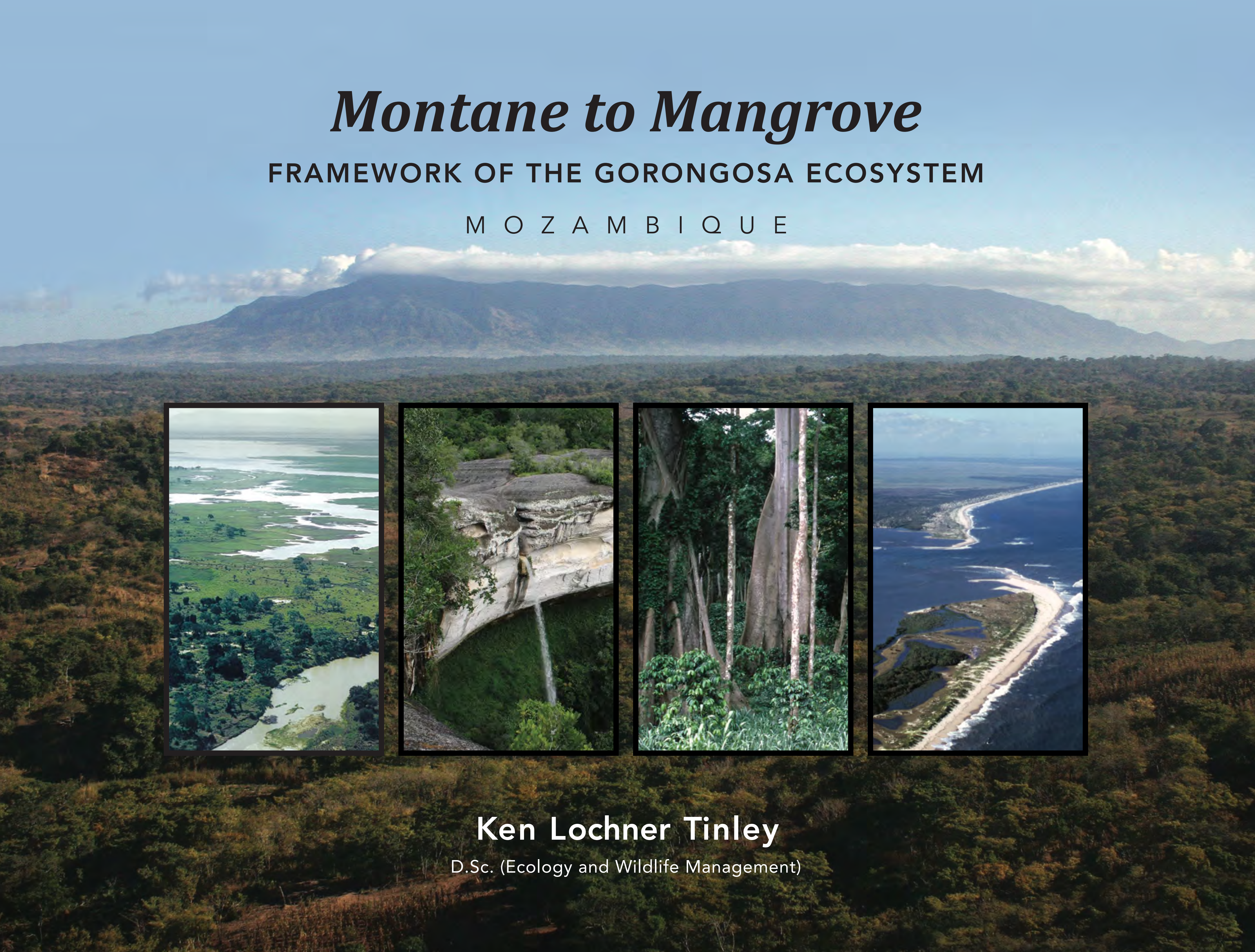


Montane to Mangrove

FRAMEWORK OF THE GORONGOSA ECOSYSTEM

MOZAMBIQUE

Ken Lochner Tinley

D.Sc. (Ecology and Wildlife Management)

Annotations for cover photos (the water story in a nutshell).

Background photo: Gorongosa Mountain — sentinel and perennial water catchment — © Bart Würsten
Small photos: Urema Lake and floodplains on the Rift Valley Floor — © Ken Tinley
Ancient limestone ravines on eastern Rift Valley rim — © James Byrne
Tall coastal rain forest — © Ken Tinley
Mangrove estuary emptying into the Indian Ocean — © Ken Tinley

Back cover: Red Mangroves *(Rhizophora mucronata)* on the Cheringoma coast. — © Eco Pic

Montane to Mangrove

FRAMEWORK OF THE GORONGOSA ECOSYSTEM

MOZAMBIQUE

Ken Lochner Tinley

D.Sc. (Ecology and Wildlife Management)

Parque Nacional da
Gorongosa

Publisher: Hamilton-Fynch
3 Neil Street, Steiltes, Nelspruit, 1213, South Africa
www.hamiltonfynch.com
https://www.facebook.com/hamiltonfynch

Funded by the Gorongosa Project – Mozambique
www.gorongosa.org
https://www.facebook.com/gorongosa

Publishing Manager: Hamilton-Fynch
Designer: Lesley Lane — Hamilton-Fynch
Proof Reader: Barbara Jay
Indexer: Marlene Burger
ISBN: 978-0-620-90482-7

Cover Photos
Main backdrop, Gorongosa Mountain — Bart Würsten
Photo block left to right:
Urema floodplain — Ken Tinley
Cheringoma cliffs — James Byrne
Coastal forest — Ken Tinley
Zambezi estuary — Ken Tinley

To the peoples of Mozambique
and to my wife and companion Lynne

'. . . we emerged on the vast plain bordering the Urema-Zangue marsh, over which we toiled for hour after hour in the intense heat, sighting a few wildebeest, zebra and waterbuck in the distance, looking like dancing motes in a sunbeam as they stood in the heat-haze. The plain seemed waterless, and shade there was none, for the track took us fully three miles from the nearest belt of palm trees, and such a track! Over hard, sun-baked mud, cracked into gaping fissures at every few yards, its surface irregularities made more painfully rough by yawning holes, which represented the old spoor of the herds of game which visit these plains in the summer. '

F. VAUGHAN KIRBY
Hunter-naturalist
1894

'. . . this sojourn by the Sungue (Urema) Plains will remain one of the
most vivid of my memories. The thousands of animals, scattered over
the arid plains, the flocks of wading, web-footed, and many other kinds
of birds which fly over at sunrise to feed; the peaceful, solemn, yet
imposing landscape, bounded on the blue horizon by the
mountains of Gorongosa and Cheringoma; all these
things will remain graven on my memory.'

W. VASSE
Hunter-naturalist
1904

Foreword

I saw Gorongosa National Park for the first time, from a helicopter, on March 30, 2004. It looked magnificent from above. There were multiple forest and woodland types, grasslands, rivers, a lake and fascinating geological formations. When we landed, however, it was clear we had trouble. The historic Chitengo camp lay in ruins—former buildings were rubble. Where tourists once wandered, burned-out vehicles lay amongst grass that was higher than my head. That year, the Mozambican government asked me to help restore Gorongosa, once one of the most popular wildlife parks in all of Africa.

In the 1960s scientists said that Gorongosa had the densest abundance of wildlife of any natural area on the continent. This was no longer true. On our visit in 2004, we could drive an entire day and perhaps see one warthog or one baboon. Whatever other wildlife there was, hid in dense forests and had every reason to fear vehicles. Approximately 95% of the large animals were killed during and in the aftermath of one generation of war. How could we possibly restore a landscape of 400,000 hectares (one million acres).

If we were going to help the Government of Mozambique re-wild this ecosystem, we needed to understand it. We needed to create a document known as a Park Management Plan.

