiversité du Mont Cameroun (CCBMC) sont impliqués dans une multitude des activités et des relations avec les institutions de recherché étrangères, les agences gouvernementales, et les communautés locales. Au cours des années antérieures, une revue de la politique et le processus de développement étaient entrepris afin de mettre effectivement en application les provisions de la Convention sur la Diversité Biologique (CBD) qui ont un impact sur le travail de JBZL/CCBMC, en particulier ceux sur 'l'accès et le partage du bénéfice'. Ceci a impliqué une série des réunions internes, des consultations avec les groupes variés et les individuels Camerounais et étrangers, et la mise sur pieds de l'ébauche du paquet des documents politiques. En plus, les protocoles d'accord particuliers qui reflectent le besoin de JBZL/CCBMC étaient mis sur pieds afin d'enoncer les termes pour le fournissement et l'acquisition des matériels biologiques et la connaissance traditionnelle associée.

Key words: Access, agreement, benefit-sharing, policy, CBD, LBZG/MCBCC

1 Introduction

1.1 Why develop an institutional policy?

The Limbe Botanical and Zoological Gardens (LBZG), working to become the Mount Cameroon Biodiversity Conservation Centre (MCBCC), is an attractive institutional base for researchers from Cameroon, Africa and overseas. It is ideally located, one hour drive from the Douala International Airport, at the base of Mount Cameroon, the highest mountain in West and Central Africa and opened to the Atlantic Ocean in Limbe, a town of 60,000 inhabitants within the South West Province of Cameroon. It is a semi-autonomous institution under the Cameroon Ministry of Environment and Forestry (MINEF) with the mission "*to provide facilities, information and services to support biodiversity conservation and improve livelihoods in the Mt Cameroon region and beyond*". It is the most functional botanical institute within the Congo Basin and is increasingly seen as having the crucial role in the initiative of collaborative research programmes. Research collaborations and the exchange of biological materials are central to its objectives and to the development of an understanding of the genetic, species, ecosystem, and cultural diversity found within and around Mt Cameroon. It recognizes the value and importance of collaborations with national and international research institutions in building our institutions and achieving our mission. Research must, however, be conducted in a way that does not damage genetic, species, or ecosystem diversity, and must benefit stakeholders fairly and equitably, particularly local communities. Research activities in which it is involved must reflect 'best practice' and must honour the letter and spirit of relevant international and national laws concerning biodiversity and traditional resource rights. It recognizes the close links between cultural and biological diversity, and legal and ethical obligations to local communities. The informed consent of local communities to any research undertaken on their knowledge, resources, or lands must be acquired prior to the initiation of any research, and their culture, traditions, and customary laws respected.

Since 1990s LBZG/MCBCC has been receiving increasing numbers of requests from researchers around the world to act as an institutional base for their work in the region. In most cases, these "requests" came in the form of research proposals in which the institution was, often unknowingly, featured as a local counterpart – commonly with little or no provision for formal institutional support. Many overseas researchers saw national research institutions within Cameroon as little more than a jumping-off point for their work, and relationships were almost always formed on a personal – rather than institutional – basis. In order to build the scientific and technical capacity of the institution, therefore, staff came to realize that they must also work to redefine the role of the tropical country institution in science. Formalizing research relationships through a written policy and agreements with researchers was seen as one way to work towards this end.

2 Objectives

- To ensure that the activities of LBZG/MCBCC are consistent with the provisions of the Convention on International Trade in Endangered Species, the Convention on Biological Diversity and other international, regional and national laws and policies concerning biodiversity, access and benefit-sharing, and protection of traditional knowledge;

- To promote co-operation between LBZG/MCBCC and other botanical gardens, scientific institutions, conservation projects, and individuals throughout the world;
- To establish conditions that facilitate access, according to current standards of best practice, to the biological resources within the Mt Cameroon region and collections held by LBZG/MCBCC, and that enable LBZG/MCBCC to access the genetic resources of others according to the same standards, whether found in *situ* or *ex situ* conditions;
- To establish conditions that will lead to the smooth collaboration between the LBZG/MCBCC and any institution(s) or individual(s) interested in carrying out research in the Mt Cameroon area or that wish to use LBZG/MCBCC data and collections;
- To promote the fair and equitable sharing of the benefits arising from the use of genetic resources with LBZG/MCBCC, local communities, and the Government of Cameroon.

3 Policy development

In 1987, a new plant species, *Ancistrocladus korupensis* was discovered within the Korup National Park of Cameroon. Its compound, michellamine-B, subsequently showed great promise in the U.S. National Cancer Institute's natural products screening program. A few years later, the government of Cameroon was involved in a complex debate with research institutions, the university, NGO, and protected area circles over issues relating to "access and benefit sharing" and "equitable research relationships". The staff at LBZG/MCBCC felt that, as a national research institution, it was their obligation a) to ensure that the operating principles underlying any research collaborations in which the botanic garden was involved were clear, and b) to clarify the responsibilities of visiting researchers. For that an institutional policy was drafted and circulated for comment in 1994. A long process began in which staff capacity to address these issues was developed, and the various elements of implementing an institutional policy were explored. For example a "Unified System of Charges for Scientists Visiting the Mount Cameroon Project Area" was developed and put in place to address one aspect of research relationships. The broader range of issues that must be considered in an institutional policy, however, were not fully expressed until the formulation of the 1999 draft 'Policy on Access to Genetic Resources and Benefit-sharing, Collaborative Research, Data, and Information Exchange', which was adopted two years later as an institutional policy document.

Importantly, parallel to the policy-development process, institutional structures were examined, and a "research co-ordinator" post, with responsibility to achieve transparency, mutually agreed terms, shared objectives, and benefit sharing was established. It is a truism to say that institutional policies are only as good as the staff and institutional structures that exist to implement them. However all too often resources are not made available to implement policies effectively. A major concern on the part of researchers worldwide is that institutions and managers of protected areas will draft policies but lack the staff to implement their terms, so all research will grind to a halt, or reaching an agreement will take many months.

The 'Policy on Access to Genetic Resources and Benefit-sharing, Collaborative Research, Data, and Information Exchange' adopted in 2001 was "developed to implement the provisions of the CBD and national laws on access and benefit-sharing, to provide sufficient information for partners to understand what they can expect when they deal with LBZG/MCBCC and to promote dialogue and good practice within the international community". The policy covers:

1. the acquisition of genetic resources;
2. the supply of genetic resources;
3. conditions relating to access to the LBZG/MCBCC-Mount Cameroon Project data;
4. collaborative research;
5. the fair and equitable sharing of the benefits arising from the use of genetic resources.

The LBZG/MCBCC policy developed in large part from the Botanic Garden Policy on Access and Benefit-sharing Pilot Project, funded by the UK Department for International Development and co-ordinated by the CBD Policy Unit of the Royal Botanic Gardens, Kew. However, it grafts onto the framework policy document developed by the seventeen botanic gardens involved in this project, and the better elaborated Royal Botanic Gardens, Kew Policy on Access to Genetic Resources and Benefit-sharing, a range of issues and relationships with local communities, and conditions attached to the use of the extremely valuable data collected by and house in the Mt Cameroon Project/Limbe Botanic Garden.

3.1 Acquisition

Collections strategies

LBZG/MCBCC acquires biological materials and associated knowledge through its collecting activities and by receiving materials sent or brought to LBZG/MCBCC in accordance with the strategies set out in the Herbarium, Living Collection, Wildlife, Socio-economic, and Conservation Technology Development Protocols, and by working with collaborators and counterpart institutions.

Criteria for suppliers

LBZG/MCBCC abides by the CBD, CITES, and all international and national laws governing access to genetic resources, biodiversity conservation, and protection of traditional knowledge, and acquires materials or associated knowledge only from organisations and individuals that also abide by the obligations arising from these laws.

Material acquisition agreements

When obtaining access to biological materials and associated knowledge, LBZG/MCBCC makes reasonable and sincere efforts to clarify in writing the respective roles, rights and responsibilities of LBZG/MCBCC, the Provider, the country of origin and relevant Stakeholders, as appropriate. In order to do so, all material accepted into LBZG/MCBCC collections is acquired according to the Agreement for the Acquisition of Biological Material for Non-Commercial Use.

3.2 Supply of genetic resources

Supply strategy

LBZG/MCBCC supplies biological material and associated knowledge to recipients including botanical gardens, scientific institutions and individuals throughout the world. Materials will be supplied by LBZG/MCBCC on terms that oblige recipients to provide LBZG/MCBCC with a fair and equitable share of benefits arising from recipients' use of the material or its progeny or derivatives. Material is supplied under separate agreements – Agreement for Supply of Biological Material for Non-

Commercial Use, Agreement for the Supply of Duplicate Herbarium Specimens, and Agreement for the Loan of Herbarium Specimens. Emphasis is placed on supplying genetic resources and associated knowledge to support conservation and sustainable use of biological diversity, and to build capacity in taxonomy and related research that will help to meet LBZG/MCBCC objectives.

Criteria for recipients

LBZG/MCBCC abides by the CBD, CITES, and all international and national laws governing access to genetic resources, biodiversity conservation, and protection of traditional knowledge, supplies materials or associated knowledge only to organisations and individuals that also abide by the obligations arising from these laws.

Material supply agreements

LBZG/MCBCC supplies biological material and associated knowledge subject to material transfer agreements – the Agreement for Supply of Biological Material for Non-Commercial Use – between LBZG/MCBCC and recipients. The terms of this agreement oblige each recipient to share benefits arising from use of the genetic resources, their derivatives, and associated knowledge fairly and equitably with LBZG/MCBCC, local people and the Cameroon Government. It also prohibits the commercialisation of the genetic resources, their derivatives, or associated knowledge without the prior written agreement of LBZG/MCBCC and the Government of Cameroon. Recipients cannot pass materials or associated knowledge onto third parties for commercial purposes without ensuring that the third parties enter into similar agreements with LBZG/MCBCC (a modified version of the LBZG/MCBCC Agreement for Supply of Biological Material for Non-Commercial Use is available for this purpose).

Conditions for loan or supply of duplicate herbarium specimens

All recipients receiving duplicate herbarium specimens sign the Agreement for the Supply of Duplicate Herbarium Specimens, an umbrella agreement for a fixed period between LBZG (MCBCC) and the recipient, governing all supplies of specimens within that period. Recipients of loan material sign and observe the conditions laid down in the Agreement on Conditions for Loan of Herbarium Specimens.

Conditions for loan or supply of other biological materials

LBZG/MCBCC is building its wildlife collections, and in future foresees loaning or supplying materials to other institutions. An agreement will be developed to guide such loans and supplies.

3.3 Conditions relating to databases

LBZG/MCBCC has compiled valuable taxonomic data on the flora and fauna of South West Province in general, and the Mt Cameroon area in particular. LBZG/MCBCC recognizes the value of sharing data in order to further scientific understanding and promote the conservation of biodiversity in the region. It seeks, therefore, to place minimum restrictions on the use of this information, but wishes to ensure that it is used in accordance with international and national laws, and with proper integrity and acknowledgement of the source. Intended recipients of data will be asked to agree to and sign an Agreement on Access to LBZG/MCBCC Databases, which lays out terms for access and benefit sharing associated with the supply of this information.

3.4 Collaborative research

LBZG/MCBCC has worked for many years on the sustainable use and management of biological resources around Mt Cameroon. It is thus in a unique position to play a leading role in the conservation of Mt Cameroon's native flora, fauna, and ecosystems. To be effective in this role, LBZG/MCBCC recognizes the important contribution that can be made by national and overseas research institutions, and seeks to develop joint research programmes that promote the objectives of LBZG/MCBCC. In order to ensure that these more involved partnerships are transparent, effective, and live up to current standards of best practice under international and national law, LBZG/MCBCC has developed Research Guidelines and a summary of core elements for an Agreement/Memorandum of Understanding for Collaborative Research. Such an Agreement will be mutually agreed to and signed by LBZG/MCBCC and collaborators prior to the initiation of research projects.

Conditions to carry out research

Attached to the policy are copies of the standard "Agreement for the Supply of Biological Material", standard "Conditions for Loan of Herbarium Specimens", standard "Agreement on Conditions on Access to the Mount Cameroon Project Data in BRAHMS and TREMA databases", and a standard "Research Agreement". The LBZG/MCBCC "Research Agreement" requires that (www.mcbcclimbe.org):

- Researchers obtain appropriate permits from the Ministry of Scientific and Technical Research (with assistance from LBZG/MCBCC if necessary);
- Work with LBZG/MCBCC staff providing appropriate training;
- For any research involving collection of plant material, a duplicate set of all specimens collected as well as their label information is left with the LBZG/MCBCC and the National Herbaria;
- Correct documents (e.g. phytosanitary certificate, certificate of origin, CITES exportation permit – where necessary) are acquired for any plant material before it is dispatched;
- Plants or materials may not be passed to a third party without written consent from LBZG/MCBCC/MCP;
- Benefits are shared with communities, LBZG/MCBCC/MCP, and government, including research results, copies of publications, and acknowledgement of MCP/LBZG/MCBCC in publications;
- Commercialization of plant "material or any progeny or derivatives thereof" are not commercialized without the written permission of MCP/LBZG/MCBCC, subject to a separate agreement;
- Ethnobotanical information and indigenous knowledge is appropriately acknowledged in publications and agreements reached with local experts supplying the information on equitable sharing of benefits arising from the research, including financial payments;
- Copies of reports and publications are provided to LBZG/MCBCC; joint publications are preferable;
- Upon completion of their field work, researchers agree to be invited to give a lecture or presentation of their work, and/or to conduct training prior to departure;
- Researchers pay research related charges as agreed and as set by the LBZG/MCBCC.

Financial benefits and responsibilities of researchers include set fees for vehicle use, employment of village guides and porters, LBZG/MCBCC staff; a contribution to village development funds; bench fees for use of LBZG/MCBCC facilities (e.g. the herbarium, nursery, Garden) and a management fee that ranges between 10 to 20% of local costs incurred as part of the overall budget. Fees are set according to use of vehicles, equipment, staff time, etc.

3.5 Towards national and regional policy

Cameroon like many African countries, is a contracting party to the Convention on Biological Diversity (CBD) and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). LBZG/MCBCC intends to honour the letter and spirit of these conventions, and other international, regional and national laws and policies concerning the conservation and sustainable use of biological diversity, access and benefit-sharing, and the protection of traditional knowledge. National laws of particular importance to research relationships include the 20 January 1994 Law Regulating Forestry, Wildlife, and Fisheries, and its implementing decrees, and the 1996 Framework Law on the Environment. Under Article 65(1) of the Framework Law on the Environment, "scientific exploration and biological and genetic resource exploitation in Cameroon shall be done under conditions of transparency and in close collaboration with national research institutions and local communities, and should be profitable to Cameroon. The exploration and exploitation should be done under the conditions stipulated by the international conventions relating thereto, duly ratified by Cameroon, especially the Rio Convention of 1992 on biodiversity". The 1994 Forestry Law (Section 11) stipulates that "the genetic resources of the national heritage shall belong to the State of Cameroon. No person may use them for scientific, commercial, or cultural purposes without prior authorization". Policy on "access and benefit-sharing" becomes paramount for regulatory purpose.

The LBZG/MCBCC Policy was therefore introduced to the Cameroon Ministry in charge of forest and environment (MINEF) who reviewed and endorsed it. However, the biodiversity conservation in Cameroon involved other ministries such as Agriculture, Livestock and research. For that an inter-ministerial meeting was organised led by MINEF and involved other international NGOs such as WWF and CIFOR. It was agreed that each stakeholder should study the policy proposed by LBZG/MCBCC and MINEF in order to generate fruitful amendments that will lead to the elaboration of the national policy on the issues. Although it has not yet been formally adopted nationally, this policy is gradually being implemented and many actors and decision makers are also working to implement it at least in spirit. The concrete example is the increasing commitment of Cameroon and other African countries to address illegal activities in forest/natural resource management. In partnership with the G8 they launched the Africa forest law enforcement and governance (AFLEG) in Yaounde in October 2003. They recognised the importance of existing subregional, regional and international organisations and agreements, including the New Partnership for Africa's Development (NEPAD), Conference of the Ministers of Central African Forests (COMIFAC), African Timber Organisation (ATO), Economic Community of West African States (ECOWAS), Southern African Development Community (SADC), Interstate Committee to Fight Drought in the Sahel (CILSS) and the Brazzaville process (CEFDHAC-Conference des Etats en charge des Forêts Denses Humides d'Afrique Centrale). They are committed to provide effective governance, including laws, policies and institutional capacity to enforce those laws in order to eliminate illegal timber and other natural resource exploitation.

3.6 Potential benefits

Indicative benefits elaborated in the policy that might result from the use of data and research collaborations include:

- taxonomic, ecological, and other information, through research results, publications and educational materials;
- the transfer of technology such as software and know-how;
- training in science, *in-situ* and *ex-situ* conservation, information technology and management and administration of access and benefit-sharing;
- joint research and development, through collaboration in training and research programmes, participation in product development, joint ventures and co-authorship of publications;
- training of the local communities in para-taxonomy, village mapping, PRA, and ethnobotanical techniques;
- Paid use of local guides, scientists, and facilities;
- In the case of commercialization, monetary benefits such as fees, milestone payments and royalties.

3.7 Successful cases

Good news from the Mt Cameroon region is encouraging. One is from *Prunus africana*, a mountain tree medicinal plant with high commercial value. A policy implementation on this forest product has led to its conservation and livelihood improvement of the local people involved. In fact harvesters have been brought to a union with agreed regulations including sustainable harvesting principles and benefit-sharing mechanism to both individuals and a village community development fund. A similar successful story is from wildlife hunters who have come into a union with sound monitoring and hunting guides for both conservation and poverty reduction at individual and village levels.

4 Conclusion

The development, adoption and implementation of a sound policy on access to genetic resources and benefit-sharing, collaborative research, data and information exchange is vital for developing countries. Those who often depend largely on their natural resources for economic development, should ensure that effective law enforcement operates in the fields and that governments should internalize independent and rigorous monitoring of such operations. Increasing calls for clarity and transparency in their activities is paramount for both country credibility internationally and poverty alleviation of their citizens. This must start with institutions involved in biodiversity research and LBZG/MCBCC is committed to address the challenges. This policy is a positive step towards meeting the urgent need for reinforced and efficient national, regional and international co-operation aimed at eradicating illegal exploitation and associated trade in forest and wildlife resources.