My very small team and I searched the literature. We found popular accounts of Gorongosa in newspapers and even in the prestigious National Geographic, dating back to the early 1960s. However, we also needed scientific data. A Harvard University friend found a reference to a doctoral thesis called 'Framework of the Gorongosa Ecosystem' published in 1977 by a Kenneth Lochner Tinley, but not the actual thesis. At the time, Google was a 'child', just six years old, and one did not find nearly every imaginable piece of information online. We learned that a physical copy of the thesis existed in the University of Pretoria, South Africa. We used 'interlibrary loan' to get that actual document (not a facsimile) sent by the postal service to Harvard and then to us. Helping me was Sydney Kwiram - a brilliant young woman and recent Harvard graduate.

The manuscript's abstract included this paragraph: 'The chapter titled "Process and Response" is the central pivot of the thesis containing the kinetic aspects of geomorphological landscape changes with coevolutionary sequences of biotic communities which change (expand, contract and recombine) kaleidoscopically in space and time, in appearance and content.'

Wow. I am not a biologist. I wondered if I should return to the friendly, popular newspaper articles about Gorongosa! However, the Tinley masterpiece is written by an incredible hand. It is the kind of literature that a layperson can follow if one reads carefully, even as an expert will gather much more from the same page. Sydney and I devoured this tome. The thesis had chapters on landscape setting, geology, soils, hydrology, climate, wildlife—covering an area in central Mozambique larger than the Park boundaries themselves—under the labels of Gorongosa Mountain Summit, Gorongosa Mountain Slopes, Midlands, Rift Valley, Coast Plateau, and Land-sea Junction. There were graphs of data and hand drawn maps by Dr. Tinley. He did all of this prior to the existence of the personal computer, GPS, digital photography, drones and the Internet. He with his spouse, Lynne Tinley and their two small children lived in Chitengo (the place where I landed in March 2004), from 1968 to 1973.

© Charlie Hamilton James

© Charlie Hamilton James

We had the document, but what about Ken Tinley? Was he still alive, did he live in South Africa? We would not find those answers in 2004.

Meanwhile, our team of scientists used insights from the Tinley thesis as we wrote a proposal to the Government of Mozambique to co-manage and restore Gorongosa. Among many critical observations, Ken Tinley—speaking through his thesis—told us that in order to save the ecosystem over the long-term, Mount Gorongosa needed to be added to the Park. Mount Gorongosa holds one of only two true rainforests in Central Mozambique, full of endemic and near-endemic species, and critically the mountain is the source of most of the Park's surface water during the dry season, and at this time it had no protected status.

We continued our studies, our visits to Gorongosa and our talks with the Government of Mozambique. I expanded our team. In 2005, on one of the luckiest days of my life, I met a man named Vasco Galante. Vasco became the Director of Communications for the nonprofit 'Gorongosa Restoration Project'. He is a human connector. He makes friends, then he becomes friends with their friends. He remembers everyone, every encounter, every event. We call him 'Vascopedia'. Vasco's records tell me that we found Ken Tinley in 2005. I sent him an email (which, of course, Vasco saved) on November 28, 2005 that says: 'We are in communication with Dr. Tinley (who now lives in Australia) and we have his thesis, which you will enjoy. I'll ask Bridget to send you a copy.'

'In communication with Dr. Tinley' actually meant that we had found an email address for his spouse Lynne (from someone who knew someone), and contacted her. Lynne is equally brilliant and is Ken's lifelong teammate. She is an artist of Nature. She wrote "Drawn from the Plains", a book about living in Chitengo Camp, Gorongosa for five years. The book includes her original artwork. We located a copy.

I remember reading my first email reply from Lynne. I now felt that the legendary Gorongosa of the 1960s was no longer just a storybook place to read about in articles. I was talking to someone who had lived there, seen it, smelled it, heard it, and breathed it. Soon, I started receiving messages on Lynne's email account written by Ken. I was finally talking to the person who had written 'Framework of the Gorongosa Ecosystem' when I was still in middle school.

We corresponded with Ken steadily from 2005 on, sharing ideas and receiving welcome advice. Ecologist Dr. Marc Stalmans was a consultant to us and later became Director of Science for Gorongosa National Park. He helped us plan the restoration.

'Ken was truly ahead of his time', Dr. Stalmans explains, 'applying a landscape ecological perspective well before this approach gained popularity in the 1980's—1990's. Ken manually applied GIS principles before the electronic tool was available. Whereas many studies conventionally only provide a snapshot in time, Ken's work takes a long term, geomorphic and geo-ecological view of the Park in terms of the formation, evolution and long-term outcome of its ecosystems and constituting components. That's why the work is still hugely relevant one half-century later. Even more astonishing is that this magnum opus resulted from Ken spending only five years in the Gorongosa ecosystem.

On top of that, he still found time to sketch landscape perspectives of Banhine National Park in Mozambique and an area next to the Kruger National Park in South Africa that would later become part the Limpopo National Park. Thirty years later, in the early 2000s, these perspectives became the foundation for the first landscape maps for both parks, which now form part of the Greater Limpopo Transfrontier Conservation Area .'

In 1990, well after his five years living in Gorongosa Park, Ken worked with landscape architects in Pretoria. They agreed that the existence of a large number of national parks and nature reserves along the frontier between Mozambique, South Africa, Zimbabwe and Swaziland opened the possibility for multi-national trans-frontier resource areas (referenced by Dr. Stalmans above).

It was exciting to think that existing protected areas could be linked by some of the little populated areas in between, to create one of the largest conservation zones in the world. Rural communities living within the resource areas, as well as the governments of the various countries, would benefit. Ken was one of the originators of the idea that became known as 'Peace Parks'. President Nelson Mandela, a founder of the Peace Parks Foundation, believed national parks could link nations or regions that had previously seen conflict. His theory: the connected ecosystems would be good not only for wildlife, but deliver benefits and peaceful relations to people as well.

We completed the first draft of our Park Management Plan and finalized our co-management contract with the Government of Mozambique. In January of 2008 I signed a 20-year agreement with the Government to co-manage and restore the Gorongosa ecosystem, and to bring human development services to the communities that live adjacent to the Park. (That agreement has now been extended to 35 years.)

In 2008 we revitalized the ranger team. They began removing wildlife traps and snares from the Park, some left over from the war. We started a health care program in nearby communities. We began our first attempts at tourism.

Yet, I had still not met Ken Tinley. I invited him to come and see what we were doing. In October 2010 Ken spent 5 days with us in Gorongosa.

On the last day of his visit Ken shared a poignant story with us. This trip was not the first time he had been to Gorongosa since 1973. In 1994, after the war ended, Ken and a man named Paul Dutton with José Tello (ex-warden of Gorongosa) were contracted by IUCN to survey the condition of the National Park. Like Ken, Paul had begun his career as a Game Ranger in the Zululand Provincial Game Reserves, and later continued his education to earn a graduate degree in Ecology. They became lifelong friends. Paul and his own small Piper Cub helped Ken and José perform the first aerial surveys of the vast herds of large ungulates during the first year of Ken's research in Gorongosa. In 1994 they then found what I saw a decade later: no wildlife and destroyed infrastructure.

The Gorongosa Restoration Team has made great progress from 2010 to 2019. Our rangers removed 27,000 traps and snares. We reintroduced some species that we obtained from other national parks, such as buffalo and wildebeest. But mostly, in a safer environment, the remaining small


© Charlie Hamilton James

RIGHT:

Ken Tinley (left) meets Greg Carr at Chitengo.

populations of wildlife were able to increase on their own. In 2018 we conducted an aerial wildlife survey and counted more than 100,000 large animals. This was just the fifteen largest species we could count from the air, not the innumerable smaller species that are also thriving. The press is kind to us. National Geographic refers to us as perhaps Africa's greatest wildlife restoration story.

We also made headway on our human development program in the traditional communities that share the greater ecosystem with the Park. Our after-school 'Girls' Club' keeps teen girls in school and out of child marriage. We help small farmers get better yields on their land. We provide health care to more than 100,000 people per year.

Recall, this idea that national parks should benefit the local people was one of Ken Tinley's early insights—that the local people living adjacent to national parks are an integral part of the region and that their knowledge, expertise and wellbeing needs to play an interactive role with science in the healthy functioning of the ecosystem, particularly in water source areas, drainage and wildlife populations.

Greg Carr
September 30th, 2019.