Acknowledgement

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Appendix 1. LBZG/MCBCC Agreement for the Supply of Biological Material for Non-Commercial Use.

Upon receipt of this Agreement, signed by Recipient below, and because Recipient has agreed to comply with the terms and conditions set forth in this Agreement, LBZG/MCBCC will supply to Recipient Biological Material and associated knowledge requested by Recipient as is, in LBZG/MCBCC's judgement, reasonable and appropriate.

Such Biological Material and associated knowledge as is supplied to Recipient will be accompanied by a copy of this Agreement, on the reverse of which the Biological Material being supplied ("the Material") will be itemized in the Notification of Material Transferred.

LBZG/MCBCC, when using its collections, intends to honour the letter and spirit of the Convention on Biological Diversity (CBD), the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and laws relating to access and benefit-sharing within Cameroon, including those relating to traditional knowledge.

Biological Material and associated knowledge is supplied on the condition that it is only used for the purpose or purposes agreed with LBZG/MCBCC at the time of application. Recipients of Biological Material will be deemed to have accepted the following conditions:

1. Subject to clauses 2 and 3 below, Recipient may use the material, any progeny or derivatives thereof such as modified or unmodified extracts), and associated knowledge, for non-commercial purposes only.

2. Recipient will provide LBZG/MCBCC, the local community and the Cameroon Government with a fair and equitable share of benefits obtained by the Recipient arising out of any utilisation by the Recipient of the Material or its progeny or derivatives, or associated knowledge, including benefits such as research results and copies of publications (see Section 9 of the *LBZG (MCBCC) Policy on Access to Genetic Resources and Benefit-Sharing* for a list of indicative benefits). In addition, Recipient shall acknowledge LBZG/MCBCC in all research publications resulting from the use of the Material. Access to all biological material and associated data lodged in Recipient Institution and supplied by LBZG/MCBCC will be facilitated for any Cameroonian researcher or student.

3. Recipient may not commercialise (for definition of terms see the attached *LBZG (MCBCC) Policy on Access to Genetic Resources and Benefit-Sharing*) the material, associated knowledge, or any progeny or derivatives thereof. If at any point in the future Recipient wishes to use the genetic resource or its derivatives for purposes (such as commercial use) other than those allowed by the terms and conditions under which the material was originally acquired, the Recipient must obtain the written permission of LBZG/MCBCC and specify in writing the terms and conditions of use, including fair and equitable benefit-sharing as set out in LBZG/MCBCC's policy. Any commercialisation to which LBZG/MCBCC agrees will be subject to a separate agreement between Recipient, LBZG (MCBCC) and the relevant Ministry of the Republic of Cameroon.

4. Recipient may not transfer the material, associated knowledge, or any progeny or derivatives thereof to any third party other than Recipient or LBZG (MCBCC) without the prior informed consent, in writing, of LBZG/MCBCC, and then only under a legally binding written agreement containing terms and conditions no less restrictive than those contained in this Agreement unless otherwise agreed in writing by LBZG/MCBCC.

5. LBZG/MCBCC makes no representation or warranty of any kind, either express or implied:
   - as to the identity, safety, merchantability or fitness for any particular purpose of the Material or its progeny or derivatives or that
   - the Material provided to Recipient under this Agreement is or will remain free from any further obligation to obtain prior informed consent from, to share benefits with or to comply with restrictions on use imposed by the Cameroon Government.

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Seyani, J.H. (2006). Adding value to African biodiversity and traditional knowledge: a pilot study from West Africa. In: S.A. Ghazanfar & H.J. Beentje (eds), Taxonomy and ecology of African plants, their conservation and sustainable use, pp. 741–742. Royal Botanic Gardens, Kew.

ADDING VALUE TO AFRICAN BIODIVERSITY AND TRADITIONAL KNOWLEDGE: A PILOT STUDY FROM WEST AFRICA

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Abstract

Africa is endowed with a rich biological diversity, which is the natural capital for basic needs of life (food, fodder, shelter, medicines, chemicals, genetic resources, recreation). Biological diversity and its associated traditional knowledge have great potential for creating new goods, services and wealth for sustainable development and poverty alleviation. In response to the Convention on Biological Diversity, in particular Article 8j – protection of traditional knowledge, and Article 15 – access to genetic resources and benefit-sharing, the Commonwealth Science and Commonwealth Secretariat are assisting traditional medicine practitioners (TMPs) in West Africa (Cameroon, Gambia, Ghana, and Nigeria) to generate income and share benefits arising from the use of biological resources and traditional knowledge through the pilot project on 'Multi-stakeholder development of bioprospecting, marketing, and benefit-sharing arrangements of biological resources at the local level'. This initiative has facilitated the establishment of the Association of Commonwealths Traditional Medicine Practitioners for West Africa (ACTMPWA) and had helped TMPs and other stakeholders to indentify critical issues that hinder derivation of maximum benefits from biological diversity and traditional knowledge. Key areas identified for actions included bioprospecting, marketing, benefit-sharing, capacity building and networking. Training workshops and education visits have improved the knowledge and skills of 107 TMPs, manufacturers, policy makers, legal and medical experts, and natural products scientists. Awareness has been created on protection and documentation of traditional knowledge, control of access to and benefit-sharing of biological resources. Capacity developed on processing of herbal medicine, quality control and packaging, and networking has improved processing and marketing of herbal medicines at local level. Furthermore, there is improved understanding and collaboration between TMPs and researchers at national level. The provision of computers with internet facilities has improved the exchange and sharing experience among ACTMPWA members as well as accessing relevant information on traditional medicine. The review of legal, policy and administrative frameworks being undertaken by the participating countries will further protect and benefit TMPs and other stakeholders, traditional knowledge and biological diversity. AETFAT has a potential role to promote the addition of value to biodiversity and traditional knowledge for the benefit of the African people and their collaborators in a fair and equitable manner.

Résumé

Valoriser la biodiversité africaine et les savoirs traditionnels: une étude pilote en Afrique de l'ouest. L'Afrique est dotée d'une riche diversité biologique qui constitue le capital naturel pour répondre aux besoins vitaux (nourriture, fourrage, abri, médicaments, substances chimiques, ressources génétiques, besoins récréatifs). La diversité biologique et les savoirs traditionnels qui y sont liés, ont un fort potentiel pour créer de nouveaux biens, services et richesses afin d'assurer le développement durable et diminuer la pauvreté. En réponse à la Convention sur la Diversité Biologique, et en particulier à l'article 8j – protection des savoirs traditionnels, et à l'article 15 – accès aux ressources génétiques et partage des bénéfices, le 'Commonwealth Science' et le 'Commonwealth Secretariat' soutiennent les praticiens de la médecine traditionnelle (TMPs) en Afrique de l'ouest (Cameroun, Gambie, Ghana et Nigeria). L'objectif est de générer des revenus et de partager les bénéfices de l'utilisation des ressources biologiques et des savoirs traditionnels à travers le projet pilote sur le 'développement pluriparticipatif de la bioprospection, du marketing et d'accords sur le partage des bénéfices obtenus grâce aux ressources biologiques au niveau local'. Cette initiative a facilité l'établissement de l'Association des tradipraticiens du Commonwealth pour l'Afrique de l'Ouest (ACTMPWA) et a aidé les TMPs et d'autres acteurs à identifier les points critiques qui empêchent de retirer le maximum de bénéfices de la diversité biologique et des savoirs traditionnels. Des régions clés ont été identifiées pour y mener des actions de bioprospection, de marketing, de partage des bénéfices, d'amélioration de potentiel et de mise en réseau. Des séminaires de formation et des visites éducatives ont amélioré la connaissance et la compétence de 107 TMPs, artisans, décideurs politiques, experts juristes et médicaux et scientifiques travaillant dans le domaine des produits naturels. Une prise de conscience de la protection et de la documentation des savoirs traditionnels a vu le jour, ainsi que de la nécessité de contrôler l'accès aux ressources biologiques et d'en partager les bénéfices. Le potentiel en matière de pratique de la médecine à base de plantes, de contrôle de qualité et de conditionnement, et de création de réseau a augmenté les techniques et le marketing des plantes médicinales au niveau local. Par ailleurs, la compréhension et la collaboration entre TMPs et chercheurs a été améliorée au niveau national. Le nombre d'ordinateurs avec connexion à internet a augmenté tant l'échange et le partage d'expériences entre membres de l'ACTMPWA que l'accès aux informations sur la médecine traditionnelle. La révision du cadre légal, politique et administratif entreprise par les pays participants protègera et bénéficiera aux TMPs et autres acteurs, à la connaissance traditionnelle et à la diversité biologique. L'AETFAT a potentiellement un rôle à jouer pour promouvoir la valorisation de la biodiversité et des savoirs traditionnels au bénéfice des peuples africains et de leurs collaborateurs de manière honnête et équitable.

Key words: benefit-sharing, biological resources, bioprospecting, traditional knowledge, West Africa

Golding, J.S., Timberlake, J.R. & Hedberg, I. (2006). Introduction to the session on threatened plants. In: S.A. Ghazanfar & H.J. Beentje (eds), Taxonomy and ecology of African plants, their conservation and sustainable use, pp. 743–744. Royal Botanic Gardens, Kew.

INTRODUCTION TO THE SESSION ON THREATENED PLANTS

JANICE S. GOLDING, JONATHAN R. TIMBERLAKE & INGE HEDBERG

At the VI^th^ AETFAT Congress, organised by Inga and Olov Hedberg in Uppsala in September 1966, concerns on the conservation of African vegetation and its constituent species were the main focus of the proceedings. This was perhaps the first time that such a large group of botanists had addressed themselves to the issue. Accounts of rare, threatened and endemic plants were prepared for 21 countries, forming the basis for many Red Lists that are in use today. These were submitted to the IUCN Threatened Plants Committee that was then based at the Royal Botanic Gardens, Kew. Now, forty years later, national and regional lists are widely available, and there are even some preliminary accounts of threatened species. Yet there remains much to be done. An extract from the VIth Congress is still relevant today "*...the lists illustrate the degree of floristic knowledge for each country and reflect a level of commitment to conservation...*".

Conservation agencies are active in many places, and are often better resourced than research institutions. Paradigms of conservation have come and gone, the more recent focussing on community involvement and economics. But fundamentally there is now a much greater awareness of conservation problems, manifested in the recently adopted Global Strategy for Plant Conservation (GSPC) with its targets for the year 2010. All this at a time when taxonomists and their research institutions are, in many instances, less well funded and coming under more pressure to justify their mandates.

The purpose of this Symposium on Threatened Plants at the XVIIth AETFAT Congress was to look at what progress has been made regarding our knowledge of threatened species in Africa, to raise awareness on how taxonomists and other botanists can contribute towards plant conservation, and to see where future collaborative work needs to be done. Chaired by Dr Inga Hedberg, who organised the first AETFAT Congress on the topic, seven presentations were given.

The papers were encouraging and allow us to reflect on how we have progressed since 1966, as well as where we still need to go. Now we have better data (such as Red Lists), we have political contexts and global movements that justify linking taxonomy and conservation, and there is a new wave of young botanists from Africa and elsewhere who are keen to contribute to conservation initiatives.

Stella Simuyu provides the global policy framework – the Global Strategy for Plant Conservation – that justifies why it is important for taxonomists and conservationists to tackle problems jointly. The GSPC is composed of goals and targets and is thus especially useful in guiding conservation-oriented botanical research. Next, Janice Golding presents a southern African case study from the SABONET Red List project, and shows the inconsistencies between new and previous accounts of threatened plants. Factors that are frequently overlooked when doing RDL work – collaboration and data sharing – are regarded as crucial because they ultimately influence the accuracy of data and subsequent recommendations for conservation.

This is followed by Schatz & Lowry's account of rediscovering 'lost' species on Africa's most speciose island, Madagascar — a powerful reminder that field surveys and taxonomic science can help clarify whether it is reasonable to assume extinction if species were last collected many years ago, or if they are taxonomically problematic.

The work of Cheek *et al.* in Cameroon is an inspiring narrative of how co-ordinated field surveys and collaboration between specialists and amateurs can greatly improve existing information. It also highlights how information products – detailed checklists, Red Lists and posters – can lead to better conservation decisions and an appreciation of the natural environment.

Vivero, Kelbessa & Demissew provide a detailed account of the threatened and endemic flowering taxa of Ethiopia and Eritrea, pointing out the priority areas. From the *Flora Zambesiaca* region of southern Africa, Timberlake, Golding & Smith demonstrate how Red Lists and herbarium data can be used to obtain a general understanding of endemism and threat. They also give a first estimate on the number of plant taxa confined to the region.

Alan Rodgers quotes Prof. Peter Crane from the Congress keynote address, "*In the heart of every taxonomist is a conservationist*". He presents a passionate reminder that taxonomists have a critical role to play, a role that he spells out very clearly. He then goes further by providing examples from across Africa on how Red List information can have useful conservation impacts.

In addition to the presentations, there was a later open discussion on how taxonomists can improve the relevance of their services to the conservation fraternity – how to bring taxonomists and conservationists closer together. Several significant points resulted. These included: the provision of more detailed information on collecting labels such as ecological and abundance data; the collation and provision of botanical information to users such as land managers in the form of annotated checklists, lists of name changes and distribution data; provision of data in monographs and floras that enable assessments to be made on threat and Red List status; preparation of field guides for poorly known areas; encouraging management at an institutional level to promote approaches that ensure responsibility to plant conservation; ensuring incorrect or dubious information on distribution and status is not needlessly repeated; developing stronger links with CBD country focal points; and encouraging the holding of 'end-user' workshops so that taxonomic products can be appropriately targeted and readily used. Finally, a plea was made to win hearts and minds – passion is needed to drive taxonomic contributions towards conservation.

Rodgers, A. (2006). Linking taxonomy and practical conservation. In: S.A. Ghazanfar & H.J. Beentje (eds), Taxonomy and ecology of African plants, their conservation and sustainable use, pp. 745–748. Royal Botanic Gardens, Kew.

LINKING TAXONOMY AND PRACTICAL CONSERVATION

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Professor Peter Crane's plenary lecture at the opening of this AETFAT Congress was inspiring. He said, "in the heart of every taxonomist is a conservationist!". I believe that ultimately we all share a common vision in that we want a sustainable world with equity and a functional natural resource base that includes a full complement of species. Taxonomy – how we go about it, and what we do with it – is one of the components that can lead us to this vision. Unfortunately our use of taxonomy as a conservation tool has not been very creative in the past.

I note that two of my favourite topics diverge, and do not always work together on this issue. On the one hand, I enjoy the stimulating thinking that can go on in Red List process and its potential as a bridge between taxonomy and conservation. But, on the other hand, the high number of threatened species in the world is thoroughly disillusioning for a practical conservationist (see various editorials and letters in the literature). Are we fighting a losing battle against extinction? How can we strengthen co-operation between taxonomy and conservation? Are these numbers real?

There seems to be a disconnect between taxonomists, who help to compile Red Lists, and conservation agencies who, in theory, should take information from Red Lists and use it for conservation implementation (such as reserve planning, ecosystem rehabilitation, re-introductions, and so forth). My task today is to discuss the importance of the linkages between taxonomy, Red Lists and real conservation. (What is real conservation? It is practical on-ground activity, leading to tangible impact). And I specifically wish to discuss what we can do about minimising biodiversity loss.

Where are we now?

Red Lists help us identify those species most in need of conservation attention. They help us set conservation priorities. They are important for a number of reasons if we are to reduce global extinction rates:

- To assess the risk of extinction (i.e. knowing the conservation status) of all species;
- To establish benchmarks (e.g. biodiversity indicators) for monitoring change in the status of populations, species and the habitats that they occupy; and
- To provide a context (social, economic and legal) for the establishment of conservation priorities and threat mitigation at international, national and local levels.

There are many Red Lists currently available, both globally (representing international concerns) and nationally (defining national priorities). These range across taxonomic groups, from lists of cryptic taxa such as lichens and fungi, to the better-known large mammals. Red Lists differ with regard to the institutions involved in their compilation, such as SABONET's Southern African Plant Red List programme which developed national level lists, based on canvassing opinion across wide-ranging groups of national expertise within "expert workshops", and the IUCN, and many others. All these Red Lists communicate the implications for research and conservation.

Southern Africa's SABONET Red List process has undoubtedly moved forward the conservation process in Southern Africa. For example, we now have computerised information outputs – databases, distribution ranges and threat status – for a number of plant species in that region. The process enabled the viewpoints of users of this information (the "end-users" in emerging conservation jargon) to be taken into account. The process has provided an opportunity for taxonomists and conservationists to work together, not just for the sake of working together, but to give well-considered attention to the most important issues relevant to conservation success.

Despite their obvious advantages, why do the many Red Lists in the world not allow us to prioritise and carry out effective conservation (i.e. conservation that filters down to the ground)? I try to answer this question by making some observations.

Firstly, I think there are two "sorts" of Red Lists: (a) those written by the "scientific few" in academic institutions, and (b) those written by national working groups combining taxonomy, field botanists and conservation groups. The processes for compiling Red Lists differ, but if there is greater "end-user" involvement, the likelihood for Red Lists to be useful, practical and credible is greatly increased.

Secondly, despite being a major scientific advance, the new IUCN Red List System (the method for determining the conservation status of species) is extremely information-greedy. Much paper work and data entry is required for hundreds of species, and this requires the most precious of all conservation resources, namely people's time and money. This view is upheld by a great number of people. One has to ask whether identifying and listing threatened species is a means to an end or an end in itself? A Tanzanian colleague of mine remarked many years ago that "counting elephants does not conserve them". Similarly, listing plants does not conserve them. We need to get on with the job of conservation. Is this new IUCN Red List system a conservation advance? The jury is still out.

Thirdly, the depressing information we hear on an almost day-to-day basis about the high levels of extinction is not particularly motivating. There are relatively few encouraging stories of conservation successes. Or is it simply that we choose not to highlight them? Also, how do we decide what is true and what is not true about threat and status because facts and figures about species extinction are so varied? Are 50% of the world's plant species really threatened with extinction? If the Red List process is so useful (I cannot use the word successful), then why are extinction rates on the increase? Changes in facts and figures can lead to different perceptions about what the priorities are, and it may even lead to different conservation decisions and management solutions.