Acknowledgements

First and foremost I want to give thanks to the memory of my friend and mentor Ian Player. It was Ian who recommended my work to Dr Alexandre de Sousa Dias prior to my employment by the Mozambique government in 1968 as the first ecologist for the territory.

I also acknowledge with gratitude Chief Chitengo's early support and acceptance of the National Park within his territory. In 1994, when José Tello, Paul Dutton and I did an IUCN survey of what was left of the animal populations and the people at the end of the Civil War, Chief Chitengo welcomed us back and supported the recovery of the National Park.

DURING THE 1960s AND 70s:

My sincerest thanks to the following people who aided my work in Mozambique—Dr F.C. Paisana (Director of Veterinary Services at that time); Dr A.H. de Sousa Dias (Director of the Fauna Conservation Section of the Veterinary Services); Dr J.L. Nunes Petisca and his successor Dr F. Valadao (Directors of the Veterinary Institute); and at Gorongosa, Dr F.M.P. Romao for resolving all logistic and administrative problems. To José Tello, Chief Warden of Gorongosa, Carlos Saraiva, Paul and Ann Dutton thanks for their friendship, interest, great enthusiasm and help in many ways. Thanks too to the Trig Survey Department of Mozambique for permission to publish the air photos.

Dr Don Broadley, of the then Umtali (Mutari) Museum, Rhodesia (Zimbabwe), helped with materials for small mammal collections and trained one of my assistants to produce fine study skins.

Special thanks to Signet and Vasco Matondo, my two field assistants from the local Chegorongosa people. Vasco, especially, was a man of many parts, hunter-naturalist, tracker, philosopher and good companion. Throughout my life the indigenous people have taught me so much of what I know about the land and I am eternally grateful to them.

During the torrid summer months my wife and I were particularly appreciative of the great hospitality of Mr and Mrs John Wright and later of Mr and Mrs Geoff Harrison in the only cool haven in the region, the ranch on the southern slope of Gorongosa Mountain.

At the University of Pretoria while I was writing up the thesis the following organisations and people provided much needed and valuable assistance: Farrell & Van Riet Landscape Architects and Ecological Planners; The Council for Scientific and Industrial Research (CSIR); The South African Nature Foundation (affiliated with the World Wildlife Fund); the Wildlife Society of South Africa; the Okavango Wildlife Society; Ted and Liz Reilly of Swaziland; Francis I. Morrison of White River; Clem Haagner; Dr D.M. Joubert; Norah and Roland Kreher; John Hosken; Lynn Hurry and the Bond van Oud Studente van Universiteit van Pretoria. Some of the figures in the thesis were redrawn by Lindsay Miller and in particular by Mike Isakov—a master draughtsman.

I am particularly grateful to Mr. R.B. Drummond, then head of the Rhodesian National Herbarium, Salisbury (Harare), for the enormous work he did in naming my woody plant collections from Mozambique. Mrs. K.E. Bennett at the same institute kindly identified the grasses. Elizabeth Retief and Dr Jeff Morris from the Botanical Research institute in Pretoria provided valuable assistance.

Dr Brian Walker, at that stage head of the Botany Department at the University of Rhodesia and later professor of botany at the University of Witwatersrand, gave me valuable advice on field techniques in quantitative vegetation analysis. Robin Barnard of the Soil Faculty of the University of Pretoria gave creative criticism of the chapter on soils and organised lab analysis of my soil collection.

Special mention must go to Willem van Riet, a landscape planner who sees things in the round, and my biologist/artist wife, Lynne, for their enthusiastic role as sounding boards against whom ideas were tested. To my promoter Professor Fritz Eloff (Zoology and Wildlife Management, University of Pretoria), great thanks for his forebearance and encouragement at all times.

IN PRESENT TIMES: 2017 TO 2020

Firstly, I want to thank with deepest gratitude Greg Carr and the Gorongosa Team for initiating and funding the publication of this historical document. Their friendship and support have been without measure.

Great thanks and admiration to Karl and Lesley Lane (Hamilton-Fynch, Nelspruit) for their tireless dedication in the digitisation, compiling and designing of this superb publication from an ancient photocopied original with poor quality photographs!

Editor Barbie Jay and indexer Marlene Burger both did wonderful and painstaking work on these complex tasks.

Thanks to Dr Marc Stalmans (Director of Scientific Services) for his present day scientific advice and his help with Vasco Galante (Director of Communications) in co-ordinating the publication process.

My final profound thanks go to Lynne, my darling wife of 55 years. Without her computing and organisational help this publication might never have been completed.

RIGHT:

Ken and his team outside the first Field Research Centre at Gorongosa 1971 (from L to R — Pedro, Antonio, Ken, Vasco, Signet).

Introduction

A holistic evolutionary approach is used in the Gorongosa thesis in which emphasis is on the salient reciprocal relations and kinetic succession of land surfaces and biotic communities, influenced by landscape processes and prime mover components.

As correlations of these relations and processes require both a total interacting framework and the details of its prime components, the thesis is divided into three main parts: (1) synopsis of the essence of the Gorongosa ecosystem and the approach used in field ecology (Perspective); (2) correlation of the physical and living components of the ecosystem; and (3) synthesis. The study attempts to relate the salient features of processes and correlations into a coevolutionary whole, caught at that particular stage in space and time by the study.

The chapter titled **Process and Response** is the central pivot of the thesis combining the kinetic aspects of geomorphological landscape changes with coevolutionary sequences of biotic communities which change (expand, contract, and recombine) kaleidoscopically in space and time, in appearance and content.

The prime movers in ecosystem change are: on the physical side, nickpoint headward eroding sequences and edaphic change in soil moisture balance, and on the biotic side, the frugivores and large ungulate components which affect geomorphic and habitat modification are central.

Of these, soil moisture appears to be the master factor. All climatic influences too, appear to be expressed through the edaphic controls which change in-situ, or with each geomorphic surface replacement sequence. This factor seems to orchestrate the opportunities and constraints from below on the community evolution possible in a particular time and place.

From this, a template of salient factors of the Gorongosa ecosystem is provided for management, based on causes and trends in the kinetic evolution of the various ecosystems. To maintain a diversity of ecosystems in Gorongosa, the fundamental management action is to reinforce or reinstate the natural local base level sills which cause ponding of floodwaters responsible for the mosaic of grasslands and slack marshes of high primary productivity and ungulate carrying capacity. Concomitantly reductions of certain overpopulated ungulate species, chiefly hippo, are required so that management is effective.

As natural processes are dynamic, it is necessary to identify and evaluate those salient factors operating at a particular time, as these key controls are altered and replaced by others through natural kinetic succession of landscapes and biotic communities. The salient factors governing the dynamics of an ecosystem or community thus require to be mapped at intervals, to provide templates of the trends and changing importance of key and master factors, in order to anticipate or predict what will result from their influences. With these data valid evaluation can be made with the other correlated information for meaningful management action.

Forty-five years later, a lot has changed in the greater Gorongosa ecosystem but the basics have remained the same so that this ecological framework is still relevant for future scientists and explorers to build upon. Perhaps the work is even more relevant in these times of drastic dynamic changes in climatic/geomorphic/biotic relationships.

The Latin names for many of the plants and animals that are listed in this work have changed over the years, the updated names are listed in Appendix 3. A number of place names have changed in the past 45 years especially in South Africa and Zimbabwe. These have been noted as the old and new (eg. Eastern Transvaal/ Mpumalanga) at first mention in the book, thereafter only as the old names.

RIGHT:

Selous zebra
Equus quagga selousi

© Clem Haagner

Background

PREVIOUS STUDIES

The collection of plant and animal specimens from the Gorongosa region and surrounding parts of Central Mozambique is a rich story still to be told, involving some of southern Africa's most famous names in natural history—Frade, Grant, Haagner, Kirk, Livingstone, Peters, Roberts (on the north side of the Zambezi Delta in 1908), Selous, Serpa Pinto, Sheppard, Swynnerton, Vaughan-Kirby, Vasse and others. The background noted here relates to actual field studies as opposed to collections of which only two are mentioned. These are by the famous hunter-naturalists Vaughan-Kirby (1899) and Vasse (1909) whose books, now valuable Africana, deal specifically with the Gorongosa region. Both these men recorded many observations of ecological importance as well as valuable proof of such species as tsessebe and roan which are extinct in the Park today. The locality of the Gorongosa–Cheringoma area is depicted in Fig. i.

Kirby arrived at Chinde at the Zambezi mouth in 1894 and travelled upriver to near the Chire junction before exploring inland on the Cheringoma Plateau. Passing south of Inhaminga he describes the deep ravines of the Riftward drainage and then descending to the floor of the Rift, camped near the Muaredzi stream. He traversed the Urema plains to the NW of Gorongosa Mountain (Bárué area) and returned to hunt elephant extensively on the Cheringoma Plateau. Thereafter he explored the Zambezia district, hunting chiefly in the area between the Chiperoni and Namuli mountains.

Vasse, a Frenchman, spent almost all of three years hunting and collecting in what is defined above as the Gorongosa ecosystem. His book, though biased to the hunt, is a remarkable record of conditions as they were in the first part of the 1900s. In addition he explored and mapped the area, including an ascent to the highest summit area of Gorongosa Mountain. His collections sent back to the Pasteur Institute and Paris Museum comprised 53 ungulates, 118 birds, 18,000 insects, 500 plants, 63 reptiles and amphibians, mollusca, worms etc., and 250 mineralogical specimens (Vasse 1909: 157).

In the early 1900s detailed geological exploration of the region was made by various geologists including Teale and Wilson (1915), Teale (1924) and Abrard (1928) amongst others, and is summarised in a major work on the geology of the Mozambique sector of the Zambezi Basin (Real 1966). Mouta (1957) published a short account of the Urema Trough.

After Vasse, more than fifty years elapsed before a biological study was made by the ornithologist Rosa Pinto (1959). In 1965 a photographic and written record of wildlife in Gorongosa was published by João August Silva, who had for many years been Administrator at Vila Paiva (now Vila Gorongosa) on the Midlands between Gorongosa Mountain and the Rift Valley.

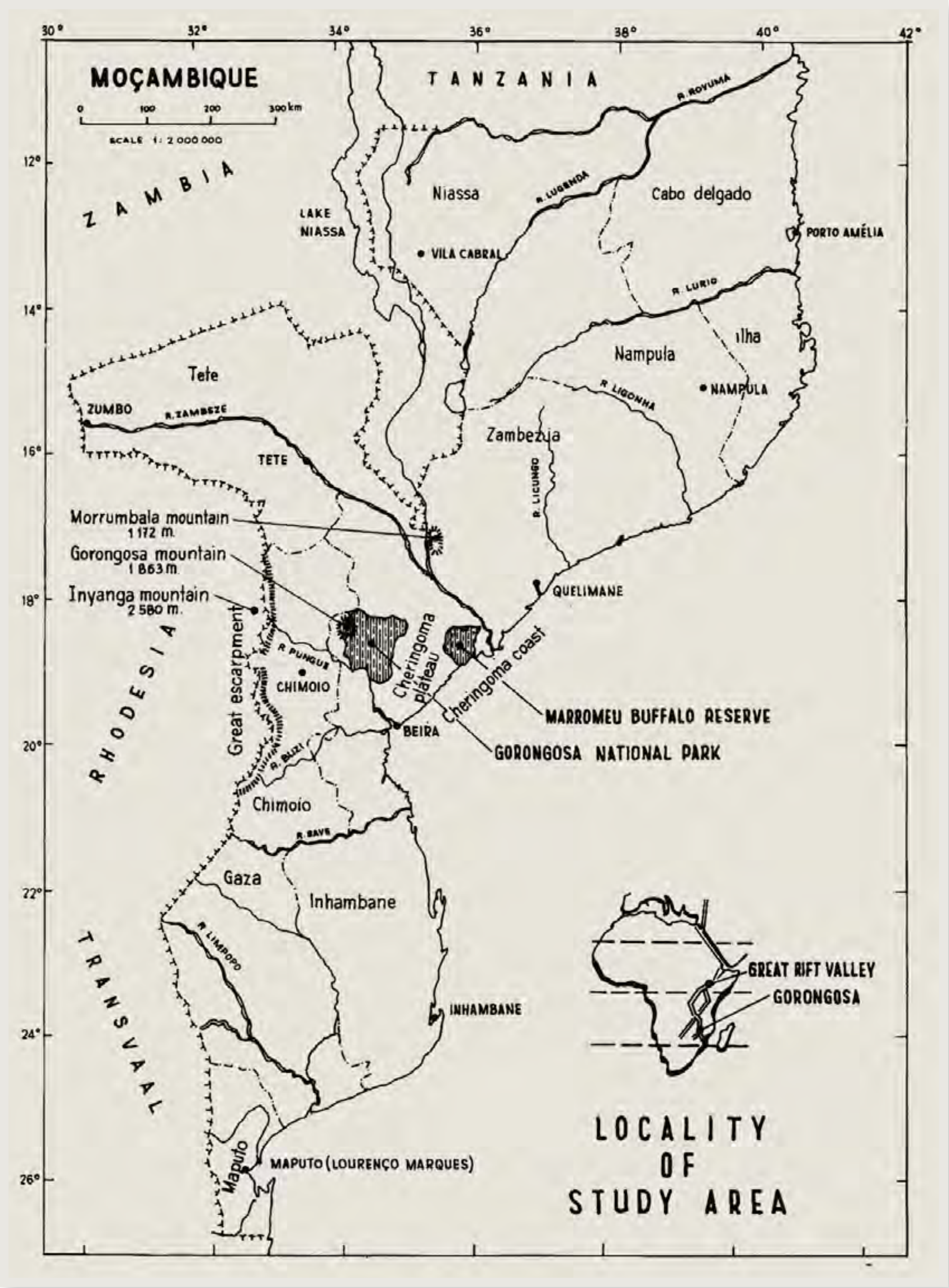
Mendes da Rocha Faria (1966) published the first attempt at describing the climate of the region by using statistics collected at stations on the higher ground on either side of the Rift (Vila Paiva and Inhaminga), and as the Chitengo station was only initiated in 1966, used Vila Machado as a Rift example (40 km to the SW of the Park on the Beira–Rhodesia main road). The present study has benefitted from 10 years of climate statistics recorded at Chitengo (in the centre of the Rift Floor), and on a ranch halfway up the southern slope of Gorongosa Mountain. The latter records were kept first by Mr and Mrs John Wright (1963-1969) and later by Mr and Mrs Geoff Harrison (1970-1973).

The botanist José Aguiar de Macedo (1966) made the first botanical survey of the region, but unfortunately this work remained incomplete as most of his collections were unnamed. He later published two works on the flora of Gorongosa Mountain (Macedo 1970a, 1970b) and as so many specimens had still not been named by this time, was forced to list the majority with his collection numbers, as reference. The present author made extensive plant collections in the process of analysing the various ecosystems and communities and was fortunate to have these named by the Salisbury Herbarium.

Plant collections were made in the region by many Portuguese botanists including A. Rocha da Torre, F. A. Mendonça, J. Simão, Pedro and Pedrogão, A. Gomes e Sousa (1966), J. Gomes Pedro, L. A. Grandvaux Barbosa. These last two authors were responsible for the first comprehensive vegetation map of Mozambique (Pedro and Barbosa 1955). Important plant collections were also made by expeditions and members of the Zimbabwe (Rhodesian) Herbarium. In addition to Rosa Pinto, collections of birds were made by the Durban Museum and bird, reptile and small mammal collections by the Rhodesian Museums.

A soil survey of the region was made by the pedologist Fernandes (1968a, 1968b), who compiled maps of both the mountain area and the Park by airphoto interpretation as determined from samples at intervals along roads.

This sums the totality of studies made of the region and, apart from Vasse (1909), they were all single disciplinary thus leaving an unlimited field for original ecological research.