Fourthly, and very importantly, the reality today is that there remains inadequate political will to conserve natural habitats. For example, the President of Ethiopia delivered a keynote address at this AETFAT Congress which emphasised the importance of conserving vegetation and soil in the Ethiopian context. But will this encouraging message of political endeavour be reflected in reality? (Several months after the congress there is no sign of follow-up!) In Kenya, the previous Government de-gazetted huge areas of forest for political expediency. Will this be repeated within the new Government? So far, so good.

A final observation relates to how Red Lists are used – how they are integrated into conservation decisions and decision-making. Conservation is about identifying areas on the ground in which protection measures are put into practice. Conservation decisions that make use of Red Lists therefore, need application at habitat level and not just focus on individual species. The conservation of Red List species also has application in the productive landscape that typically buffers natural areas and are associated with human activity. Red List species such as threatened tree species (*Pterocarpus*, *Widdringtonia*, *Prunu*s, etc.) need regulations allowing sustainable use regimes within public lands. Its utility goes beyond the species and habitat, and it goes beyond just natural and semi-natural environments.

Moving forward to link taxonomy, conservation and action

After these last perhaps rather depressing paragraphs on our past failures, we can think more positively. How can we move forward; what are the tools we have available? I use Southern Africa as an example, where we have SABONET's Plant Red Lists – some 4,000 taxa. But how do we start conserving these? Perhaps, in some cases, we can manage on a species-by-species basis, and intensify management of prioritised species in conservation areas. It is rather worrying that management plans for many of Africa's better known National Parks have no emphasis on conserving plants. We can perhaps start by analysing the main threats if we are interested in reducing and managing them. We can also start by looking for high concentrations of threatened endemics if we are interested in identifying key conservation areas where we can establish reserves, or develop species- and habitat-based conservation action plans in the productive environment, as two immediate examples.

Important Bird Areas (IBAs) have proved to be a useful conservation tool. They use detailed species-based criteria (endemism, richness, threat, etc.) to identify priority conservation areas. Tanzania has 90 identified IBAs, Ethiopia 40 and Uganda 40. Such sites or specific habitats help direct funding and enable us to find better management inputs. And from IBAs we can move on to Important Plant Areas (IPAs), as is being done very effectively in Europe. As there is often much congruence between organismal groups, we should perhaps be thinking of moving on to that other IBA, Important Biodiversity Areas.

The Global Strategy for Plant Conservation (GSPC), an element of the Convention of Biological Diversity, gives us an excellent political tool for conservation and practical tools for conservation of IPAs. The strength of the GSPC is that it has targets and indicators, timed milestones and responsibilities, including setting up IPAs. It also links into the real-world concerns such as poverty relief and sustainable development, and is based on an ecosystem approach. Stella Simuyu gave us more detail on this in an earlier presentation, but there are five components that I think are pertinent here:

1. List all known plant species
2. Provide an assessment of the conservation status of all known plant species
3. Develop models and protocols for plant conservation and sustainable use
4. Ensure that at least 10% of each of the world's eco-regions are effectively conserved
5. Ensure that at least 50% of the most important areas are effectively conserved

From identified and prioritized targets, we need to move into appropriate action or management. In Tanzania we identified the Eastern Arc Mountains as a priority, and have managed to move from that into conservation action as well as target applied research. We must ask such questions as what needs doing. Should we maintain a closed canopy in this forest, reduce cutting, or stop fire? Research questions might involve determining the detailed distribution and requirements of target species, and what the regeneration requirements are. And we need to monitor in order to determine progress and assist adaptive management.

Most importantly, we must build on what we have and get a wider range of people involved.

We botanists are the people that have the data that can direct conservation input. We must use these data sets wisely, share them, publicize them, carry out advocacy!

Some conservation activists tie themselves to trees in front of bulldozers: an activity that can be effective. But which trees should they tie themselves to? Where are the priority trees for such sterling action? We, the taxonomists with an interest in conservation, are the brains behind this call for action, and we must go out and use these brains for real conservation on the ground as well as in the herbarium.

Timberlake, J.R., Golding J.S. & Smith, P. (2006). A preliminary analysis of endemic and threatened plants of the Flora Zambesiaca area. In: S.A. Ghazanfar & H. Beentje (eds), Taxonomy and ecology of African plants and their conservation and sustainable use, pp. 749–760. Royal Botanic Gardens, Kew.

A PRELIMINARY ANALYSIS OF ENDEMIC AND THREATENED PLANTS OF THE FLORA ZAMBESIACA AREA

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Abstract

The compilation of national plant Red Data Lists for southern Africa, during which particular attention was given to endemics, allows us to carry out a preliminary analysis of both threatened and endemic taxa. The analysis looks at (a) the proportion of the total flora that is threatened in one or more of the five Flora Zambesiaca countries, (b) the threat categories, (c) the proportion of country endemism, and (d) the distribution of these taxa. Given that data are presented by country and not for the FZ region as a whole, the analysis must be considered as only preliminary.

The level of country endemism (around 8.4%) is relatively low compared to the Flora of Southern Africa area, possibly reflecting lower vegetation type diversity. The level of nationally threatened taxa (around 5.2% of total flora) is also low. But a major caveat to these findings is that the floras are insufficiently known in terms of species distribution and threat status, particularly for Zambia and Mozambique. Overall, however, it appears that a relatively low proportion of known country endemics are threatened.

The paper concludes by showing that patterns useful to conservation managers can be obtained even from incomplete and poor-quality data, much of it derived from herbarium specimens. Herbaria and taxonomists can play an important role in conservation and should grasp this opportunity even if data is not considered sufficiently "scientific". Major future activities will have to include targeted field surveys aimed at obtaining a better knowledge of species distributions and the actual status of threatened taxa of limited distribution.

Résumé – Une analyse préliminaire des plantes endémiques et menacées de la zone couverte par la 'Flora Zambesiaca'. La compilation des listes rouges nationales pour l'Afrique australe, avec une attention particulière accordée aux endémiques, nous permet une analyse préliminaire des taxons menacés et endémiques. Cette analyse s'intéresse à: (a) la proportion de la flore totale menacée dans un ou plusieurs des cinq pays couverts par la 'Flora Zambesiaca', (b) les catégories de menace, (c) la proportion d'endémisme par pays, et (d) la distribution de ces taxons. Ces données sont présentées par pays et non pour l'ensemble de la région couverte par la FZ, leur analyse doit donc être considérée comme préliminaire. Le niveau d'endémisme par pays (environ 8,4%) est relativement faible comparé à la région couverte par la 'Flora of Southern Africa' et reflète probablement la diversité inférieure des types de végétation. Le pourcentage de taxons menacés au niveau national (environ 5,2% de la flore totale) est également faible. Un bémol à ces résultats est que les flores sont insuffisamment connues en terme de distribution des espèces et de menace, particulièrement en Zambie et au Mozambique. Néanmoins, dans l'ensemble, il apparaît qu'une proportion relativement faible d'endémiques connues des différents pays soient menacées. La conclusion de l'article montre que des modèles utiles pour les conservationnistes peuvent même être obtenus à partir de données incomplètes et de mauvaise qualité, une grande partie provenant d'échantillons d'herbier. Les Herbiers et les taxonomistes peuvent jouer un rôle important dans la conservation et devraient saisir cette opportunité même si les données ne sont pas considérées comme suffisamment «scientifiques». Les principales activités à mener devront comporter des enquêtes de terrain ciblées afin d'obtenir une meilleure connaissance de la distribution des espèces et le statut actuel des taxons menacés dont la distribution est limitée.

Key words: conservation, Flora Zambesiaca, endemics, Red Data Lists

1 Introduction

How to stem the loss of biodiversity is one of the greatest challenges facing conservationists today. Increasingly, many species are under threat from human activities, directly or indirectly. Given that resources – human and financial – for conservation are limited, particularly in southern Africa, it is important that conservation efforts are focussed on species or areas that can yield concrete results.

One of the means of measuring actual biodiversity loss, or the risk of it, is through the compilation of Red Lists (Hilton-Taylor, 2000). These are lists of taxa categorised using carefully-structured criteria, applicable across all taxonomic groups and across the globe. The criteria (see IUCN 1994, 2001) reflect the risk of extinction owing to changes in species' distribution and status. Such changes may be due to a reduction in the numbers of individuals, a reduction in the extent of occurrence, population fragmentation or an intrinsically very low number of individuals. Red Lists can help serve as a barometer for the state of biodiversity of a country or region; indeed some Northern Hemisphere countries have integrated Red List concepts into national and regional planning processes (e.g. Schnittler & Günther, 1999). Within southern Africa, however, the limited concern that does exist for threatened species is fragmented and not yet part of any coherent strategy aimed at conservation and sustainable use goals (but see Barnard, Shikongo & Zeidler, 2002).

One of the most significant groups of potentially threatened species are endemics – species that only occur in a particular defined area, usually a country or smaller region. National governments have particular responsibility for conservation of such species under the Convention on Biological Diversity (CBD 1992, Preamble) as, by definition, species endemic to a country are not found elsewhere. Yet within the southern African region there are few lists of endemic species, and national governments are often not aware of their responsibilities.

In this paper we attempt to determine patterns in the distribution and status of endemic and threatened vascular plants found in the Flora Zambesiaca region of southern Africa, based on data derived from the recently-published Southern African Plant Red List

(Golding, 2002). Lists of endemic plant taxa from countries within the region (i.e. country endemics) are examined and general patterns with respect to their threatened status are given. We conclude with broad recommendations that can help improve existing Red List initiatives and help focus the limited conservation resources available in the region for better conservation impact, as well as enhancing the role of taxonomists in conservation.

1.1 The Flora Zambesiaca region

The Flora Zambesiaca (henceforth FZ) region of south-central Africa is a large area (2.65 million km^2) comprising Botswana, the Caprivi Strip (Namibia), Malawi, Mozambique, Zambia and Zimbabwe. It represents a floral initiative (*Flora Zambesiaca*, current editor G.V. Pope) and is estimated to contain at least 9860 plant species (G.V. Pope, pers. comm.). The total number of taxa (including subspecies and varieties) is estimated by us to be around 11,400 (see later).

Floristically the region is homogeneous over large areas, comprising a range of broad-leaved woodlands interspersed with natural grasslands (Wild & Barbosa, 1967). In high rainfall areas woodlands are tall and dense, often with an evergreen understorey, while woodland becomes increasingly shorter and spaced out towards the drier south and west. Much of the lowland flora shows relatively low levels of diversity with few endemics, except along the coastal belt in Mozambique. In the east there are a number of mountain ranges supporting moist forests on the slopes, and montane grasslands at higher altitude. It is here that some of the highest levels of diversity and endemism are found.

Using the Ecoregion terminology of the World Wide Fund for Nature, WWF (defined as relatively large units of land or water that harbour a characteristic set of species, communities, dynamics and environmental conditions), the great majority of the FZ region falls within the Miombo Ecoregion or ‘super-ecoregion’ (WWF-SARPO 2002). Major vegetation types include wet and dry miombo woodland, *Baikiaea* woodland, *Colophospermum* (mopane) woodland, *Burkea-Terminalia* woodland, *Acacia-Combretum* woodland, dry evergreen *Cryptosepalum* forest, wetland and floodplain grasslands, dry deciduous (Itigi) forest and Afromontane forest and grassland (Frost, Timberlake & Chidumayo, 2002). The dominant tree genera are Caesalpinoid – *Brachystegia*, *Julbernardia*, *Isoberlinia*, *Colophospermum*, *Baikiaea*, *Cryptosepalum* and *Burkea* – while non-Caesalpinoid genera, including *Terminalia*, *Combretum* and *Acacia*, are more common in drier areas (White, 1983).

1.2 Endemic plant taxa

Most work on endemic plant species in southern Africa has been focussed on particular groups, such as succulents (Van Wyk & Smith, 2001) and cycads (Golding & Hurter, 2003), or biomes with high levels of endemicity such as fynbos in South Africa (e.g. Hall, 1993; McDonald & Cowling, 1995). Major centres of endemism in the region have been described (Wild, 1964, 1965; Davies, Heywood & Hamilton, 1994; Van Wyk & Smith, 2001). The first list of endemics was produced for Malawi (Hargreaves, 1982), and recently a detailed list and analysis of the endemic taxa of Zimbabwe has been produced by Mapaura (2002). However, countries such as Mozambique and Zambia have been particularly poorly covered. This paper is an attempt to enumerate endemic and threatened taxa from across the FZ region and discern any patterns.

It is important to emphasise that we restrict ourselves to country endemic taxa only, species that are endemic to a single country within the FZ region or restricted to a limited area that crosses an international boundary. We do not have data on taxa that are endemic to the FZ region as a whole, i.e. those taxa that are confined to the region rather than to individual countries.

1.3 Threatened plant taxa

Over the last decade global Red Lists have been produced for flowering plants (Walter & Gillett, 1998; Hilton-Taylor, 2000) and specifically for trees (Oldfield, Lusty & MacKinven, 1998), while plant Red Lists for certain southern Africa countries (South Africa, Lesotho, Swaziland, Namibia and Botswana) include Hall *et al.,* 1980 and Hilton-Taylor, 1996. However, each of these Red Lists differs in the system of categories used to assess extinction risk, their geographic coverage, species representation and application of taxonomic nomenclature. They also have limitations owing to incomplete knowledge of the flora and the lack of specialists familiar with the species in the field, particularly for areas north of the Limpopo River.

The most recent plant Red List covers Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland, Zambia and Zimbabwe (Golding, 2002), and uses the 1994 IUCN Red List criteria. It is the most comprehensive yet compiled and also incorporates poorly known taxa (those known only from single herbarium collections or type localities) as well as country endemics and utilised species. Hence it is an appropriate source from which to draw general conclusions about overall patterns of distribution and threats to plants in south-central Africa.

2 Data and methods

We use the term ‘taxa’ to refer to named species, subspecies and varieties. Taxa confined to a single country are termed national endemics, irrespective of the extent of the distribution range in that country. Near-endemic taxa are those known to occur in relatively restricted adjacent areas across national borders (e.g. Chimanimani mountains, Nyika plateau), including with countries outside the FZ region. Hereafter, endemics and near-endemics are collectively referred to as endemics.

2.1 Information sources

Data were sourced from the CD-ROM version of national Red List assessments (Golding, 2002), which in turn were derived primarily from specimen information contained in Flora volumes (Flora Zambesiaca, 1960–), specimens from herbaria at Kew, Harare, Pretoria, Gaborone, Lusaka, Zomba and Maputo, and also from expert knowledge. The Caprivi Strip was not included in this study as it was not possible to separate taxa confined to this area from those in Namibia as a whole. Taxa falling into any of the IUCN Red List categories of Extinct (EX), Critically Endangered (CR), Endangered (EN) or Vulnerable (VU) were termed threatened (IUCN, 1994). Taxa that were Data Deficient (DD) and Lower Risk were not considered in this study. A few taxa were categorised as Extinct (11 taxa were given as nationally extinct, although five of these are probably found in adjacent FZ countries), but none were categorised as Extinct in the Wild (ExW).

Figures for national floras were taken from the best or most recent available information. No figure is available for the total number of taxa (in contrast to species) found within the FZ area, as the Flora itself is only around 70% complete. In order to calculate this figure we used the estimated figure for total number of species (described or in press) for Flora Zambesiaca of 9860 (G.V. Pope, pers. comm.). This was then corrected for taxa (i.e. including recognised subspecies and varieties) by using the recently completed FZ volumes covering the large families of Euphorbiaceae and Orchidaceae. These families have 15% more taxa than full species, hence we added 15% to the estimate of 9860 to give an approximate upper total of 11,400 taxa for the whole area.

Two data sets were compiled. The first lists all the endemic taxa from the five countries, while the second lists all threatened taxa. Duplications within each set were removed. However, as threatened taxa were based on national assessments, a taxon assessed as being in a particular threatened category in one country might be assessed in a different threat category in another. In such cases, where a particular national threat category was thought to be too high (e.g. on the Chimanimani Mountains) the overall category was reduced. Otherwise a precautionary approach was adopted and the higher threat category used.

Six tree taxa (*Afzelia quanzensis*, *Baikiaea plurijuga*, *Dalbergia melanoxylon, Pterocarpus angolensis*, *Sterculia appendiculata* and *Sterculia quinqueloba*) regarded as threatened in some countries were excluded because although they may be threatened commercially, they are not threatened biologically. Oldfield *et al.* (1998) list the first four taxa as not-threatened globally (Lower Risk-near threatened), and do not list the latter two.

2.2 Threat categories

In order to classify threats to taxa, quantitative criteria are used to place them into a particular threat category (IUCN, 1994). The IUCN Red List system uses five sets of criteria (Criteria A to E), singly or in combination. Criterion A assigns a threat category in terms of percentage population decline over a ten year or three generation time period (which ever is less). Criterion B considers declines or fluctuations in the distribution range of a taxon, while Criterion C looks at declines of small populations. Criterion D assigns a threat category based on very small or restricted populations. Criterion E (based on quantitative analysis of population data) was not used.

3 Results

3.1 Endemic taxa

The total number of taxa recorded as endemic to any of Botswana, Malawi, Mozambique, Zambia or Zimbabwe, or to transfrontier areas within the region (e.g. Nyika Plateau and Chimanimani mountains), was 954 (Table 1). A full list of these is available from the authors. This represents 8.4% of the total FZ flora, although this figure excludes taxa endemic to the region as a whole but not to any particular country.

The number of endemic taxa found in each country is not similar across the region, being highest in Zambia and very low in Botswana (Table 1). Zambia has 334 endemic taxa (6.4% of the national flora), although a large number of these are only known from one or two collections from the far north west or north east of the country. The lowest levels of endemism are found in Botswana, with 15 taxa, most of which are of uncertain status. Malawi, with 154 endemic taxa, has fewer endemics than Mozambique and Zimbabwe (with 251 and 224, respectively), but a similar proportion of its flora is endemic (4.1% compared to 4.4% and 3.8%). A large number of Mozambique's endemics are of uncertain taxonomic status or are only known from the type specimen. Of interest is that across the region there are 387 endemic taxa, particularly Cyperaceae, that are considered Data Deficient (DD), i.e. of dubious taxonomic status or about which insufficient is known.