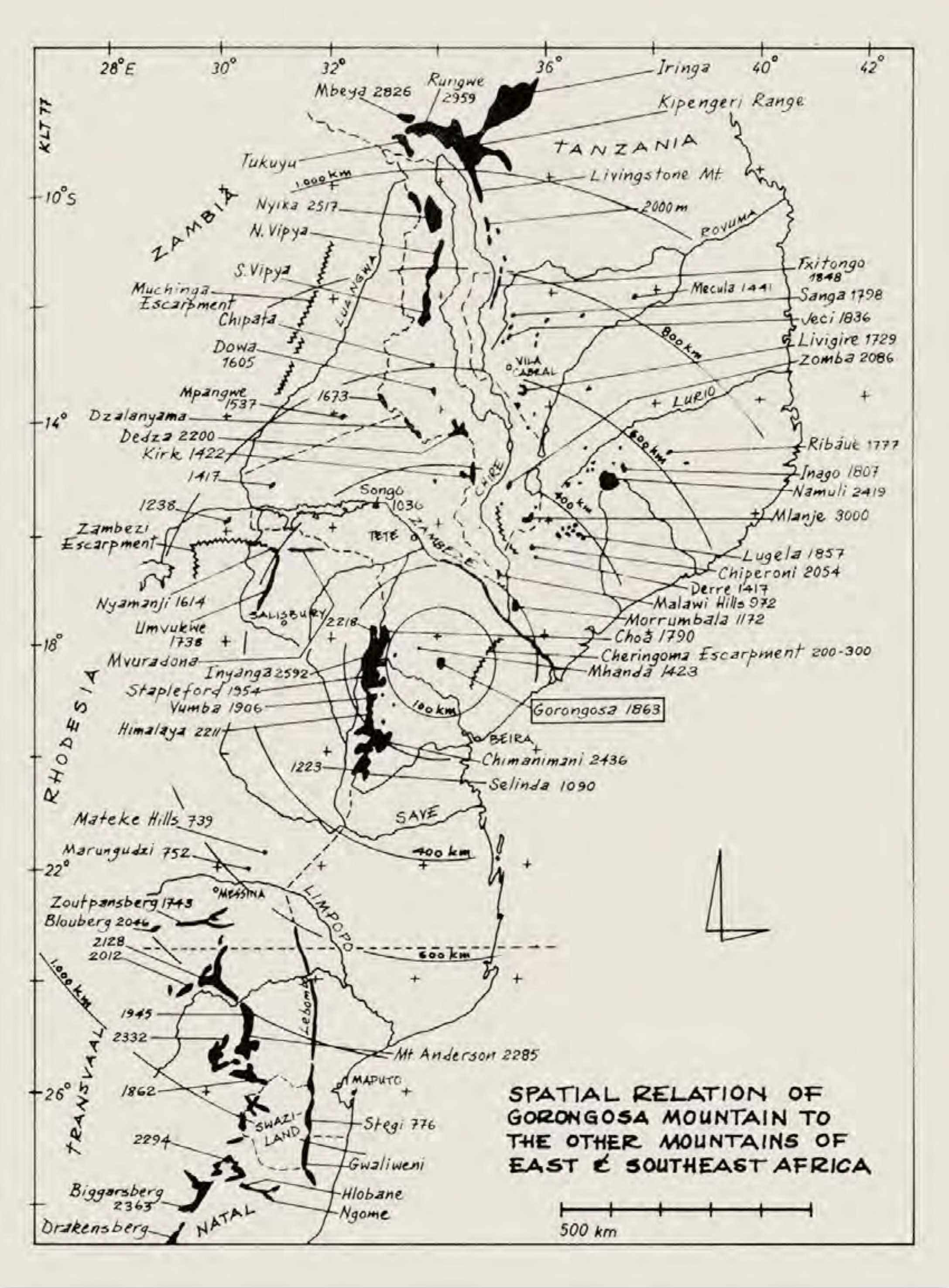
RIGHT: Fig. i

Locality of study area.

AMBIENT OF PRESENT STUDY

In August 1968 on arrival at Gorongosa, which was to be my base for the next four years, I was faced with the task of determining the ecological limits of the national park. All previous boundary limits had been arbitrary or political, that is straight lines, roads or rivers, and the authorities were concerned about the space requirements for seasonal wildlife migrations, the sufficiency of wildlife habitats, and the constant pressure by companies and tribal cultivators for park land. The report of this first major study was presented to the Mozambique Government in August 1969 (Tinley 1969b). After this base work was completed, it was clear that the highest conservation priority in Mozambique was not the further detailed study of Gorongosa wildlife alone, as no in-depth study could alter the fundamental importance of the salient factors, but the urgent need was to define the unique ecosystems throughout the territory which still required proclamation as national park areas. As the only wildlife ecologist in the territory it was important, therefore, for me to work on a priority basis covering as much of the territory as possible as well as keeping the study of Gorongosa as the main ongoing theme (see References). ln the fifth year I moved to head office in Lourenço Marques and left Mozambique in April 1974. Wildlife conservation and national parks was then, and remains, the responsibility of the Fauna Section of the Veterinary Department.

A prerequisite for meaningful ecological research is the use of a light aircraft for studying geomorphology,



LEFT: Fig. ii

Locality map of study area.

seasonal changes in habitats, and for air census of the larger wildlife species. To prove its efficacy to the Mozambique authorities, I arranged with Paul Dutton (then Ranger-in-Charge of the Ndumu Game Reserve in Zululand) who had his own highwing Piper aircraft, to initiate the air studies in November 1968. As Mozambique at this time of the year is covered by a dense pall of smoke from veld fires, Paul and Ann Dutton flying in from Zululand were only able to find the Park's main camp by navigating at tree-top level up the Pungue River from the coast! In this way the first air count of wildlife in Mozambique was made. The report emanating from this air survey also highlighted the crucial part played by Gorongosa Mountain in providing the perennial surface water which traversed the heart of the Park system (Tinley et al. 1968). This historic air survey and the resulting report had the desired effect of enthusing the authorities to provide a light aircraft for all ensuing research in the territory, and twice a year for air census of Gorongosa and the Marrameu Buffalo Reserve in the Zambezi Delta. An agreement was made by the Veterinary authorities with the Chimoio Airclub for the use of a highwing Cessna monoplane which could be called on, even at short notice. Soon after, the first air count of the legendary buffalo herds of Marromeu in the Zambezi Delta was made in December 1968 (Tinley 1969a).

In October 1969 an ecological survey was made of the Southern Coast in the Bazaruto region which resulted in the proclamation of the first marine park and second national park in Mozambique, the Bazaruto Marine National Park (Tinley 1970a). The survey was continued inland in November to cover the entire Arid Savanna region between the Limpopo and Save Rivers (Tinley 1970b) known as Gazaland, which later resulted in the proclamation of Banhine and Zinave (Save) areas as national parks.

The programme of activity outlined above, and by the references, shows that the study of the Gorongosa ecosystem did not enjoy unbroken attention during those four years. As most of the interruptions were not much longer than a month, and the writing of reports and publications was all done at the Gorongosa main camp, it was possible to maintain a semblance of recording continuity, especially in phenological events. The collation of these data into a related whole serves as an ecological base for future studies and management in Central Mozambique and as a record of a unique piece of wild Africa, whose future as a viable, productive, natural system remains an open question.

On arrival at the University of Pretoria to write up the Gorongosa data for thesis puposes, I soon found, through access to excellent reference libraries, that many of my findings merely substantiate or elaborate those of older studies, of up to nearly a century ago. Thus readers should not be surprised at finding references in this study going back to the last century. It would appear that the 'old' schools, which produced Darwin, Wallace, Woodworth, Adams, Cowles, Smuts, Fraser Darling, Monod and others, were integrative and holistic and the subsequent 'modern' schools have been divisive, or mereological, and compartmented.

Though it is superflous to use the prefix 'geo-' for ecological dynamics, it is used here in emphasis because most students of ecology in southern African approach the subject purely from a plant or animal viewpoint. In this regard, only one amongst the many definitions of ecology and ecosystems (that of Dyksterhuis 1958), includes energy relations, and the climatic and geological processes as an integral part of the definition. His definition reads: '... the ecosystem involves the accumulation, circulation and transformation of energy and matter through such biological processes as photosynthesis, herbivory and decomposition, with the non-living part involving precipitation, erosion and deposition, reacting to the living part and with coactions between organisms' (Dyksterhuis 1958).