There are 353 taxa that are both endemic and threatened, 37.0% of the total number of endemics. Of the 334 endemics in Zambia, only 95 are considered threatened (28.4%), while this proportion is much higher in Malawi (55.8%), but intermediate in both Mozambique (43.4%) and Zimbabwe (31.7%). Botswana has by far the lowest number of threatened endemics.

TABLE 1. Number of threatened and endemic taxa for the FZ region (Source: Golding, 2002). Figures in parentheses are percentage of total flora.

Country	Total flora	Endemics(%)	Threatened (%)	Threatened endemics (%)
Botswana	2157[a]	15 (0.7%)	13 (0.6%)	2 (0.1%)
Malawi	3765[b]	154 (4.1%)	131 (3.5%)	86 (2.3%)
Mozambique	5692[c]	251 (4.4%)	119 (2.1%)	109 (1.9%)
Zambia	5233[d]	334 (6.4%)	144 (2.8%)	95 (1.8%)
Zimbabwe	5930[e]	224 (3.8%)	211 (3.6%)	71 (1.2%)
FZ region	11,400	954 (8.4%)	595 (5.2%)	353 (3.1%)

Sources: a= PRECIS 2002; b=WCMC; c=Mozambique SABONET checklist; d=M.Bingham unpublished checklist; e=Mapaura & Timberlake (2004). Figures in columns do not add up as some taxa are present in two or more countries.

Details on locality and habitat within countries for each taxon were generally missing from the original data set (with the exception of Zimbabwe), so it was not possible to determine directly areas or habitats with high endemism. However, examination of the data shows that there are some significant centres of endemism, as shown in Fig. 1.

In addition, certain taxonomic groups appear to be disproportionately represented in the endemic and threatened taxa lists. The reasons for this should be explored when a more complete data set is available.

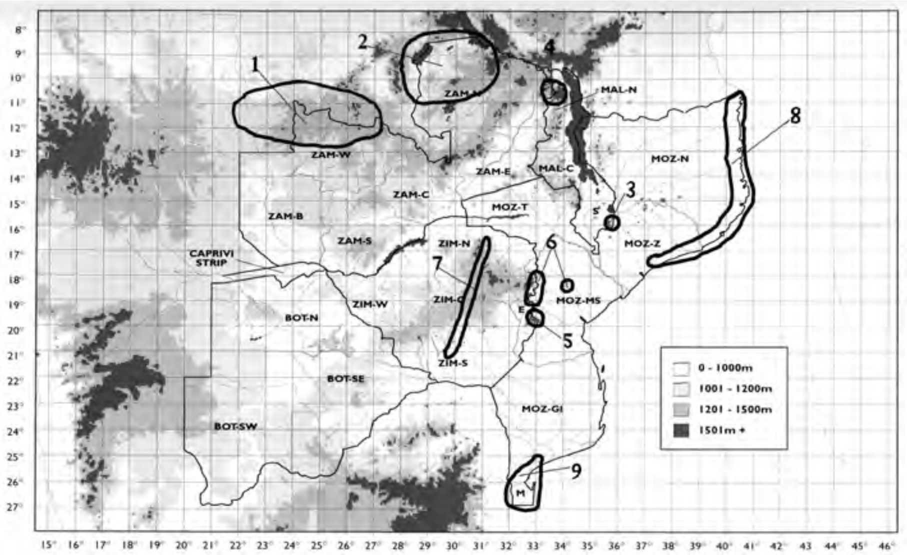

FIG. 1. Areas of high endemism.

3.2 Threatened taxa

There are 595 taxa that are considered threatened in at least one country (Table 1), representing 5.2% of the total estimated flora. A full list is available from the authors. Botswana has by far the lowest number of threatened taxa (13), most of which are in the Vulnerable category. Given the country's comparatively depauperate flora, low human population density and the limited extent of arable agriculture, this is only to be expected. Malawi (131 threatened taxa) has a significant number of taxa where the B criterion was used, indicating small populations in a very limited geographical range coupled with marked habitat fragmentation and loss. On the other hand, for Mozambique with a similar number of threatened taxa (119), distribution data is poor and the threat status is often unclear. Most threatened taxa here were categorised as VU D2, i.e. known from only a few locations but with no available evidence of population decline.

Zambia has a surprisingly low number of threatened taxa (144) given the size of the flora and number of endemics. This is as much a reflection of our poor knowledge on plant distribution as of a relatively stable situation regarding threats. The great majority of threatened taxa were categorised as VU D2. A more even spread of level and type of threat is seen for Zimbabwe (211 threatened taxa), perhaps reflecting a better and more comprehensive knowledge of the country's flora rather than differences in actual threat category. Here, a relatively high number of taxa were categorised as CR owing to very small population sizes in a very restricted habitat under great threat (e.g. small forest patches).

4 Discussion

This paper is the first detailed account of the endemic and threatened plant taxa of the *Flora Zambesiaca* region. It demonstrates the value of specimen-based data from herbaria coupled with local expertise in poorly-known areas. In developing countries, specimen data residing in herbaria and floras often provide the only reliable information to guide conservation decisions as information on population status and full distribution is not often available (Golding, 2001; 2004). The results are interpreted primarily from a conservation perspective rather than from a biogeographical viewpoint.

4.1 Endemism

The level of country endemism for the FZ area is estimated to be 8.4% (Table 1). Significantly, this figure excludes those taxa endemic to the region as a whole but found in more than one FZ country. In addition, it is likely that the number of country endemics is actually higher than the figure given owing to incomplete recording. For example, Mapaura (2002) recently carried out a study of the endemics of Zimbabwe and listed 232 taxa, an increase of eight on that given here. On the other hand, Balding (2003, paper presented at this Congress) reassessed the listed endemics for Botswana and found that only six taxa were endemic (with a possible further three), rather than the 15 given in the Botswana list used here. A number of endemics from Zambia and Mozambique are of uncertain taxonomic status or known only from the type collection. On further collecting or taxonomic revision these may well be subsumed under other taxa, thus reducing the number further.

Given the size of the FZ region and its relative stability over geological time, the recorded level of endemism is rather low. This may be due to environmental homogeneity over large areas compared to coastal and escarpment environments,

TABLE 2. Areas of plant endemism within the FZ region.

1. Mwinilunga (NW Zambia)
2. Mbala, Lake Mweru, Lake Mweru-Wantipa, Mporokoso plateau (NE Zambia)
3. Mt Mulanje (S Malawi)
4. Nyika plateau (N Malawi)
5. Chimanimani mountains (E Zimbabwe – C Mozambique)
6. Eastern Highlands (E Zimbabwe – C Mozambique)
7. Great Dyke (C Zimbabwe)
8. North Coastal Mozambique
9. Maputaland (S Mozambique)

which are not well represented in the FZ area. The Flora of Southern Africa region (South Africa, Namibia, Botswana, Swaziland and Lesotho) has around 80% endemism in a flora of around 23,000 taxa (Cowling & Hilton-Taylor, 1997), while Madagascar also has more than 80% endemism (12,000 taxa) in an area of 587,000 km^2 (Phillipson, Schatz & Lowry, 2003, this Congress), more than five times smaller than the FZ region. Endemism in the fynbos biome of the Cape Floristic Region of South Africa is known to be exceptionally high (according to Goldblatt & Manning (2000) more than 50% of the endemics of South Africa are found in the Cape and Karoo areas), as is endemism among succulents in the Karoo region (Van Wyk & Smith, 2001).

4.2 Centres of endemism

The patterns of endemism within the FZ region possibly reflect the limited range of environmental variability and the distribution of special habitats. The main areas of endemism are shown in Fig. 1 and listed in Table 2. Botswana, with a depauperate arid flora and without the development of desert and succulent species as in Namibia and the Karoo, is particularly poor in endemics. The endemics of Zimbabwe are mostly found on unusual impoverished quartzite soils in the Chimanimani mountains (29%) and on the mineral toxic soils of the Great Dyke (13%) (Mapaura, 2002), while those in Malawi are principally found in the montane areas of Mulanje and Nyika (58%). Interestingly, in most of these cases the habitat is grassland or heathland, which is a comparatively rare habitat across the region. In Zambia where endemism is comparatively high, most endemic taxa are found in the north-west (Bingham, 1994), where the Guineo-Congolian flora meets and interdigitates with the Zambesian (White, 1983), and in a broad area in the north east covering Mbala, lakes Mweru and Mweru-Wantipa and the Mporokoso plateau (Fig. 1). In both cases, many taxa are likely to be also found in a limited area of the neighbouring Democratic Republic of Congo.

In Mozambique many of the endemics are found in coastal forests, thickets and grasslands of the Zanzibar-Inhambane Regional Mosaic (White, 1983), or what Clarke (1998) now terms the Swahelian regional centre of endemism and the Swahelian/Maputaland regional transition zone. In addition, Van Wyk & Smith (2001) describe the very southern part of Mozambique as a separate phytogeographical area termed the Mapautaland-Pondoland regional mosaic. There are a number of endemics here, some shared with adjacent parts of South Africa and Swaziland.

4.3 Threats

Only 5.2% of the total FZ flora has been classified as threatened, considerably less than the level of endemism. This calls into question Pitman and Jorgensen's (2002) assumption that the number of species endemic to a country is a reasonable proxy for the number of threatened plants there. Bramwell (2003) has also recently questioned this assumption, his own analysis suggesting that threatened species make up an average of 15% of the floras of countries for which reliable Red Data Lists exist.

Among the 595 taxa identified as threatened in the FZ region, 11 are listed as Extinct. Most are known only from very old types, putting their taxonomic reliability in question. Of these 11 taxa, five are thought to be globally extinct because of extensive urban degradation of their limited habitat. Four of these occur in Malawi and one in Mozambique: *Suaeda* sp. (Caldeira & Marques, 599) (Chenopodiaceae) is known only from coastal Inhambane in Mozambique; *Deinbollia nyasica* Exell (Sapindaceae); *Encephalartos* sp. (*Greenway*, 6283) from near Zomba; *Dovyalis spinosissima* Gilg (Flacourtiaceae); and *Polystachya kaluluensis* P.J.Cribb & la Croix (Orchidaceae). The first three were known only from the type specimen. *Angraecopsis trifurca* (Rchb.f.) Schltr., an epiphytic orchid from Zimbabwe, is now thought to be extinct to the FZ region, although it is still found on the Comores. The ephemeral annual *Triceratella drummondii* Brenan, a monospecific genus in the Commelinaceae, appears to be extinct in the type locality in southern Zimbabwe, but has recently been recorded from coastal dunes in northern Mozambique. The other four taxa are extinct in one FZ country but present in another or in South Africa.

From the criteria cited in the original dataset, it appears that the major threat for plants across the FZ region is loss of habitat. This is often a generalised diffuse threat rather than something specific that can be readily targeted for action. The implication is that conservation actions in general will also have to be diffuse and deal with such issues as development and land use planning, rather than with legislation and its enforcement, as would be the case if the major threats were utilization or collection. In some cases, e.g. the Chimanimani mountains along the Zimbabwe-Mozambique border and Mulanje Mountain in Malawi, formal protection may be the most appropriate action. But this is not likely to be the case in north eastern Zambia where species of concern are widely distributed.

Our results suggest that species with narrow ranges, such as endemics, appear to be the most affected by threats, while widespread species are least affected. The inference is that threats currently do not appear to operate at a scale or at an intensity to cause significant reduction in the number of individuals in a population or its distribution range, except for range-restricted or endemic species (i.e. those known from few localities).

4.4 Dataset limitations

The dataset used is far from complete, but presents the best available information (Golding, 2002). There are four main limitations: (1) assessments were made at a national level – if a taxon was assessed in one country, it was not necessarily assessed in another; (2) a standardised taxonomic approach was not used as Floras are incomplete and there is no recognised checklist for the FZ region; (3) a considerable level of subjectivity was used when dealing with uncertainty in the application of Red List criteria, and this was not consistent between countries; and (4) national assessments used greatly differing levels of knowledge of the flora and its status. Most of these problems can be overcome by using a standardised taxonomy and by using a single team to carry out revised regional assessments. We consider this to be an important future activity for the region.

4.5 Implications for conservation

Although species and ecological processes do not respect political boundaries, it is recognised that conservation action primarily takes place at national or sub-national levels, and not at ecological or habitat level. It is also primarily at national level that changes in policy and legal instruments are made and enforced. But to be most effective, conservation needs to take place within an ecological or regional context (WWF, 2002). Under the Convention on Biological Diversity, endemics are the major responsibility of national governments. They should be national conservation priorities as no other government can be held responsible. Hence conservation of the 353 threatened endemics must be the major priority.

Given the scale of conservation action and resources required, and the number of taxa across the region, it is important that focal points are identified and some logical system of prioritisation outlined if conservation efforts are not to be so diffuse as to be ineffective. This study provides some preliminary data towards three important requirements for conservation: (1) focal points for conservation action, (2) a rational basis for conservation prioritisation, and (3) the identification of gaps and weaknesses in our current knowledge.

Apart from actual conservation, the other important task is the compilation of regional lists of taxa endemic to the FZ region as a whole (i.e. those taxa that are not endemic to any single country), and similarly for threatened taxa with regional threat categorisation. These lists would help focus conservation action at regional and continental levels and help clarify “hotspots” of both endemism and threat. At present the actual threatening processes are not always clear, so focussed conservation action is hard to achieve.

There is also need for further field survey and taxonomic research. Most of the present data are qualitative, reflecting our poor knowledge both of distribution and population status. Such research is particularly important for taxa in the Critically Endangered category. In addition, many taxa were recorded as Data Deficient, and a major effort is needed to clarify their status. Are they indeed endemic or threatened? Some may not be good taxa, and hence require a critical analysis by taxonomists. It is here that taxonomists can play an important role in conservation (Golding & Smith, 2001; Golding & Timberlake, 2003), something that is sorely needed.

Although a start has been made on identifying both the endemic and threatened plant taxa across the FZ region, as well as describing the levels and patterns of endemicity and threat, the results so far are only indicative. But they do provide a good basis for targeted conservation action, both nationally and regionally, and also indicate priorities for survey and research work, work that needs to encompass taxonomists, ecologists and conservationists.

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PROGRESS ON THE RED LIST OF PLANTS OF ETHIOPIA AND ERITREA: CONSERVATION AND BIOGEOGRAPHY OF ENDEMIC FLOWERING TAXA

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Abstract

A first assessment of threat to the endemic flowering plants of Ethiopia and Eritrea is made, and their biogeography is outlined. This is based on the published accounts of the Flora of Ethiopia and Eritrea (FEE), unpublished manuscripts, bibliography and collections at the National Herbarium (ETH). This information includes data on the taxonomic status, chorology, and ecology of the endemic plants. We have applied the IUCN categories, A1cd, B1ab and B2ab (i, ii, iii, iv) to 596 taxa using the most conservative approach due to the scanty information available. The resulting new Red List contains 464 threatened taxa (CR, EN, VU), three times more than the previous 1997 Red List (an increase of 435 new taxa). Overall endemism is 9.7%, and species endemic to a single province represent 38.6% of the endemic flora. More than 200 taxa are found in a single locality, 72 are known only from type material, and 13 taxa have not been collected since the 19th Century; at least seven are presumed to be extinct. These data illustrate the pronounced narrow endemism among the endangered taxa in the region. The floristic regions of Shewa and Gondar have the highest numbers of endemic taxa, Sidamo and Harerge have the highest number of narrow endemics, and Arsi and Shewa are the most endemic-rich areas. Welo appears as a poor region with only one narrow endemic, the lowest species richness, and with the lowest afroalpine endemic richness (despite having more than 4000 km^2 above 3000 m). This coldspot requires further collections and biogeographical research. Gondar and Sidamo have more than half of the total number of endemics (344), reaching up to 70% when Shewa is taken into account. Nine local centres of endemism are specified for Ethiopia, four in the highlands and five in the lowlands. The transitional belt between the Southern Highlands and the Ogaden-Borana lowlands appears as an important endemic plant area, and requires a thorough conservation and chorology assessment. Finally, in light of recent data on plant and animal endemism, we consider the possibility of designating the Horn of Africa as a world hotspot; it has more than 1500 endemic plants, high plant and animal species richness, and an overwhelming habitat modification.

Résumé

Avancement de la liste rouge des plantes d'Ethiopie et d'Erythrée: conservation et biogéographie des taxons endémiques de spermatophytes. Une première estimation de la menace pesant sur les spermatophytes endémiques d'Ethiopie et d'Erythrée est présentée et des modèles biogéographiques pour les plantes endémiques sont décrits sur base des volumes publiés de la ‘Flora of Ethiopia and Eritrea’ (FEE), de manuscrits inédits, de la bibliographie et d’échantillons du ‘National Herbarium’ (ETH). L’information rassemblée comprend des données sur le statut taxonomique, la chorologie et l’écologie. Les catégories IUCN, basées sur les critères A1cd, B1ab et B2ab (i,ii,iii,iv) appliqués en utilisant l’approche la plus conservatrice en raison de l’insuffisance d’information, sont affectées à 596 taxons. Cette nouvelle liste rouge contient 464 taxons menacés (CR, EN, VU) et triple la précédente liste établie en 1997 avec une augmentation de 435 taxons. Les espèces endémiques d’une seule province représentent 38,6% de la flore endémique et le pourcentage d’endémisme est de 9,7%. En fait, plus de 200 taxons ne sont présents que dans une seule localité, 73 sont seulement connus de l’échantillon-type et 14 n’ont plus été récoltés depuis le XIXème siècle, huit au moins ayant probablement disparu. Ces données illustrent le stenoendémisme prononcé parmi les taxons menacés de la région. Shewa et Gondar sont les régions floristiques avec le plus grand nombre de taxons endémiques, Sidamo et Harerge ont les valeurs les plus élevées en terme d’endémisme à petite échelle, alors que Arsi et Shewa viennent en tête en ce qui concerne la richesse endémique par région. Wello, au contraire, se révèle une région anormalement pauvre avec un endémisme à petite échelle, la richesse spécifique la plus faible et la richesse en endémiques afroalpines la plus basse (malgré le fait qu’elle comprend plus de 4000 km^2 au-delà de 3000 m d’altitude). Ce ‘coldspot’ nécessite des missions de récolte et des recherches biogéographiques complémentaires. Gondar et Sidamo totalisent plus de la moitié des endémiques (344), atteignant jusqu’à 70% lorsque Shewa est pris en compte. Neuf centres locaux de plantes endémiques sont indiqués pour l’Ethiopie, quatre dans les régions d’altitude et cinq à basse altitude. La zone de transition entre les ‘Southern Highlands’ et les terres basses de Ogaden-Borana semble être une région importante d’endémisme végétal. Une conservation minutieuse et une évaluation de la chorologie par un important travail de terrain sont considérés de la plus haute importance pour terminer l’établissement des listes rouges. Finalement, à la lumière des données récentes sur les endémiques animales et végétales, les auteurs discutent de l’égilibilité de la corne de l’Afrique en tant que ‘hotspot’ mondial avec plus de 1500 plantes endémiques, une richesse spécifique animale et végétale élevée et une modification inquiétante de l’habitat.

Key words: conservation, endemism, Ethiopia and Eritrea, hotspot, Red List

1 Introduction

The richness of Ethiopia’s biological resources is well-documented. The country exhibits an enormous variety of plants and animals, many of them being endemic to this area (Yalden & Largen, 1992; Hillman, 1993; Fjeldså & Klerk, 2001; Vivero, 2001). Vavilov (1951) indicated that 38 species have their primary or secondary centre in Ethiopia, whereas Zohary (1970) identified 11 cultivated crops as having their centres of diversity in the area. The Flora of Ethiopia and Eritrea (FEE hereafter) area has a truly unique environment for its region and this, together with its isolation, has been a potent stimulus for rapid speciation in its colonists (Kingdon, 1989).

Ethiopia, including Eritrea, is considered to be a minor core area for endemism and biodiversity (Harlan, 1969; Hamilton, 1982; Davis *et al.*, 1994). However its importance as a threatened biodiversity hotspot has not been duly acknowledged due to the scanty, outdated and incomplete knowledge about its flora and fauna. Thus, out of the 25 terrestrial hotspots identified by Myers *et al.* (2000), neither the pair Ethiopia-Eritrea nor the Horn of Africa as a whole have been eligible. Previous studies of the flora of

Ethiopia and Eritrea[1], always based upon estimations or incomplete species lists, indicate figures ranging between 6000 and 7000 species, with levels of endemism between 12–20% (Cufodontis, 1953–72; Brenan, 1978; Friis, 1983; Tewolde Berhan, 1986, 1991). As a rule, the higher the knowledge about Ethiopian flora, the lower the figure of plant endemic species: 1182 in 1972, 804 in 1986, 596 in this paper. Only partial Red Lists of plants of Ethiopia and Eritrea have been published to date (Oldfield *et al.*, 1998; Walter & Gillett, 1998; Hilton-Taylor, 2000), all of them based on published volumes of FEE or partial lists for afroalpine, endemic or woody taxa (Hedberg, 1957; Viswanathan, 1986; Ensermu *et al.*, 1992; Friis, 1992). Red-listing assessments of the conservation status of all known plant species at national and regional levels are among the sixteen specific outcome-oriented global targets for 2010 of the Global Strategy for Plant Conservation, adopted during the Convention of Biological Diversity COP-6 in The Hague (Simiyu, 2003).

The purpose of the present study is twofold: a) to provide a preliminary assessment of the flowering endemic plants of Ethiopia and Eritrea, assigning IUCN categories to the taxa, and b) to outline some biogeographical patterns of the endemic plants of Ethiopia and Eritrea. Finally the authors, in light of the evidence presented in the paper, discuss the consideration of the area as world hotspot, according to the three evaluating criteria used by the international organization Conservation International (Mittermeier *et al.,* 1999).

2 Materials and methods

The taxa included in the Red List of Flowering Plants of Ethiopia and Eritrea have been drawn from the published volumes of the Flora of Ethiopia and Eritrea (FEE) Vols. 2 (part I, II), 3, 6, 7 (Hedberg & Edwards, 1989; Edwards *et al.*, 1995, 1997, 2000; Hedberg *at al.*, 2003) and from the manuscripts under preparation for the same flora. These unpublished manuscripts were under different stages of preparation, thereby making necessary in some cases a complementary work to be carried out by the authors and member of the National Herbarium staff to complete the data. Moreover, detailed research on the funds of the National Herbarium of Addis Ababa University (ETH) was conducted to validate areas of occurrence and dubious taxonomic aspects. Other unpublished material was also used to complement the existing data. The nomenclature of the taxa and the floristic regions follow the FEE. Those regions are based on the old administrative regions of imperial Ethiopia, and they have already been used for phytogeographical purposes (Friis *et al.*, 2001; Nordal *et al.*, 2001). Within the Horn of Africa, Ethiopia and Eritrea encompass a homogeneous block, having the high plateau (northern and southeastern) in the middle, surrounded by the savanna lowlands. Thus, although two different sovereign countries since 1994, Ethiopia and Eritrea form one ecological unit and so they will be considered in this paper. Endemism will be therefore assigned to those taxa restricted to the administrative boundaries of both countries.

More than 5600 species from 200 families have been reviewed and relevant information has been collected for the endemic flowering taxa. Table 1 shows the number of families and species per volume in the Flora of Ethiopia and Eritrea. For unpublished volumes, the estimations are made based on personal communication from corresponding authors and reviewed manuscripts provided by the Editorial Board. The numbers per volume correspond to species level only.

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[1] References to Ethiopia before 1993 refer to Ethiopia and Eritrea

TABLE 1. Families and species for published and unpublished volumes of Flora of Ethiopia and Eritrea (estimates based on manuscripts and ongoing research).

Volume	**Year of publication**	**Families**	**Species**[1]
2 (part 1)	2000	61	676
2 (part 2)	1995	26	687
3	1989	49	1097
4 (part 1)	2003	13	381
4 (part 2)	2005	1	480
5	in prep. (2006)	24	946
6	1997	38	757
7	1995	1	618
TOTAL		200	5642

[1] Including additional species described since publication

TABLE 2. IUCN categories and criteria assigned to flowering endemic plants of Ethiopia and Eritrea.

2003 Initiative	**CR**	**EN**	**VU**	**NT**	**LC**	**Total taxa**	**Total spp**	**N° spp**	**%**
Criteria	196 (32.7%)	135 (22.5%)	133 (22.2%)	66 (11%)	66 (11%)	596	550	5642	9.7
A	52	19	27						
B1	133	71	68						
B2	155	76	78						
1997 Red List	**Ex**	**Ex/E**	**V**	**R**	**I**	**Total**		**N° spp**	**%**
	0	3	69	46	14	163		6603	2.5

The taxa information included the right citation, chorology, ecology (habitat and altitude) and former IUCN categories. All the taxa were assessed according to the IUCN criteria (IUCN, 2001). To calculate the endemism percentage in the FEE area, all the endemic subspecies have been gathered in the corresponding species level, accounting just for one species. As the first assessment for more than 400 taxa was based on scanty resources and the available information to date, only IUCN criteria A1cd, B1ab and B2ab (i, ii, iii, iv) were applied. The category Extinct has been discarded because consistent information and extensive field work is needed before we can certainly assume a taxon is extinct. Criteria A relates to declining population, with 1c being used when there is an observed, estimated or suspected reduction in the area of occupancy or extent of occurrence; whereas 1d was applied when levels of exploitation were considered as a threat for the species survival. Geographic range size and fragmentation, criteria B, was the most frequently applied, either for severe fragmentation or limited number of locations (1a, 2a) or for continuing decline (1b, 2b). Only the first four qualifiers were used, as the number of mature individuals was unknown. This was considered by the authors the most conservative approach, as information related to other criteria was not available at the time of the study, it was almost absent or it would have required extensive field work. In any case, any person conducting an assessment is expected to use the best available information in combination with inference and projection to test a taxon against the criteria (IUCN, 2003). The IUCN Red List categories are primarily meant to be applied at global level, which happens to be the case in this paper because the taxa are endemic and their range is therefore the global range. Species have been assigned the higher risk categories if known only from a single or few localities, and/or it has not been collected for many years.

3 Results and discussion

3.1 The enlarged Red List of Ethiopia and Eritrea

The red listing exercise presented in this paper contains 596 taxa, species and subspecies, what represents more than a threefold increase compared to the previous 1997 Red List of Ethiopian and Eritrean plants (Walter & Gillett, 1998). This new Red List contains 464 taxa in the higher risk categories (CR, EN, VU), with an increase of 392 threatened taxa compared to the 1997 Red List. These threatened taxa, considered as Globally Threatened Plants due to their endemism, represent 8.2% of total flora. This figure is expected to increase once fern and fern allies are reviewed, and especially when near-endemic species are assessed (those also present in neighbouring countries such as Somalia, Sudan and Kenya). As there are 550 species and 46 subspecies in the Red List, and the total figure for the reviewed flowering flora of both countries is 5642 species, the most updated endemism percentage for Ethiopia and Eritrea is 9.7%. This percent may vary slightly when the remaining families are included, but we shall not expect much variation considering the considerable figure of reviewed species. Table 2 summarizes the IUCN categories assigned to each taxon, and the criteria used in each category.

There are 137 woody taxa (32 trees and 105 shrubs), that represent 13% of the total woody plants estimation for the FEE area (Demel *et al.*, 2001). Following life forms presented in FEE, the non-woody taxa are distributed as follows: 376 herbs, 57 succulents, 12 climbers, 8 epiphytes, 3 weeds, 2 geophytes and 1 submerged herb. Among the species present in the Red List there are crops (*Avena abyssinica*), useful trees (*Erythrina burana, Boswellia pirottae*), spices (*Aframomum corrorima*), medicinal plants (*Pycnostachys abyssinica, Taverniera abyssinica*), weeds (*Pentaschistis trisetoides, Avena vaviloviana*), species not collected for more than 150 years (*Blepharis cuspidata, Phagnalon phagnaloides, Leptagrostis schimperiana, Onobrychis richardii*), species presumably extinct by human action (*Crotalaria boudetii, Crotalaria heterotricha*), dubious species (*Orthosiphon grandiflorus, Pavonia steudneri*), two monotypic endemic genera (*Pseudoblepharispermum bremeri* and *Nephrophyllum abyssinicum*), and species restricted to but widely distributed within the FEE area (*Acanthus sennii, Echinops longisetus, Satureja paradoxa*). The endemic-rich families are *Asteraceae* (98), *Leguminoseae* (67), *Euphorbiaceae* (43) and *Poaceae* (38), which indicates the importance of semi-arid savanna-like areas in the lowlands and afroalpine moorlands in the mountains as major centres of endemism. Numbers of endemics per family are shown in Table 3.

3.2 Biogeography of endemic flowering plants

The study revealed numerous species with extremely narrow distribution (area of occurrence). Species endemic to a single province represent 38.6% of the endemic flora. Actually, more than 200 taxa are just found in one single locality, out of those 72 are only

TABLE 3. The endemic-rich families in FEE.

Asteraceae	98	Urticaceae	3
Leguminosae	67	Aïzoaceae	2
Euphorbiaceae	43	Anacardiaceae	2
Poaceae	38	Araliaceae	2
Asclepiadaceae	31	Balsaminaceae	2
Lamiaceae	30	Callitrichaceae	2
Orchidaceae	29	Capparidaceae	2
Aloaceae	27	Combretaceae	2
Acanthaceae	21	Commelinaceae	2
Scrophulariaceae	16	Eriocaulaceae	2
Convolvulaceae	14	Moraceae	2
Cyperaceae	14	Passifloraceae	2
Crassulaceae	11	Verbenaceae	2
Caryophyllaceae	8	Violaceae	2
Lobeliaceae	8	Zingiberaceae	2
Sterculiaceae	8	Alliaceae	1
Iridaceae	7	Amarathaceae	1
Hyacinthaceae	3	Amarylidaceae	1
Portulacaceae	3	Chenopodiaceae	1
Urticaceae	3	Guttiferae	1
Rubiaceae	7	Hydrocharitaceae	1
Brassicaceae	6	Menispermaceae	1
Ranunculaceae	6	Moringaceae	1
Anthericaeae	5	Plantaginaceae	1
Asphodelaceae	5	Plumbaginaceae	1
Celastraceae	5	Potamogetonaceae	1
Loranthaceae	5	Rutaceae	1
Vitaceae	5	Santalaceae	1
Boraginaceae	4	Sapindaceae	1
Geraniaceae	4	Saxifragaceae	1
Malvaceae	4	Simaroubaceae	1
Polygalaceae	4	Tiliaceae	1
Rosaceae	4	Velloziaceae	1
Araceae	3	Zygophyllaceae	1
Burseraceae	3		

TABLE 4. Altitudinal distribution of endemic taxa in Ethiopia and Eritrea.

	Lowlands		Highlands		Mountains
Ecological zones (Daniel 1977)	Bereha (0–800 m)	Kolla (801–1500 m)	Woina Dega (1,501–2300 m)	Dega (2301–3000 m)	Wirch (>3000m)
Restricted to this range	25	28	24	44	52
Total*	44	149	241	67	55

*42 taxa with no altitudinal data and thus the total sample is restricted to 554 known from the type specimen and 13 have not been collected since the 19th Century, with at least seven presumably extinct (*Crotalaria boudetii, Crotalaria heterotricha, Crotalaria trifoliolata, Kalanchoe angustifolia, Stachys hypoleuca, Cirsium straminispinum, Vernonia buchingeri*). Sidamo and Harerge are the provinces with the highest figures and relative weight (% of total taxa present in the province) of stenochorous species, called province-restricted taxa (see Table 5). These data illustrate the pronounced narrow endemism among endangered taxa in the region, specially in the lowlands. According to the altitudinal distribution shown in Table 4, there are 193 taxa present in the lowlands, with 53 being narrowly restricted; 308 in the highlands up to 3000 m, with 68 restricted to that range; and 52 above 3000 m (afroalpine endemics according to Hedberg, 1957).

Shewa (SU) and Gondar (GD) are the floristic regions harbouring the highest numbers of endemic taxa, followed by Sidamo (SD) and Bale (BA). Sidamo and Harerge (HA) have the highest figures of narrow endemics, with Bale and Gondar falling far behind; whereas Arsi (AR) has by far the highest endemic richness per area (see Table 5). It is worth stressing the importance of Arsi as an important area for plant richness harbouring 103 endemic taxa, with 4 montane species restricted to its administrative boundaries (*Eriocaulon aethiopicum, Pennisetum thulinii, Trifolium chilaloense*, and *Bidens microphylla*). Welo (WU), on the contrary, appears as an anomalously poor region with only one narrow endemic found in the intermediate belt between the lowlands and the highlands (*Indigofera cana*), extremely low endemic richness and the lowest taxa richness. More oddly, Welo has the lowest afroalpine endemic richness in the FEE area, despite the fact of having more than 4000 km^2 above 3000 m and three peaks above 4000 m, representing 18% of total for FEE area (Yalden, 1983). The explanation could be this apparently coldspot has been overlooked by 19th and 20th Century botanists (Moggi, 1976), but it surely holds an important afroalpine flora yet to be discovered in mountains such as Abune Yosef, Delanta and Amba Farit, and therefore deserves further collecting trips and biogeographical research. Recent research in Abune Yosef has contributed to the taxonomy of afroalpine *Senecio* (Ortiz & Vivero, 2005).

Shewa, with a medium size area and 43% of land above 2000 m, contains more endemic taxa than any other floristic region. Its pivotal position in the core of the FEE area, comprising semi-arid, savanna, highland and afroalpine ecosystems, enables Shewa to become a reservoir of endemic plants as well as highway for afroalpine plant movements (northwards and southwards) and subsequent speciation, as well as displacement along the Rift Valley. That explains why Shewa stands for the second place in plant diversity, just after Sidamo (Friis *et al.*, 2001). Nevertheless, Shewa still lacks protected areas to cover this rich flora (Nordal *et al.*, 2001). Finally, as shown in Table 6, Gondar and Sidamo accumulate more than half of total endemics (344) thus outlining the importance of being centres of endemism, mainly Simien mountains and the V-shape area Moyale-Mega-Yabello and the Liben Plains (see below). The last figure reaches up to 70% (422 taxa) when Shewa is taken into account, thereby demonstrating the importance of the North-South axis through the Highlands as a major centre of endemism in the Horn of Africa, with Shewa at its heart.

3.3 Local centres of endemism

Based on the data contained in the Red List of Endemic Flowering Taxa, and fine-tuning the broad-based figures for each floristic region displayed above, nine local centres of endemism have been considered in Ethiopia and Eritrea. The centres of endemism are specific areas displaying considerable numbers of endemic species, and they are the following: Simien Mountains, Bale Mountains, Agere Maryam-Yabello-Mega and Harerge Highlands in the high plateau, and Liben Plains, Bale Eastern Plains, Jijiga Lowlands, Borana Lowlands and Ogaden Desert in the lowlands. It is not the intention

TABLE 5. Number of endemic taxa in Ethiopia-Eritrea per administrative provinces[1]. Abbreviations for administrative provinces follow FEE.

	ER	**AF**	**AR**	**BA**	**GD**	**GG**	**GJ**	**HA**	**IL**	**KF**	**SD**	**SU**	**TU**	**WG**	**WU**
Total endemic taxa	100	4	103	173	208	59	122	138	47	100	182	229	143	78	58
Area (in 1000 km^2)	125.7	85.4	21.5	131.2	80.2	39.5	62.2	261.2	53.5	53.5	111.7	82	60.2	77.2	93.5
Endemic Richness (endemics/10,000 km^2)	7.9	0.4	47.9	13.1	25.9	14.9	19.5	5.2	8.7	18.6	16.2	27.9	23.7	10.0	6.2
Taxa Richness[2] (species/10,000 km^2)	84.4	–	243.2	62.4	107.6	193.4	93.4	42.6	108.2	166.7	127.3	151.8	154.3	72.6	39.3
Province-restricted taxa	15	0	4	27	26	5	4	43	2	4	54	20	21	5	1
% over total province endemics	15	0	3.8	15.6	12.5	8.4	3.2	31.1	4.2	4	29.6	8.7	14.6	6.4	1.7
Province endemic richness (endemics/10,000 km^2)	1.2	0	1.8	2.0	3.2	1.2	0.6	1.6	0.3	0.7	4.8	2.4	3.4	0.6	0.1

[1] Eritrea is treated as a separate unit.