NOTE:
All Mozambique place names in the text are spelt according to the published Portuguese maps of the territory. The 'h' used in tribal names by the Portuguese is equivalent to 'y' in English, for example 'Banhine' is pronounced 'Banyine'.

REFERENCES / BACKGROUND

Abrard, R. 1928. *L'Eocene de Cheringoma (Mozambique)*. Bulletin de la Société Géologique de France, pp.91-92.

Dutton, T.P. & Dutton E.A.R., 1973a. *A preliminary survey of the Chimanimani Mountains and adjoining area with a view to its creation as a conservation area.* Report to Veterinary Department of Mozambique Government.

—1973b. *Preliminary ecological reconnaissance of the "Reserva Especial do Gile" and the adjoining "Regime de Vigilância": District of Zambezia.* Report to Veterinary Department of Mozambique Government.

Dyksterhuis, E.V. 1958. *Ecological principles in range evaluation*. Bot. Rev., vol. 24, pp. 253-272.

Fernandes, J.F. 1968a. *Os solos da Serra da Gorongosa e sua capacidade de utilizeçao.* Instituto de Investigação Agrária de Moçambique (I.I.A.M.), communication no.7

—1968b. *Os solos do Parque Nacional de Gorongosa.* Instituto de Investigação Agrária de Moçambique (I.I.A.M.), comm. no.19.

Gomes E. & Sousa A. 1966. *Dendrologia de Moçambique.* 2 Vols. I.I.A.M. Serie Memorias. Imprensa Nacional, Lourenço Marques.

Macedo, J.M. De Aguiar 1966. *Relatório preliminar de diligência ao Parque Nacional e â Serra da Gorongosa.* Mim. report (Botanical survey).

Mouta, F. 1956. *L'effondremente de L'Urema, extreme sud des "Rift Valley" au Moçambique.* CCTA, 1st Meeting of East-Central Regional Committee for Geology, Dar Es Salaam, pp. 21-122 & Fig.

Pedro, J. Gomes & Barbosa, L.A. Grandvaux 1955. *A vegetação. Esboço do reconhecimento ecológico - agrícola de Moçambique.* Lourenço Marques: Centro de Investigação Científica Algodoeira, Mem. e Trab, No.23, Vol. II & vegetation map at 1:2 million.

ReaL, F. 1966. *Geologia da bacia do Rio Zambeze (Moçambique).* Junta de Invest. do Ultramar, Lisboa.

Rocha Faria, J. & Mendes D.A. 1966. *Algumas notas sobre o clima do Parque Nacional da Gorongosa.* Serv. Meteor de Moç. SMM 25, MEM. 23.

Rosa Pinto, A.A. Da 1959. *Um esboço da avifauna sedentária da regiaõ da Gorongosa.* Proceedings of the 1st Pan-African Ornithological Congress, Ostrich Suppl., No.3, pp. 98-125.

Silva, J. Augusto 1965. *Gorongosa: shooting big game with a camera.* Empresa Moderna, Lourenço Marques. (Translated from the Portuguese by António J.O. de Freitas).

Teale (Thiele), E.O. 1924. *The geology of Portuguese East Africa between the Zambezi and the Sabi Rivers.* Trans. Geol. Soc. S. Afr., 26, pp. 103-159.

—& Wilson, R.C. 1915. *Portuguese East Africa between the Zambezi and the Sabi River: A consideration of the relation of its tectonic and physiographic features.* J. Geog., 65(1), pp. 16-45.

Tinley, K.L. 1969a. *A first air count of the buffalo of Marromeu.* Veterin. Moçamb. 1(2), pp. 155-170.

—1969b. *The ecological limits of Gorongosa National Park. Mozambique: and the maintenance of wilderness.* Report to the Mozambique Government, Mim. (bilingual English/ Portuguese).

—1970a. *Proposed maritime national parks and a dugong and marine turtle sanctuary in the Bazaruto region of the Mozambique coast.* Report to the Vet. Dept. of the Moz. Govt.

—1970b *Parques nacionais sugeridas para a zona de savana arida de Moçambique.* Report to Vet. Dept. of Moz. Govt.

—1971a. *Lake St. Lucia and its peripheral sand catchment.* WiIdlife Soc. of S. Afr. Pub. Report to the Water Affairs Dept. of South African Govt.

—1971b *Etosha and the Kaokoveld.* African Wildlife (suppl.), vol. 25(1).

—1971c. 'The conservation of ecosystems and tourist impact upon these and their custodians'. In *Nature Conservation as a form of land use*. Proceedingsof the SARCCUS Symposium. Govt. Printer, Pretoria, pp. 27-42.

—1971d. *Determinants of coastal conservation: diversity and dynamics of the environment as exemplified by the Mozambique coast*. Ibid. pp. 124-153.

—1971e. *Sketch of Gorongosa National Park.* Ibid. pp. 163-172.

—1972. *Protection and utilization of Mozambique ecosystems: a pictorial atlas.* Presented at first Congress on Conservation in Portuguese Africa, Sa da Bandeira, Angola.

—1973a *Base plan for rescue and translocation of wildlife from the Caborabassa Dam area in Mozambique.* Report to Vet. Dept of Moz. Govt.

—1973b *Request for the establishment of an applied ecology section for the study, planning and management of all parks and reserves in Mozambique.* Mim. Report to Vet. Dept. of Moz. Govt.

—Tello, J.L.P.L. & Dutton, T.P. 1968. *Primeiro recenseamento aérea dos grandes ungulados selvagens: Parque Nacional da Gorongosa (Mozambique).* Report to Vet. Dept. of Moz. Govt.

—& Sousa Dias, A.H.G. De 1973. *Wildlife reconnaissance of the mid-Zambezi valley in Mozambique before formation of the Caborabassa Dam.* Veterin. Moçamb, vol. 6(2), pp. 103-131.

—& Dutton, T.P. 1973. *Alternativas sugeridas para os traçados da linha ferra e da estrada para que a Reserva do Maputo possa subsistir.* Mim. Report to Vet. Dept. of Moz. Govt.

—Rosinha, A.J., Tello, J.L.P.L. & Dutton, T.P. 1976. *Wildlife and wild places in Mozambique.* Oryx, vol.13 (4), pp.344-350.

Vasse, W. 1909. *Three years' sport in Mozambique*. Pitman, London. (Translated from the French by R. & H.M. Lydekker).

Vaughan-Kirby, F.V. 1899. *Sport in east central Africa*. Rowland Ward, London.