[2] Based on Friis *et al.* (2001) with data from published FEE volumes (2,959 taxa)

TABLE 6. Cumulative percentage of endemic taxa per different floristic regions pairs.

Accumulative %	N° endemic species	% total endemic species
GD-SD	344	57.8
SD-SU	343	57.6
SU-BA	319	53.5
GD-BA	317	53.1
GD-SU	315	52.8
GD-SU-SD	422	70.5

of this paper to be exhaustive while determining a local-level centre of endemism, but we aim at refining the generally-recognized centres of endemic plants, providing updated figures to help towards formulating conservation strategies, and planning protected areas for these micro-hotspots. Minor local centres of endemism in Tigray, Gojam (Nordal *et al.*, 2003), Ilubabor or Kefa have not been considered in this paper.

3.3.i Bale and Simien Mountains as major afroalpine centres of endemism in Ethiopia

There are 55 afroalpine endemic taxa (49 species and 6 subspecies), mostly herbs belonging to *Asteraceae* (17) and *Poaceae* (8), which adds 41 taxa to previous accounts (Hedberg, 1994). Gondar and Bale hold the highest numbers, 33 and 27 respectively, as expected by the importance of Simien and Bale Mountains as centres of endemism. However, when considering the afroalpine endemic richness, as the number of endemics per 1000 km^2 of area above 3000 m, Tigray stands high with 7 endemics in 350 km^2, followed by Gondar and Harerge. Welo however presents the lowest afroalpine endemics density. Simien Mountains harbour nine afroalpine taxa found only in those mountains, whereas Bale has only three. Furthermore both mountains also hold a rich afromontane flora in the *Juniperus* and *Erica* woodlands as well as in the lower altitude closed forests. Appendix 1 shows a preliminary list of endemic plants present in those two centres of endemism.

Simien Mountains, a World Heritage Site and National Park, stands as the most important centre of endemism for montane and afroalpine plants in Ethiopia, as it has 120 endemic taxa (with 21 plants narrowly restricted to that mountain). Bale Mountains, a National Park widely known for its endemic mammals and the Sanetti Plateau and Harenna Forest, holds 111 endemic plants (with 10 restricted to its limits). Bale Mountains National Parks, with an extension of 4400 km^2 and ranging from 1500 m to 4377 m, could be considered as a micro-hotspot, as one can find within its boundaries 18.8% of endemic plants, 26.5% of endemic mammals and 53.3% of endemic birds of Ethiopia and Eritrea. Endemic plant density is over 2.5 taxa per 100 km^2. Despite its legal protection, it suffers from a worrisome set of threats to its survival, such as human invasion by refugees, forest fires, illegal grazing, forest encroachment by cultivated land or animal diseases. There are 60 endemic taxa shared by both mountains, with 5 found nowhere else.

3.3.ii Southern Highlands

The Agere Maryam-Yabello-Mega centre (1500–2200 m) is confined to a long strip from the highland flat areas near Agere Maryam in the north to the gentle semi-arid slopes in the south. There are 18 taxa restricted to this area (see Appendix 2) distributed along the hills, slopes, *Acacia-Commiphora* woodlands and grasslands that cover the lower highlands. The only protected area is the Yabello Sanctuary (2540 km^2), designed to protect two endemic threatened birds, the Abyssinian Bush Crow and the White-tailed Swallow.

The Harerge Highlands (1500-2800 m) are located between Dire Dawa, Harar and Jijiga and present several minor peaks such as Mount Hakim and Mount Gara-Mulata. There are 14 taxa (see Appendix 2) in this area. The landscape is formed by a combination of dry evergreen montane forests (*Juniperus*, *Olea*), with *Acacia-Commiphora* woodlands and grasslands at lower altitudes. This area is considered as a major centre of endemic Aloe species, where a number of transgressors from lowlands to highlands are found (Sebsebe *et al.*, 2001). The combination of high altitude and low rainfall has acted as a speciation driving force.

3.3.iii South Plains and Southeastern Lowlands

The Jijiga Lowlands centre of endemism is formed by relatively flat areas in the lower contour of Jijiga lowlands up to Degeh Bur, between 800–1500 m. It holds the only populations of 11 extremely narrow plants (see Appendix 3). The habitat is largely occupied by *Acacia-Commiphora* bushland characterised by drought tolerant trees and shrubs, which have either deciduous leaves or leathery persistent leaves. The understorey mainly consists of shrubs, perennial herbs and grasses. Some of these populations could be included within the limits of the gazetted but actually unprotected Babille Elephant Sanctuary.

The Bale Eastern Plains, ranging from 1200 to 1600 m, have 13 narrowly restricted taxa (see Appendix 3). This local centre embraces a relatively sharp boundary between the lowlands and the elevated highlands, having suffered dramatic changes in vegetation and climate during the Quaternary. This area, south and south east of Bale Mountains National Park, has been pointed out as the gravitational centre of lilioid geophyte endemics of Ethiopia (Nordal *et al.*, 2001). This area has been fairly inaccessible for quite a while and therefore barely collected. Most collections have been done around S of Omar caves (type locality for 6 endemic taxa, see Appendix 3). This limestone valley is covered with shrubs, small trees (*Acacia-Kirkia-Commiphora*) and climbers.

The Liban Plains are extensive areas of comparatively flat land, lying between the Genale and Dawa rivers (EWNHS, 1996), with Negele woodlands as the northern border and Bogol Mayo as southern limit. The altitude starts at 1000 m at the edge of the Genale river gorge and rises gently to over 2000 m in the forest located on the escarpment. The landscape is formed by *Acacia-Commiphora* woodland and bushland, with *Combretum*, *Boswellia*, *Barbeya* and *Kirkia* as common species. Soils can be rocky, calcareous, granitic or limestone. This important local micro-hotspot has 22 endemic taxa (see Appendix 3), plus the only populations of two narrow endemic birds (Degodi Lark and Sidamo Lark). Overgrazing by cattle, human pressure by internal displacement due to ethnic clashes, and recurrent persistent droughts are serious threats to this open area. The road between Negele and Bogol Mayo has been the type locality for at least 10 narrow endemics (marked with * in Appendix 3).

The Borana Lowlands centre has the lowest endemic plants (6 taxa seen in Appendix 4), but it has been considered due to its clear distinction from surrounding centres. It lies between 300–1000 m, but it transgresses the Kenyan border and extends to northern Moyale province, thereby comprising many more near-endemic species not included in this Red List. It is covered by open vegetation with scattered shrubs, small trees and annual herbs, and succulents.

The Ogaden Desert, consisiting of the greater part of Somalia and the northern strip of Kenya (200–800 m), has been traditionally considered as a regional centre of plant and animal endemism (Kingdon, 1989; Davis *et al.*, 1994). This area is commonly called the Somali-Masai biome. The Ethiopian side contains 27 endemic taxa in Harerge (and Bale) provinces (Appendix 4), with one or few scattered localities for each species. The Ogaden area has been a stable habitat for thousands of years, thus it contains many arid species in the limestone woodlands and shrublands, many of which are endemic. The habitats are mostly defined by rainfall and vegetation types.

4 Conclusions

The Red List of Endemic Flowering Plants is of relevance to the biogeography and conservation of the flora of Ethiopia and Eritrea. This preliminary Red List, where only endemics have been assessed, adds considerable taxa to previous lists and accounts: 41 new afroalpine taxa, 115 new Red List trees and shrubs, and 435 new taxa. Nine local centres of endemism are proposed and preliminary endemic plants within their boundaries are listed. There is a remarkable pattern of high endemic density found in three local centres of endemism situated along the southern limit of the Highlands, a transitional area between two phytogeographical zones: the Ethiopian Highlands and the Somali-Masai biome (White, 1983). This transitional zone runs parallel to the Southern Highland block from south to northeast and contains the Jijiga Lowlands, the Bale Eastern Plains and the Liban Plains, and to a lesser extent parts of the Agere Maryam-Yabello-Mega area and the Harerge Highlands. This longitudinal area, ranging between 1000 m and 2000 m, embraces the altitudinal belt where the species richness and endemism is highest in Ethiopia (Friis *et al.*, 2001).

Although the work undertaken has been considerable, the remaining activities request a coordinated effort from different research and financial institutions to place the Ethiopian flora on the world map of conservation and biodiversity. Extensive field work needs to be done to collect data chorology and conservation. The near-endemic plants (more than 600) need to be assessed, and the most threatened endemic plants (many of them only known from the type specimen or not collected since 1870) require immediate assessment in the field for implementing conservation measures.

We have been recently informed that an ongoing exercise is being carried out by Conservation International to assess the two main biomes present in the Horn of Africa, the Ethiopian Highlands and the Somali-Masai lowlands for their consideration as world hotspots. Based on the information provided in this paper, plus the more than 300 near-endemics shared with Somalia and Kenya and the 600 taxa restricted to Somalia (Thulin, 1994), we could reasonably assume that the Horn of Africa holds more than 1500 endemic plants. The high numbers of endemic species (plants, mammals and birds), the plant richness (more than 7000 species) and the high habitat modification due to natural disasters, civil strife and cattle pressure may entitle for any of those two biomes to be upgraded to the selected group of world's major hotspots.

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APPENDIX 1. Endemic taxa in two important local centres of plant endemism in Ethiopia.

Simien Mountains

Acacia negrii
Agrostis diffusa
Aloe percrassa
Aloe steudneri
Anarrhinum forskaohlii subsp. *abyssinicum*
Anchusa affinis
*Aphanes bachiti**
Argyrolobium schimperianum
Astragalus atropilosulus subsp. *abyssinicus*
Becium grandiflorum
Ceropegia convolvuloides
*Ceropegia sobolifera**
Chenopodium ulbrichii
Cirsium straminispinum
Clematis burgensis
Clematis longicaudata
Convolvulus steudneri
*Conyza messeri**
Crepis achyrophoroides
Crepis tenerrima
Crotalaria intonsa
Cycniopsis humilis
Cyperus atronervatus subsp. *atronervatus*
Dianthus leptoloma
Disperis galerita
Disperis crassicaulis
*Disperis meirax**
Drimia simensis
*Echinops buhaitensis**
*Festuca gilbertiana**
Festuca macrophylla
Galium boreo-aethiopicum
Habenaria perbella
*Habenaria platyanthera**
Helichrysum horridum
Helichrysum sclerochlaenum
Holothrix unifolia
Hypagophytum abyssinicum
*Inula arbuscula**
Isolepis omissa
Kalanchoe quartiniana
Leucas stachydiformis
Lobelia schimperi

Bale Mountains

Agrostis gracilifolia subsp. *parviflora*
Alchemilla haumanii
Alopecurus baptarrhenius
Arisaema mooneyanum
*Bidens mesfinii**
Cineraria abyssinica
Crotalaria agatiflora subsp. *erlangeri*
Crotalaria exaltata
Cyperus holostigma
Chlorophytum ducis-aprutii
Droguetia iners subsp. *pedunculata**
Erucastrum abyssinicum
Erucastrum meruense subsp. *balense*
Euphorbia dumalis
Euryops antinorii
*Euryops prostratus**
*Gladiolus balensis**
Gladiolus longispathaceus
Haplocarpha hastata
Helichrysum elephantinum
Helichrysum gofense
Helichrysum harennensis
Inula confertiflora
Justicia schöensis
Kanahia carlsbergiana
Kotschya recurvifolia subsp. *aetiopica*
Lavatera abyssinica
Ledebouria urceolata
Lobelia achrochila
Lobelia erlangeriana
Lobelia scebelii
*Lobelia tripartita**
Maytenus addat
*Maytenus harenensis**
Panicum ruspolii
*Pentarrhinum balense**
Poa hedbergii
Rhus glutinosa subsp. *neoglutinosa*
Rubus erlangeri
*Sedum baleensis**

Both mountains

Acanthus sennii
Aeollanthus abyssinicus
Artemisia schimperi
Astragalus atropilosulus subsp. *atropilosulus*
Becium formosum
Bidens macroptera
Bothriocline schimperi
Callitriche favargeri
*Callitriche hedbergiorum***
Chiliocephalum schimperi
Chiliocephalum tegetum
Cineraria sebaldii
Cirsium schimperi
Conyza abyssinica
*Conyza nana***
Conyza spinosa
Crassocephalum macropappum
Cynotis polyrrhiza
Echinops longisetus
Erophila verna subsp. *macrosperma***
Erucastrum pachypodum
Ficinia clandestina
Habenaria lefebureana
*Herniaria abyssinica***
Hyparrhenia arrhenobasis
Impatiens tinctoria subsp. *abyssinica*
Kalanchoe petitiana
Kalanchoe schimperiana
Kniphofia foliosa
Kniphofia isoetifolia
Kniphofia schimperi
Launaea rueppellii
Lobelia rhynchopetalum
Mikaniopsis clematoides
Pennisetum humile
Pentaschistis trisetoides
Plectocephalus varians
Plectranthus garckeanus
Poa simensis
Polystachya caduca
Pseudognaphalium melanosphaerum
Ranunculus simensis

APPENDIX 1. Continued.

Simien Mountains	**Bale Mountains**	**Both mountains**
*Maytenus cortii**	*Sedum glomerifolium**	*Ranunculus tembensis***
Otostegia tomentosa subsp. *steudneri*	*Sedum mooneyi*	*Sagina abyssinica* subsp. *abyssinica*
*Paronychia bryoides**	*Senecio balensis*	*Satureja paradoxa*
*Pennisetum beckeroides**	*Solanecio harennesis**	*Senecio fresenii*
Pennisetum longistylum	*Stachys alpigena* subsp. *longipetala*	*Senecio myriocephalus*
Pennisetum uliginosum	*Stachys balensis*	*Senecio ochrocarpus*
*Phagnalon phagnaloides**	*Stolzia grandiflora*	*Senecio schimperi*
*Poa pumilio**	*Tragia ashiae*	*Senecio schultzii*
Polygala rupicola	*Trifolium spananthum*	*Senecio steudelii*
Ranunculus districts	*Uebelina kigesiensis* subsp. *ragazziana*	*Senecio unionis*
Roeperocharis alcicornis	*Vernonia tewoldei*	*Sisymbrium maximum*
*Rosularia semiensis**		*Solanecio gigas*
*Rytidosperma grandiflora**		*Sonchus melanolepis*
*Sagina brachysepala**		*Thalictrum schimperianum*
Satureja punctata subsp. *ovata*		*Thymus schimperi* subsp. *schimperi*
Saxifraga hederifolia		*Trifolium calocephalum*
Sedum epidendron		*Urtica simensis*
Senecio farinaceus		*Vernonia rueppellii*
Senecio nanus		
Senecio pinnatipartitus		
*Snowdenia mutica**		
Sparmannia macrocarpa		
Stachys hypoleuca		
Thymus serrulatus		
Trifolium bilineatum		
Trifolium decorum		
Trifolium mattirolianum		
Trifolium schimperi		
*Verbascum benthamianum**		
*Verbascum pubescens**		
*Verbascum scabridum**		
Verbascum sedgwickianum		
*Vernonia buchingeri**		
Vernonia filigera		
Vernonia leopoldii		
Veronica simensis		

* Restricted to that mountain
** Present on both mountains.

APPENDIX 2. Endemic taxa present in two local centres of plant endemism located in the Southern Highlands.

Agere Maryam-Yabello-Mega **1500–2200 m**	**Harerge Highlands** **1500–2800 mm**
Aloe yavellana	*Aloe harlana*
Asystasia ammophila	*Aloe megalacantha* subsp. *alticola*
Athroisma boranense	*Ceropegia ellenbeckii*
Barleria longissima	*Crotalaria jijigensis*
Bidens zavattarii	*Cyphostemma burgeri*
Conyza megensis	*Euphorbia rubella*
Crotalaria sacculata	*Gladiolus calcicola*
Cyperus costatus subsp. *sidamoensis*	*Gladiolus lithicola*
Cystostemon ethiopicus	*Hildebrandtia diredawaensis*
Gladiolus boranensis	*Lotus lalambensis*
Hirpicium beguinotii	*Pachycymbium sprengeri* subsp. *ogadense*
Justicia diclipteroides subsp. *megaensis*	*Pelargonium hararense*
Melhania beguinotti	*Rhynchosia erlangeri*
Senecio aequinoctialis	*Stachys jijigaensis*
Tragia triumfettoides	
Trifolium somalense	
Vernonia printzioides	
Vernonia yabelloana	

APPENDIX 3. Endemic taxa in three centres of plant endemism located in the rich intermediate altitudinal zone of Southern Ethiopia (800–2000 m).

Liben Plains **1000–2000 m**	**Bale Eastern Plains** **1200–1600 m**	**Jijiga Lowlands** **800–1500 m**
*Cladostigma nigistiae**	*Adenia pulcrha*	*Ceropegia erergotana*
*Convolvulus vollesenii**	*Chlorophytum pterocarppum***	*Euphorbia burgeri*
Crotalaria fallax	*Commiphora monoica***	*Euphorbia dalettiensis*
Dicoma aethiopica	*Convolvulus gilberti***	*Euphorbia piscidermis*
Endostemon glandulosus	*Crotalaria trifoliolata***	*Euphorbia somalensis*
*Erythrococca uniflora**	*Dicoma aethiopica*	*Gutenbergia somalensis*
Euphorbia bittataensis	*Euphorbia baleensis***	*Helichrysum jijigaensis*
*Euphorbia cryptocaulis**	*Euphorbia omariana***	*Merremia dimorphophylla* subsp. *ogadensis*
Euphorbia ellenbeckii	*Euphorbia sareciana*	*Rhynchosia ramosa*
Euphorbia furcatifolia	*Hildebrandtia aloysii*	*Stylochaeton oligocarpum*
Euphorbia gymnocalycioides	*Melhania somalensis*	*Vernonia dalettiensis*
Euphorbia uniglans	*Polygala erlangeri*	
*Gladiolus negeliensis**	*Tragia crenata*	
*Hibiscus boranensis**		
*Hybanthus puberulus**		
*Jatropha horizontales**		
*Maerua boranensis**		
Panicum vatovae		
*Phyllanthus borenensis**		
Polygala mooneyi		
*Ruellia boranica**		
Wellstedia filtuensis		

* Road between Negele and Filtu
** Around S of Omar caves area

APPENDIX 4. Endemic taxa of two centres of plant endemism located in semi-arid lower altitudes (below 1000 m).