Contents

PART 1 PERSPECTIVE

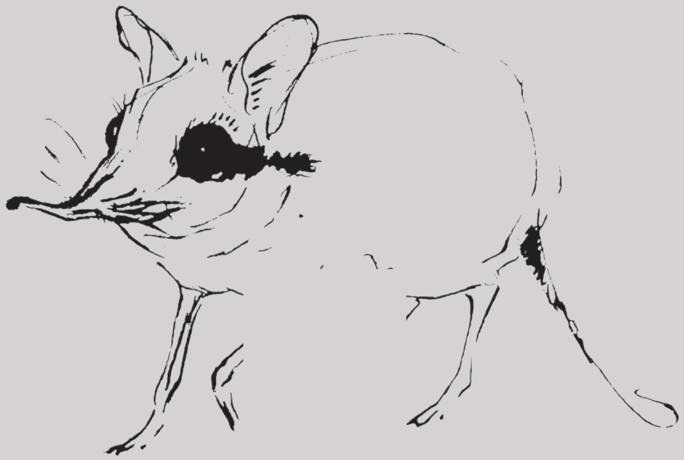
PART 2 CORRELATION

PART 3 GORONGOSA PATTERNS

APPENDIX

PART 1

PERSPECTIVE



Chapter 1

Salient Features

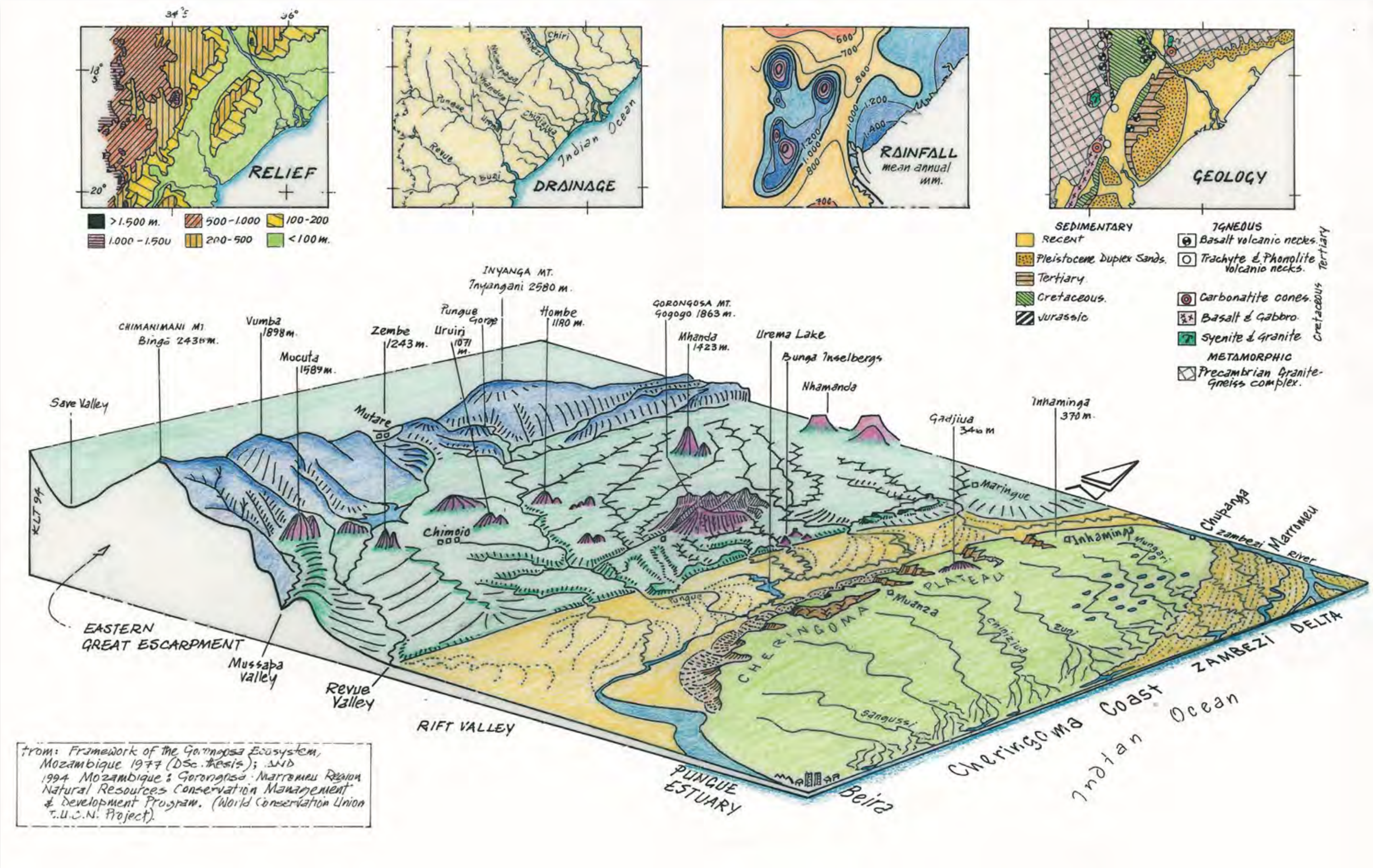
Salient Features

1.1 GEOGRAPHIC SETTING

Gorongosa National Park is situated in the geographic centre of Mozambique, astride the southern end of the Great Rift Valley system of Africa, which extends through East Africa from the Red Sea to Mozambique. The Gorongosa ecosystem is contained within the co-ordinates 18° 10'S to 19° 20'S and 34°E to 35°E, on the eastern, Indian Ocean, coast of Africa between the Zambezi and Pungue Rivers (Fig. 1.1).

Lake Malawi (Niassa) and the Shire River which drains it south to the Zambezi, lie in the Niassa Trough sector of the Rift. The Rift Valley crosses the present course of the Zambezi at the Shire junction and extends south in a rectilinear curve to inland of the port-town of Beira where it branches and runs out in a southwest direction to form the Buzi Trough, and southeast to disappear in the sea between Beira and the old Arab port of Sofala. The southern-most, Mozambican, sector of the Rift, known as the Urema Trough, is enclosed on either side by higher midlands country, that on the western margin is surmounted by the isolated block of Gorongosa Mountain at 1,863 m. The mountain is 160 km inland from the sea, and the centre of the Rift Valley within the same transect is 120 km. Inland the nearest large highland massifs to Gorongosa are the Mozambique–Rhodesian (Zimbabwean) Escarpment 100 km inland to the west rising to 259.5 m at Inyanga, and the isolated Morrumbala Mountain 150 km to the northeast near the confluence of the Shire with the Zambezi River (Fig. i).

A remnant of the former oldland coast plain was left as an isolated upland block by the downthrow of land in the trough faulting of the Rift Valley, and this remnant forms the steep eastern side of the Urema Trough, known as the Cheringoma Plateau (geologically, actually a water table in profile).



From: Framework of the Gorongosa Ecosystem, Mozambique 1977 (DSc. thesis); AND 1994 Mozambique: Gorongosa · Marromeu Region Natural Resources Conservation Management & Development Program. (World Conservation Union I.U.C.N. Project).

LEFT: Figure 1.1

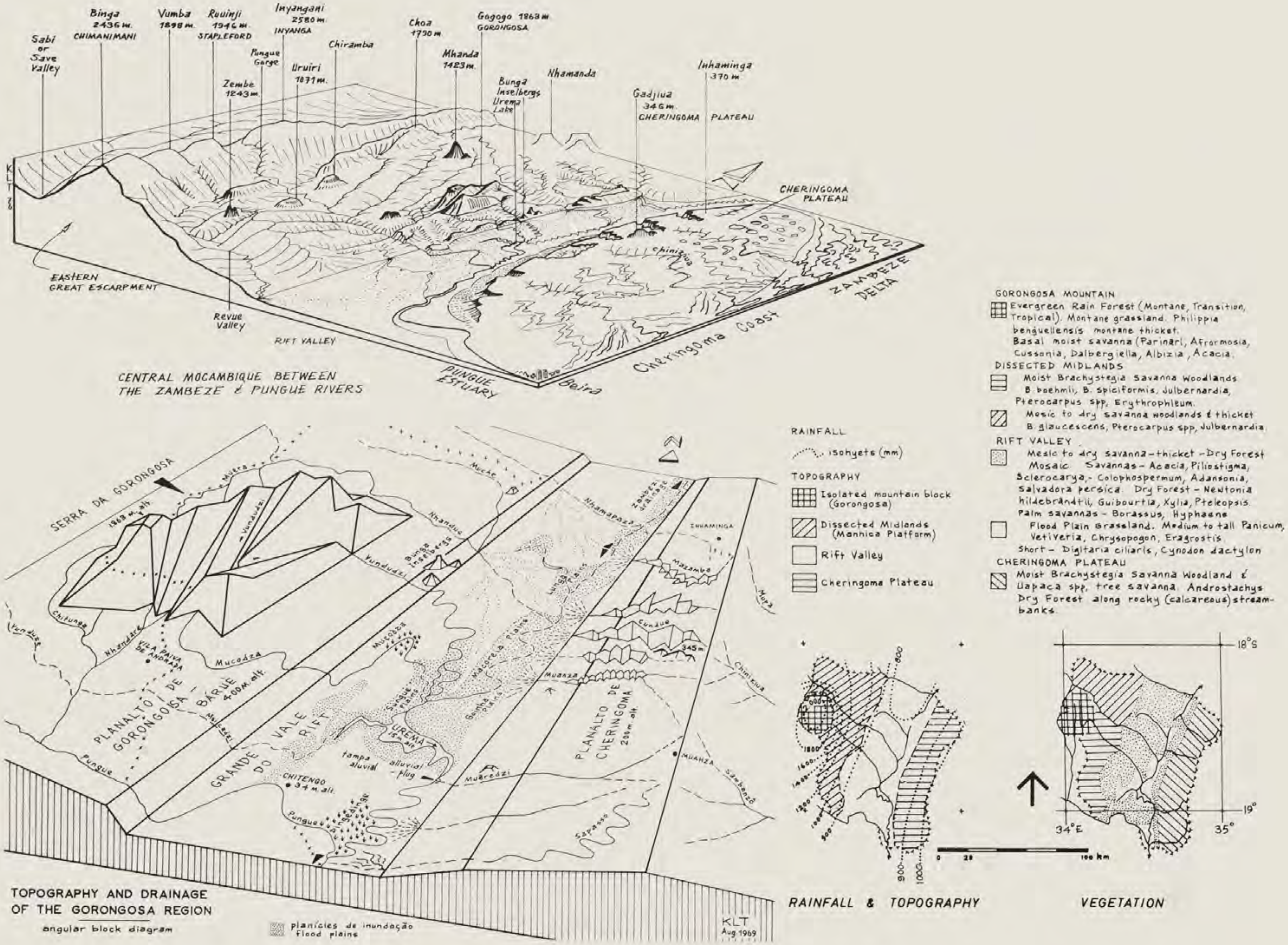
The regional landscape of the Gorongosa-Marromeu conservation area.