Borana Lowlands 300–1000 m	**Ogaden Desert 200–700 m**
Blepharis cuspidata	*Acacia bricchettiana*
Cadaba divaricata	*Acacia pseudonigrescens**
Euphorbia doloensis	*Aloe bertemariae*
Euphorbia fissispina	*Aneilema grandibracteolatum*
Indigofera curvirostrata	*Boswellia ogadensis*
Justicia vixspicata	*Cadaba divaricata*
	Crotalaria boudetii
	Crotalaria heterotricha
	Cyperus maculatus subsp. *ogadensis*
	Echidnopsis jacksonii
	Erythrophysa septentrionalis
	Euphorbia ogadenensis
	*Euphorbia tetracantha**
	Fagonia hararensis
	Hermannia erlangeriana
	Indigofera ellenbeckii
	Indigofera kelleri
	Kleinia gypsophila
	Merremia subpalmata subsp. *tenuisecta*
	Merremia warderensis
	Monadenium shebeliensis
	Orthosiphon grandiflorus
	Plicosepalus ogadenensis
	Pseudoblepharispermum bremeri
	Pseudolithos gigas
	Seddera simmonsii
	*Xerophyta rippsteinii**

* Bale narrow endemic

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CONSERVATION OF THE PLANT DIVERSITY OF WESTERN CAMEROON: A DARWIN INITIATIVE PROJECT

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Abstract

Western Cameroon (SW and NW Provinces) has been shown to rate highest in tropical Africa in terms of numbers of vascular plant species per degree square. Many of these species are locally endemic and threatened with extinction from conversion of forest to agricultural land. This paper records progress of a three year Darwin Initiative (UK Government-funded) project to catalogue and map the plant diversity of this largely-forested area using both specimens from new field inventories and historic specimens. The conservation status of these species is assessed using IUCN 2001 Red Listing criteria. The results are already being used in making decisions on gazettement of areas for conservation and for allocation of resources to manage these areas.

Résumé

Le plus important taux de diversité en nombre d'espèces de plantes vasculaires a été observé dans l'Ouest du Cameroun. Beaucoup de ces espèces sont localement endémiques et menacées d'extinction par la conversion des forêts en terres cultivables. Cet article résume une étude de trois ans grâce à l initiative Darwin (Subventionnée par le gouvernement anglais) pour cataloguer et cartographier la diversité des plantes de cette zone largement boisée, utilisant des spécimens provenant de nouvelles expéditions et de spécimens provenant de collections historiques. Le statut de conservation de ces espèces est donné en accord aux critères IUCN 2001 pour la création des listes rouges. Ces résultats ont déjà servi dans la prise de décisions pour la création de liste des aires de conservation ainsi que pour l'allocation des ressources pour le fonctionnement de ces zones.

Key words: biodiversity, Cameroon, conservation, Darwin Initiative, threatened species

1 Introduction

This paper focuses on conservation and threatened species aspects of a four year project funded primarily by the Darwin Initiative of the British Government, with fieldwork supported by Earthwatch. The main partners in the 'Conservation of the Plant Diversity of Western Cameroon' project, now drawing to a close, are the Royal Botanic Gardens, Kew and the National Herbarium of Cameroon (HNC), Yaoundé. The project is linked with six protected area-based conservation organizations, including Limbe Botanic Garden at Mt Cameroon, which provided the inspiration for the current project (Cable & Cheek, 1998). Other collaborations have been established with several international NGOs operating in Cameroon, including BirdLife International, San Diego Zoological Society's Conservation and Research on Endangered Species (CRES) and the World Conservation Society (WCS). Staff from over 15 Cameroonian NGOs have also been involved in fieldwork and have been trained in botanical surveying and inventory techniques and plant identification skills.

1.1 Why western Cameroon?

1.1.i Biodiversity

The Flora of West Tropical Africa (FWTA) (Keay & Hepper, 1954–1972) treats about 8,000 species. Western Cameroon (Northwest and Southwest Provinces) comprises only about 2% of the FWTA land area, but is home to more than 4,000 species (see Fig. 1 and Cheek *et al.*, 1996), i.e. >50% of the species known in the area of the whole flora. This exceptional concentration of plant species is most clearly shown in an Africa-wide context by Barthlott *et al.* (1996). In their world map of global biodiversity, regions of the world are divided into 10 Diversity Zones (DZs), quantified by the number of species per degree square (± 10,000 km^2). Western Cameroon merits inclusion in DZ 9, the second highest zone, with 4000–5000 species per degree square, a total unparalleled in tropical Africa and only equalled elsewhere in Africa by the Cape Floristic Province of South Africa.

1.1.ii Threats to natural vegetation and narrowly endemic taxa

Many of the species in Western Cameroon are endemic and restricted to forests threatened by logging and conversion to both industrial scale plantations and small-scale agricultural holdings. GIS analysis of satellite imagery (Moat, 2000) has shown that in one of the worst affected locations, at Mt Oku, NW Province, forest cover was reduced by 25–30% between 1987 and 1995. Cheek *et al.* (2004) calculated a percentage of endemism for Kupe-Bakossi of nearly 5%. Conservation action is urgently needed.

2 Project outputs for conservation

2.1 Conservation checklists

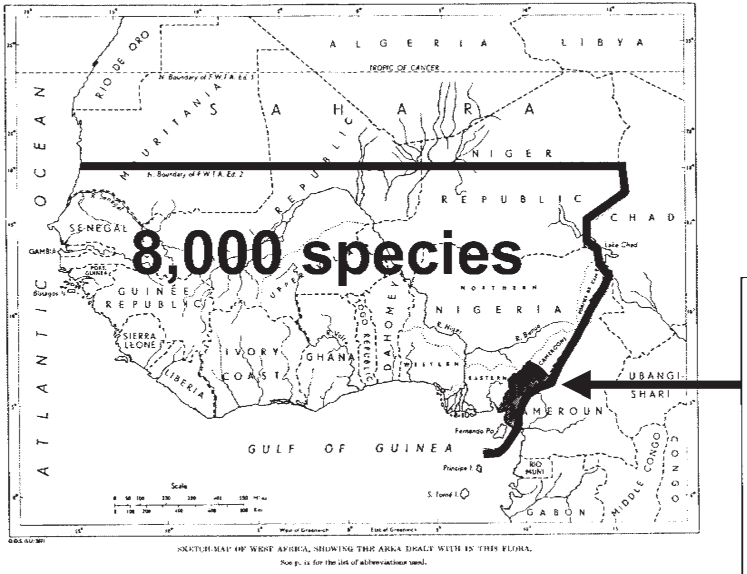
Conservation checklists of plant taxa for individual protected areas are the main products of the project, and three have recently been published in this series, based on the model of Cable & Cheek (1998): Cheek *et al.* (2000), Cheek *et al.* (2004) and Harvey *et al.* (2004).

The main user groups are:

i) Managers of National Parks and other protected areas – they need information on Red Data plant species and total plant diversity, with detailed habitat conservation assessments.
ii) The Government of Cameroon, to help them comply with their commitment to the Convention on Biological Diversity.

Below is a sample entry from one of our most recent checklists (Cheek *et al.*, 2004: 250). For each taxon at species level and below, data are provided for: generic name, species name, author of plant name, place of publication (if the name has been published since completion of FWTA), a short description to assist with field identification, typical habitat,

Flora of West Tropical Africa



8,000 species

Western Cameroon
4,000 $^+$ species
in c. 2% of the
land area

FIG. 1. The area of the Flora of West Tropical Africa, showing concentration of species in western Cameroon. B.J. Pollard.

altitudinal range within the checklist area, distribution, chorology (adapted from White, 1983), an IUCN conservation rating, and, most importantly, the specimens on which these are based which provide details of the collector's name and number, often with phenological information and the date of collection. Further notes are often provided for taxonomic points, the finer details of distributional data, or perhaps to indicate that the determinations made are not necessarily certain as the specimen(s) cited may be sterile or lack some generative stages (flowers or fruits). Where known, local names and uses are provided, following the standards proposed by Cook (1995), except for medicines which are only listed under Cook's level 1 headings (the least-detailed), to protect the rights of the local people over such sensitive information.

Impatiens letouzeyi Grey-Wilson
Fl. Cameroun 22: 25 (1981).
Epiphytic herb 50–150 cm; leaves alternate, oblong-elliptic, 14 × 5 cm; peduncles 0.4 cm, 1–4-flowered; pedicels 4 cm; flowers pink, face concave, c. 6 × 4 cm; lateral sepal 1 cm, dentate; spur c. 6 mm, tightly coiled. Forest; 1200–1350 m.
Distr.: Cameroon. (Narrow endemic).
IUCN: EN
Edib: *Etuge* 4092 fl., 1/1998; **Kodmin:** *Etuge* 4086 fl., 1/1998; *Gosline* 59 fl., 1/1998; **Lake Edib:** *Satabie* 1123 fl., 2/1998; **Mwambong:** *Cheek* 9371 fl., 10/1998.
Note: known only from the Bakossi Mts.
Local name: Fume. **Uses:** MEDICINES (Gosline 59).

2.2 Red Data assessments

A major chapter on Red Data taxa is included in the introductory part of each of the checklists to provide detailed information on each threatened species to assist conservation project managers. These typically include: plant name and author(s), IUCN rating, range, habitat, threats, management suggestions, a description (not always included) and, where possible, an illustration by way of a line drawing or colour photograph. Cheek *et al.* (2004) includes 9 line drawings and 71 colour photographs of vascular plant taxa of conservation importance.

About 300 assessments of threatened taxa have been published as part of the project, using the IUCN (2001) criteria, mostly for taxa that have not previously been assessed. Some are updates of earlier assessments made using the 1994 criteria (IUCN, 1994). These assessments have been accepted by IUCN (see www.redlist.org). It is believed the project is the main source of Red Data assessments for plants in Cameroon and west-central Africa in general. Most of the assessments have been published in the conservation checklists, but others are given in papers describing new species (see 2.3 below). In addition to the threatened species assessments mentioned above, about 2400 further assessments have been made for taxa categorised as Near Threatened or of Least Concern, and one taxon has been categorised as Data Deficient. We intend to submit these to IUCN for evaluation and hopefully inclusion in the 2006 Red List.

2.3 Publication of new species/taxonomic research

Another significant output of the project has been the ongoing description of new taxa. These descriptions have usually appeared in peer-reviewed botanical journals, including Brittonia, Lindleyana and the Nordic Journal of Botany, and particularly in Kew Bulletin. As of November 2004, 40 new taxa (including two new genera*), have been published, a further seven have been submitted for publication and five more are in preparation for publication as a result of research conducted during this project. These vary enormously in habit, and are detailed in Table 1 in chronological order by the year in which they were published. The protected area or target forest from which they are known to occur is listed under 'Region'.

Taxonomic research: a case study – *Dovyalis cameroonensis* (Flacourtiaceae)

A recent collaborative taxonomic project was conducted with Rita Lemngan Ngolan, formerly an ecomonitor at BirdLife Internatonal's Kilum-Ijim Forest Project in NW Province, Cameroon. She is currently studying for an MSc. in Tropical Forest Management at Dresden University, Germany. The BirdLife-managed project helped Kom, Nso and Oku villagers to manage the habitats around Mount Oku, which at 3011 m is the second highest mountain in west-central Africa, and supports the largest surviving montane forest block in the province. Rita completed the 2003 International Course in Plant Conservation Techniques at RBG, Kew, and her course project was to investigate the taxonomic and conservation status of 10 specimens of *Dovyalis* (Flacourtiaceae) gathered during Kew-HNC expeditions to Mt Oku since 1996. They were previously identified as *Dovyalis* sp. nov.? and considered to represent a potential Red Data species (Cheek *et al.*, 1997). Later they were included in the conservation checklist for that area (Cheek *et al.*, 2000). This investigation included a reassessment of *Dovyalis spinosissima* Gilg, which proved to be a complex of three distinct species. The Mt Oku specimens were shown to represent a species new to science, named *Dovyalis cameroonensis* ined. (Cheek & Ngolan, in prep.).

Justin Moat, of Kew's GIS department, mapped the geo-referenced specimens of this species, and a provisional IUCN conservation assessment was calculated using a novel automated GIS-based technique (Fig. 2; Willis *et al.*, 2003). Eventually this technique will be used to screen all the correctly named and geo-referenced taxa in the western Cameroon specimen database to extract a candidate Red List for assessment.

2.4 Conservation posters

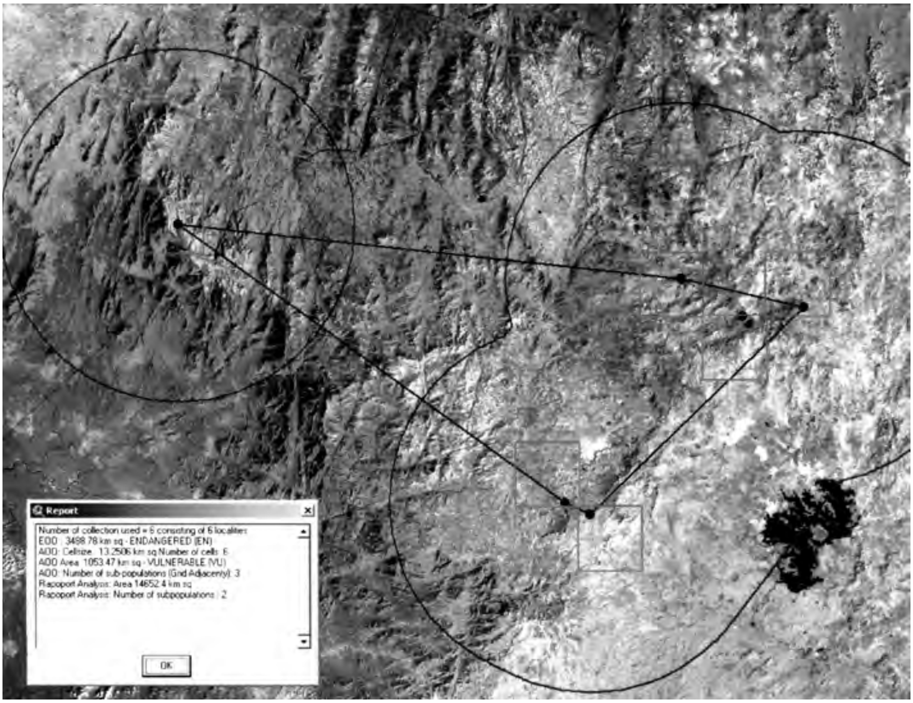
To raise awareness and increase the impact of conservation issues on people living near the protected areas in which the project has been working, a series of 16 species-specific conservation posters have been published (Fig. 3; www.kew.org/scihort/wta/index.html). Each A3 colour poster features a narrowly distributed Red Data species including, where available, a colour photograph, any known local names and uses, a distribution map and short notes explaining the discovery, rarity and uniqueness of the plant. These posters have been found to be very effective by managers of protected areas in explaining the conservation message to local people. In western Cameroon, particularly in SW Province where forest tracts are still extensive, a good, industrious individual will traditionally prove his worth by 'reclaiming' agricultural land from the forest, as the latter is often seen as being of little value, seemingly unlimited in scale and uniform in structure. The need for conservation is therefore not obvious, nor easily understood by rural villagers. Many plant species are unique to tribal village areas or adjoining forests, and the inhabitants may indeed already know of them. The fact that 'their forest' contains one or more unique species comes as a revelation to most villagers and raises local pride as well as promoting an awareness for the need to conserve at least part of it. When a new, narrowly distributed, species has been discovered by botanists, often a toponym is given to recognise its place of origin (e.g. *Coffea montekupensis*, the 'Mount Kupe Coffee', or *C. bakossii*, the 'Bakossi Coffee'). This fosters an increased local-community identity with particular threatened or endemic species.

TABLE 1. Conservation of the plant diversity of western Cameroon: new taxa described.

Scientific name	**Plant family**	**Year**	**Life form**	**Region**
Belonophora ongensis	Rubiaceae	2000	Rainforest tree	Mt Cameroon, Korup N.P., Kupe-Bakossi
Indigofera patula subsp. *okuensis*	Leguminosae	2000	Montane grassland shrub	Kilum-Ijim
Ancistrocladus grandiflorus	Ancistrocladaceae	2000	Rainforest climber	Mt Cameroon
Oxyanthus okuensis	Rubiaceae	2000	Cloud forest tree	Kilum-Ijim
Aphelariopsis kupemontis	–	2000	Rainforest fungus	Kupe-Bakossi
Chassalia laikomensis	Rubiaceae	2000	Cloud forest tree	Kilum-Ijim
Eriocaulon bamendae	Eriocaulaceae	2000	Montane grassland herb	Kilum-Ijim
Pentarrhinum abyssinicum subsp. *ijimense*	Asclepiadaceae	2000	Cloud forest climber	Kilum-Ijim
Bafutia tenuicaulis var. *zapfackiana*	Compositae	2000	Montane grassland herb	Kilum-Ijim
Plectranthus cataractarum	Labiatae	2001	Cloud forest herb	Mt Cameroon, Kupe-Bakossi
*Korupodendron songweanum**	Vochysiaceae	2002	Rainforest tree	Korup N.P.
Psychotria bidentata	Rubiaceae	2002	Rainforest shrub	Mt Cameroon
Psychotria bimbiensis	Rubiaceae	2002	Rainforest tree	Mt Cameroon, Banyang-Mbo
Psychotria martinetugei	Rubiaceae	2002	Rainforest shrub	Mt Cameroon, Kupe-Bakossi, Banyang Mbo
Psychotria moseskemei	Rubiaceae	2002	Cloud forest shrub	Kilum-Ijim
Cola metallica	Sterculiaceae	2002	Rainforest shrub	Mt Cameroon, Kupe-Bakossi, Banyang Mbo
Cola suboppositifolia	Sterculiaceae	2002	Rainforest tree	Mt Cameroon, Korup N.P., Banyang Mbo
Cola cecidifolia	Sterculiaceae	2002	Rainforest tree	Mt Cameroon
Impatiens frithii	Balsaminaceae	2002	Cloud forest epiphyte	Mt Cameroon, Kupe-Bakossi
Coffea bakossii	Rubiaceae	2002	Cloud forest tree	Kupe-Bakossi
Tricalysia lejolyana	Rubiaceae	2002	Rainforest shrub	Banyang Mbo
Rhaptopetalum geophylax	Scytopetalaceae	2002	Cloud forest tree	Kupe-Bakossi
Angraecum sanfordii	Orchidaceae	2002	Cloud forest epiphyte	Mt Cameroon, Kupe-Bakossi
Polystachya kupensis	Orchidaceae	2002	Cloud forest epiphyte	Kupe-Bakossi
Stelechantha arcuata	Rubiaceae	2002	Rainforest tree	Mt Cameroon, Kupe-Bakossi
Newtonia duncanthomasii	Leguminosae	2003	Cloud forest tree	Kupe-Bakossi, Korup N.P.
Dorstenia poinsettiifolia var. *etugeana*	Moraceae	2003	Cloud forest herb	Kupe-Bakossi
Dorstenia poinsettiifolia var. *achoundongiana*	Moraceae	2003	Rainforest herb	Mt Cameroon
Phyllanthus nyale	Euphorbiaceae	2003	Cloud forest shrub	Kupe-Bakossi

TABLE 1. continued

Scientific name	Plant family	Year	Life form	Region
Phyllanthus caesiifolius	Euphorbiaceae	2003	Cloud forest shrub	Kupe-Bakossi
Uvariopsis submontana	Annonaceae	2003	Cloud forest tree	Kupe-Bakossi
Manniella cypripedioides	Orchidaceae	2003	Rainforest herb	Kupe-Bakossi
Kupea martinetugei *	Triuridaceae	2003	Rainforest herb	Kupe-Bakossi
Ledermanniella onanae	Podostemaceae	2003	Rainforest herb	Kupe-Bakossi
Laccosperma korupensis	Palmae	2003	Rainforest climber	Mt Cameroon, Korup N.P., Kupe-Bakossi
Rinorea fausteana	Violaceae	2004	Cloud forest shrub	Kupe-Bakossi
Rinorea thomasii	Violaceae	2004	Rainforest shrub	Mt Cameroon, Korup N.P., Kupe-Bakossi
Bulbophyllum kupense	Orchidaceae	2004	Cloud forest herb	Kupe-Bakossi
Justicia leucoxiphus	Acanthaceae	2004	Cloud forest herb	Kupe-Bakossi
Peucedanum kupense	Umbelliferae	2004	Montane grassland herb	Kupe-Bakossi
Magnistipula butayei subsp. *balingembaensis*	Chrysobalanaceae	2004	Rainforest tree	Bali Ngemba
Scleria afroreflexa	Cyperaceae	subm.	Submontane grassland	Kupe-Bakossi, Bali Ngemba
Hypolytrum subcompositus	Cyperaceae	subm.	Rainforest herb	Kupe-Bakossi
Hypolytrum pseudomapanioides	Cyperaceae	subm.	Rainforest herb	Kupe-Bakossi
Cyperus microcristatus	Cyperaceae	subm.	Rainforest herb	Kupe-Bakossi
Keetia bakossii	Rubiaceae	subm.	Rainforest climber	Kupe-Bakossi
Psydrax bridsoniana	Rubiaceae	subm.	Rainforest tree	Kupe-Bakossi
Dovyalis cameroonensis	Flacourtiaceae	subm.	Rainforest tree	Kilum-Ijim, Baba II
Deinbollia oreophila	Sapindaceae	prep.	Rainforest shrub	Kupe-Bakossi, Bali Ngemba
Plectranthus abictus	Labiatae	prep.	Rainforest herb	Kupe-Bakossi
Allophyllus bakossii	Sapindaceae	prep.	Rainforest shrub	Kupe-Bakossi, Banyang Mbo
Psychotria geophylax	Rubiaceae	prep.	Cloud forest shrub	Kupe-Bakossi, Mt Etinde
Psychotria bakossiensis	Rubiaceae	prep.	Cloud forest shrub	Kupe-Bakossi



```
Number of collection used = 6 consisting of 6 localities
EOO : 3498.78 km sq - ENDANGERED (EN)
AOO: Cellsize : 13.2506 km sq Number of cells: 6
AOO Area: 1053.47 km sq - VULNERABLE (VU)
AOO: Number of sub-populations (Grid Adjacency): 3
Rapoport Analysis: Area 14652.4 km sq
Rapoport Analysis: Number of subpopulations : 2
```

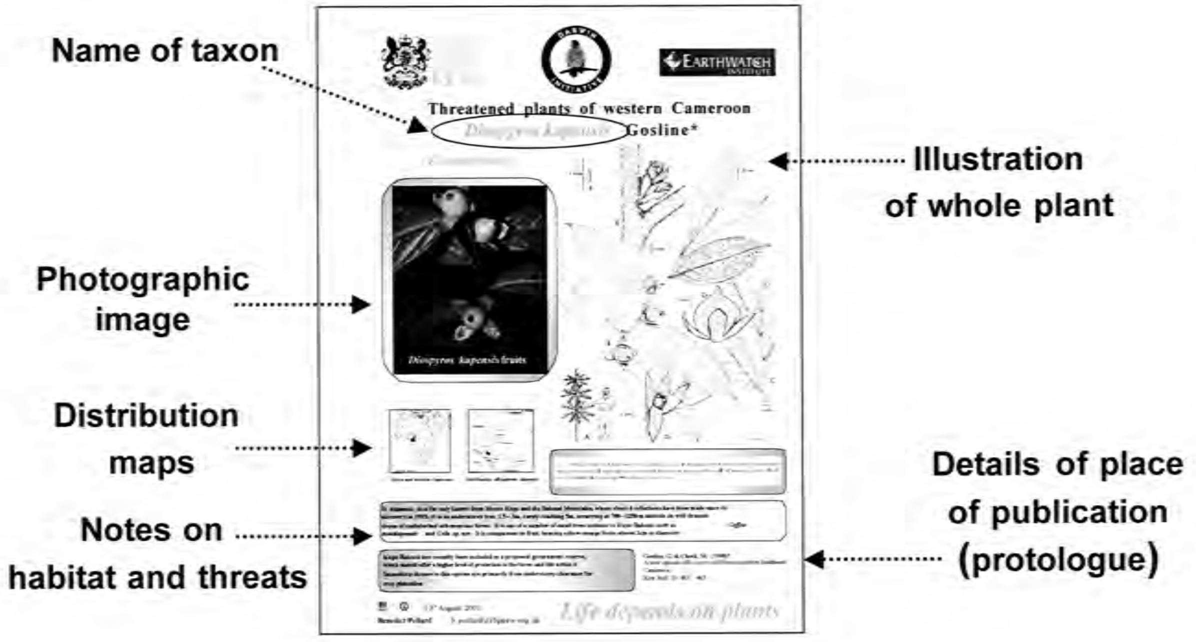
FIG. 2. Distribution map of *Dovyalis cameroonensis*, analysed for provisional Red Data assessment using Willis *et al.* GIS techniques. J. Moat.

The success of these posters was highlighted by an unusual event in 2002. An American journalist visiting Cameroon had happened to pass through a remote part of Kupe-Bakossi, one of the protected areas extensively surveyed by the project, and had been told by village elders of their unique wild coffee. Upon meeting Kew staff, she enquired, “do you, at Kew, know anything about this?” In fact, in 2001, while on a survey in the area, the project had distributed several conservation posters of *Coffea montekupensis* at a gathering of village chiefs that had met to authorize the project’s botanical work in their area. Clearly these posters had been displayed and discussed, the implications absorbed by the community, and the message disseminated.

3 Methodology

The outputs from this project are derived from information gleaned from the thousands of herbarium specimens gathered during the intensive botanical surveys manned largely by Earthwatch volunteers and Earthwatch African Fellows. In recent years, the fellows alone have numbered around 140 individuals from 14 African countries. Teams typically stay for two weeks in a Cameroonian village near a target forest, for training and evaluation on the methodology that the project uses for ‘plant inventory for conservation management’. This methodology has already been described in detail elsewhere (Cheek & Cable, 1997). Teaching of plant recognition characters is aided by lectures from Kew staff and postdoctoral researchers, often world specialists, who join the project’s field teams from institutes around Africa, Europe and North America.

Conservation Poster: *Diospyros kupensis*



Name of taxon

Photographic image

Distribution maps

Notes on habitat and threats

Illustration of whole plant

Details of place of publication (protologue)

FIG. 3. *Diospyros kupensis*, an example of a conservation poster. B.J. Pollard.

In the evenings, specimen data are transferred from field notebooks to the project's database by trained fellows and volunteers, using laptop computers powered by a petrol-driven generator. Under the Darwin grant, about 90% of the estimated 12,000 'historic' specimens from western Cameroon have now also been databased from the collections at the Kew herbarium. They have also been geo-referenced and images of types have been repatriated to the National Herbarium of Cameroon, initially as cibachromes but more recently as electronic scans using Kew's HerbScan© hardware and Adobe photoshop.

The Cameroon specimen and species database

64,000	specimen records
45,000	specimens geo-referenced
40,000	specimens reliably determined
3500	taxon accounts (in the species database) completed by end 2004

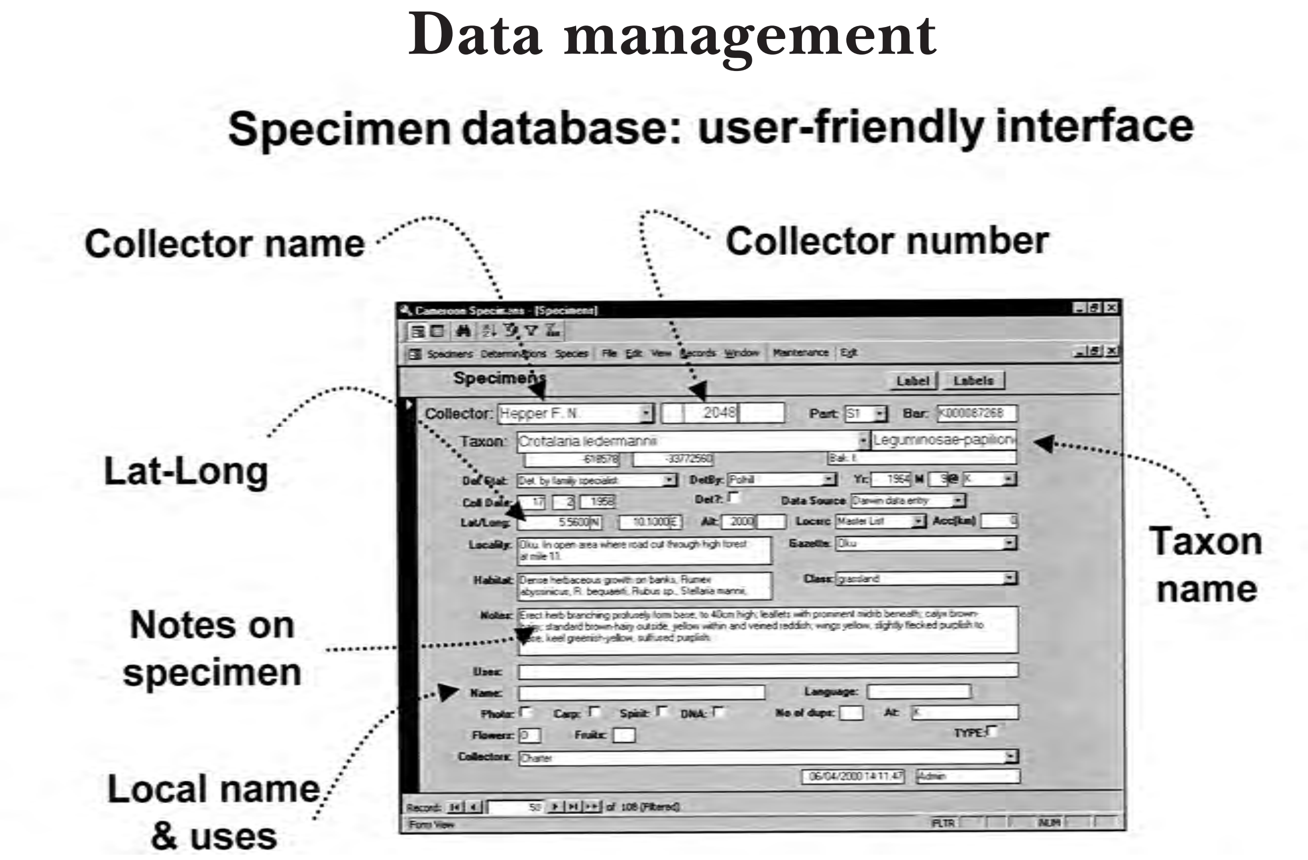
Identifications of specimens can take as much time and energy, and often more, than collecting the specimens in the first place, especially those from a poorly documented yet highly species-diverse area such as western Cameroon. In some rare cases as many as fourteen of each hundred specimens in a field book have turned out to be new to science (Cheek *pers. obs.*). Final identifications are conducted largely at the Kew herbarium by both Cameroonian and Kew-based scientists. Wherever possible, international specialists are used, so material of some families is sent away for naming, principally to scientists at the National Herbarium of the Netherlands at Wageningen.

Once the identifications have been entered into the database, checklists for an area can be produced automatically, directly from the specimen and species database. This process has been documented in greater detail by Gosline (2004), and the interface illustrated by Fig. 4.

4 Conservation action: direct examples

It is often asked of conservation projects if plants are actually being conserved on the ground, and how. Some examples of concrete conservation action where the project's results have been used in making decisions on gazetting of areas for conservation are detailed below. Other examples of more specific conservation successes for individual species are also listed.

1. In 2000 the project was asked by BirdLife International to supply information on which Red Data species were present in the Kilum-Ijim Forest at Mt Oku. The information emphasised the significance of those forests by way of the endemic and threatened taxa occurring there, and helped secure a US$ 1 million commitment from the United Nations Development Programme to keep that project running for another four years.
2. In 2002 the project learnt that forest around the crater lake of Oku was being gazetted as a Plantlife Sanctuary by the Government of Cameroon, based largely on the project's data.
3. Just two weeks before the AETFAT Congress, we learnt that the Minister of the Environment of Cameroon had issued a Public Order Notice commencing the creation of the 76,551 ha Bakossi National Park in SW Province, Cameroon. Most of the supporting plant data was provided by us through CRES and WWF, the NGOs championing National Park status. It is thought that the Park will come into effect early in 2005.



Data management

Specimen database: user-friendly interface

Collector name

Collector number

Lat-Long

Taxon name

Notes on specimen

Local name & uses

Specimens

Collector: Hepper F. N. | 2048 | Part: S1 | Bar: K000087268

Taxon: Crotalaria ledermannii | Leguminosae-papilion

618578 | -33772560 | Bak. f.

Det Stat: Det. by family specialist | DetBy: Polhill | Yr: 1964 | M 9 | @ K

Coll Date: 17 | 2 | 1958 | Det?: ☐ | Data Source: Darwin data entry

Lat/Long: 5.5600 N | 10.1000 E | Alt: 2000 | Locsrc: Master List | Acc(km) 0

Locality: Oku. In open area where road cut through high forest at mile 11. | Gazette: Oku

Habitat: Dense herbaceous growth on banks, Rumex abyssinicus, R. bequaerti, Rubus sp., Stellaria manni, | Class: grassland

Notes: Erect herb branching profusely form base, to 40cm high; leaflets with prominent midrib beneath; calyx brown-hairy; standard brown-hairy outside, yellow within and veined reddish; wings yellow, slightly flecked purplish to base, keel greenish-yellow, suffused purplish.

Uses:

Name: | Language:

Photo: ☐ Carp: ☐ Spirit: ☐ DNA: ☐ | No of dups: | At: K

Flowers: 0 | Fruits: | TYPE: ☐

Collectors: Charter

06/04/2000 14:11:47 | Admin

Record: 50 of 108 (Filtered)

FIG. 4. The specimen interface of the Cameroonian database. B.J. Pollard.

4. Mounts Kupe (4,676 ha) and Mwanenguba (5,252 ha) are to become Integral Ecological Reserves, the highest level of protection available under Cameroonian law. Again, most of the plant data supporting the application for these gazettements was provided by the project.
5. *Newtonia camerunensis* (Leguminosae-Mimosoideae), a timber tree thought to be extinct, and not seen by botanists since 1974, was rediscovered on the 2002 Kew-HNC-Earthwatch expedition. Several hundred seeds were collected and planted at the Bamenda Highlands Forest Project nursery. These will be planted out at suitable forest patches across its known former range when the saplings are robust enough to survive with a low level of maintenance.
6. We have also made a difference to the survival of individual threatened species through partnerships with biologists in local protected area projects. One good example follows on from the *Dovyalis* case study detailed above. Having discovered what the project then considered to be a probable new species of *Dovyalis,* apparently restricted to the forest surrounding the crater lake of Mt Oku, the project explained its importance for conservation to technicians of a local conservation project. On returning to this part of Cameroon three years later, the project found that not only had the technicians conducted a census of all 15 trees at the site, but that they had had located a second site, many kilometres distant, with a further eight trees. They had explained the importance of these trees to the elders responsible for that forest and they have now been included in its management plan. *Dovyalis cameroonensis*, assessed as being Critically Endangered according to the IUCN (2001) guidelines due to the very low number of individuals known, has gone from being an unprotected and unrecognized species to a known, threatened, but protected, species.

5 Conclusions

This Darwin Initiative Project has been successful in addressing and contributing to several of the 16 targets identified in the Global Strategy for Plant Conservation. It has increased our understanding of plant diversity in western Cameroon by way of a massive increase in documentation of plants and their distributions. Preliminary assessments of the conservation status of over 3,000 species are complete; these data are helping to establish protection in several important areas for plant diversity, which include many threatened species now conserved *in situ.* A wealth of expertise has been developed, at Kew, in Cameroon, and all across Africa by way of the 140 African Earthwatch Fellows, as well as staff from Kew, HNC and local NGOs who have received training in plant surveying and conservation techniques. This has built capacity for the conservation of plant diversity in western Cameroon.

Acknowledgements

Many thanks to the Darwin Initiative Grant from the Department of the Environment, Transport and the Regions, UK, now the Department for the Environment, Food and Rural affairs (DEFRA). Iain Darbyshire and Daniela Zappi are thanked for comments on an earlier version of the manuscript, and Shahina Ghazanfar for the opportunity to include this project summary, updated since the AETFAT congress.

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