1.2 FORM, CLIMATE, COVER

The build of the Gorongosa region is dominated by the Rift Valley trough, whose alluvial floor averages 40 km in width and lies between 15 and 80 m above sea level. The centripetal drainage of the Rift floor is collected by the Urema Lake which forms the lowest part and as the basin is partially endoreic it is the effective local drainage base level. When filled, the basin discharges to the Pungue River which forms the southern boundary of the park. The upper edges of the trough rise obliquely to form the Cheringoma Plateau (300 m) on its eastern side, and the deeply incised Báruè Midlands (400 m) on its western side. Perched on the western Midlands within 21 km of the trough is Gorongosa Mountain which is 20 by 30 km in size and attains 1,863 m at its highest point (Fig. 1.2).

RIGHT: Figure 1.2

Salient landscape features.



As Gorongosa Mountain is the only eminence in the region which stands in the path of moisture-bearing winds of which the most constant are the southeast trades, it forces their ascent, resulting in heavy orographic rains to its confines. The mountain is a pluton composed of fine-grained granite and is covered by rain forest with montane grassland and fynbos on the summit areas, which forms an effective sponge capturing and releasing water in a constant radial pattern of flow. The perennial streams born on this island of high rainfall, receiving more than 2,000 mm per annum, form a key to life in the surrounding midlands and adjacent Rift Valley. Three of the four main streams which rise on the mountain traverse the Rift floor and meet at the Urema Lake.

The Midland is deeply dissected spur and valley country developed on Precambrian metamorphic gneisses and migmatites. This is covered by tall *Brachystegia* (miombo) savanna woodland on sandy skeletal soils and swarms of granophyre and dolerite dykes radiate north and south of the mountain. The latter produce fertile red oxisols which break the otherwise widespread monotony of poor soils in the Midlands. Rainfall is more than 1,000 mm on the Midlands falling mainly in summer but with some rain in the winter; precipitation variability is only 28%.

By contrast, the Rift Valley has a rainfall of 840 mm with a markedly arid winter despite the frequency of heavy valley fogs. Rain variability is more than 60%. The Rift floor has the greatest variety of ecosystems in the region, supported by the mosaic of different types of alluvia and the seasonal flooding of the plains. Vast seasonally inundated grasslands are dotted with patches and fingers of tall acacia, mopane and combretum savannas, dry forest on sands and myriads of seasonally rain-filled pans and termite hill thickets.

The genesis of the surface configuration of the Rift floor has been dominated by the discharge of rivers from the sides of the trough. The alluvial fans, built outwards from the Rift sides by these rivers, have pinched off the drainage of the trough resulting in a necklace of seasonally flooded grasslands, with savannas invading all the convex surfaces.
Of these constrictions, that formed by the Muaredzi stream is unique. The greater area of floodplain grasslands (c. 600 km^2) and the Urema Lake owe their existence to this coincidence of nature— the periodic obstruction of the lake's exit by alluvium deposited by the Muaredzi stream which meets the Urema drainage at right angles from off the Cheringoma Plateau (Fig. 1.2/photos pages 10 & 11 'Key features of the Gorongosa Ecosystem'). Although the obstruction is small, it assumes extreme importance as it forms the main critical height controlling drainage of the Rift Valley plains, and is responsible for the partially endoreic nature of the Urema basin. Together with the water from Gorongosa Mountain, these are the two outstanding salient features of the Gorongosa ecosystem. The Rift Valley substrates support the greatest concentrations of wildlife remaining in Mozambique.

The Cheringoma Plateau which forms the eastern side of the Urema Trough is composed of massive Cretaceous to Tertiary limestones mantled by a cover of red and pallid sands. The red sands are deep, horizonless and compact, whilst the pallid sands of the dipslope plain have a high water table due to an impervious clay at about 1m depth. The water table has stepped steeper slopes facing the Rift into which deep cliff-sided limestone ravines have been cut. The shallowly inclined seaward dip slope ends in a broad, low coastal plain with mangrove swamp estuaries. The rainfall increases from the Rift sides parallel to the topography to just over 1,000 mm on the crest and thereafter to 1,400 mm on the coast, where rainfall variability decreases again to 28%.

In contrast to the miombo on the west of the Rift trough which occurs on deeply dissected hill country — 'hill miombo', that on the Cheringoma occurs on flat to slightly undulating terrain interspersed with fingers of waterlogged drainage line grassland (dambos) similar to the 'dambo-miombo' of the Zambezi-Congo watershed. The plateau is covered in tall miombo forming a mosaic on the seaward slopes with evergreen forest, *Philippia simii* heath, and swamp and gallery forests in the incised dambos. The seaward streams are all perennial, tea-coloured, peaty 'blackwaters'. The larger streams of the Riftward drainage are perennial only in their central parts, and only two, the Muaredzi and Musapasso, meet the Urema drainage directly, the others disappear into the sumps of sandy alluvial fans at the break in slope of the Rift sides.

RIGHT:

Ecosystem occlusion — grasslands being invaded by scrub and thicket.

PART 1

PERSPECTIVE

Chapter 2

Definition

Definition

2.1 PARK BOUNDARY LIMITS

Gorongosa National Park was the first, and until 1971 the only, national park in Mozambique. Gorongosa was first proclaimed as a game reserve of 1,000 km^2 on 2 March 1921. On 21 November 1935 the game reserve was enlarged to an area of 3,200 km^2. Gorongosa received national park status on 23 July 1960 (Diploma Legislative No. 1993), and at the same time the park area was enlarged to 5,300 km^2. In January 1966 the park area was reduced to its present size of about 3,770 km^{2,} mostly of Rift Valley floor and parts of the hill slopes forming the sides of the trough. All these straight-line and road limits excluded Gorongosa Mountain.

In 1968 and 1969 a special study, undertaken to determine the ecological limits of the park, revealed that the entire park system and a population of some 20,000 tribal cultivators west of the park were all dependent solely on the perennial water resource born on the isolated massif of Gorongosa Mountain (Tinley 1969). The ecological limits proposed in the above study enlarged the park to about 8,200 km^2 to include the greater part of Gorongosa Mountain and the remainder of the area delimited by all the local drainage received by the Urema depression on the Rift Floor. The crux of these proposals was to ensure that the park was made a viable entity by inclusion of the mountain in order to protect the primary water resource. Any effect of surrounding land misuse would thus be effectively confined to outside the Urema drainage basin. The ecological limits were determined by analysis of the salient factors governing the life requirements of man, and the large wild ungulates which require space to satisfy seasonal migrations. The third main feature was to ensure representation of viable examples of the full spectrum of ecosystems occuring in the region. The same study recommended extension of the park eastwards to the coast to include examples of the unique forests and swamps of the Cheringoma coast and to link with the Marromeu Buffalo Reserve in the southern sector of the Zambezi Delta.

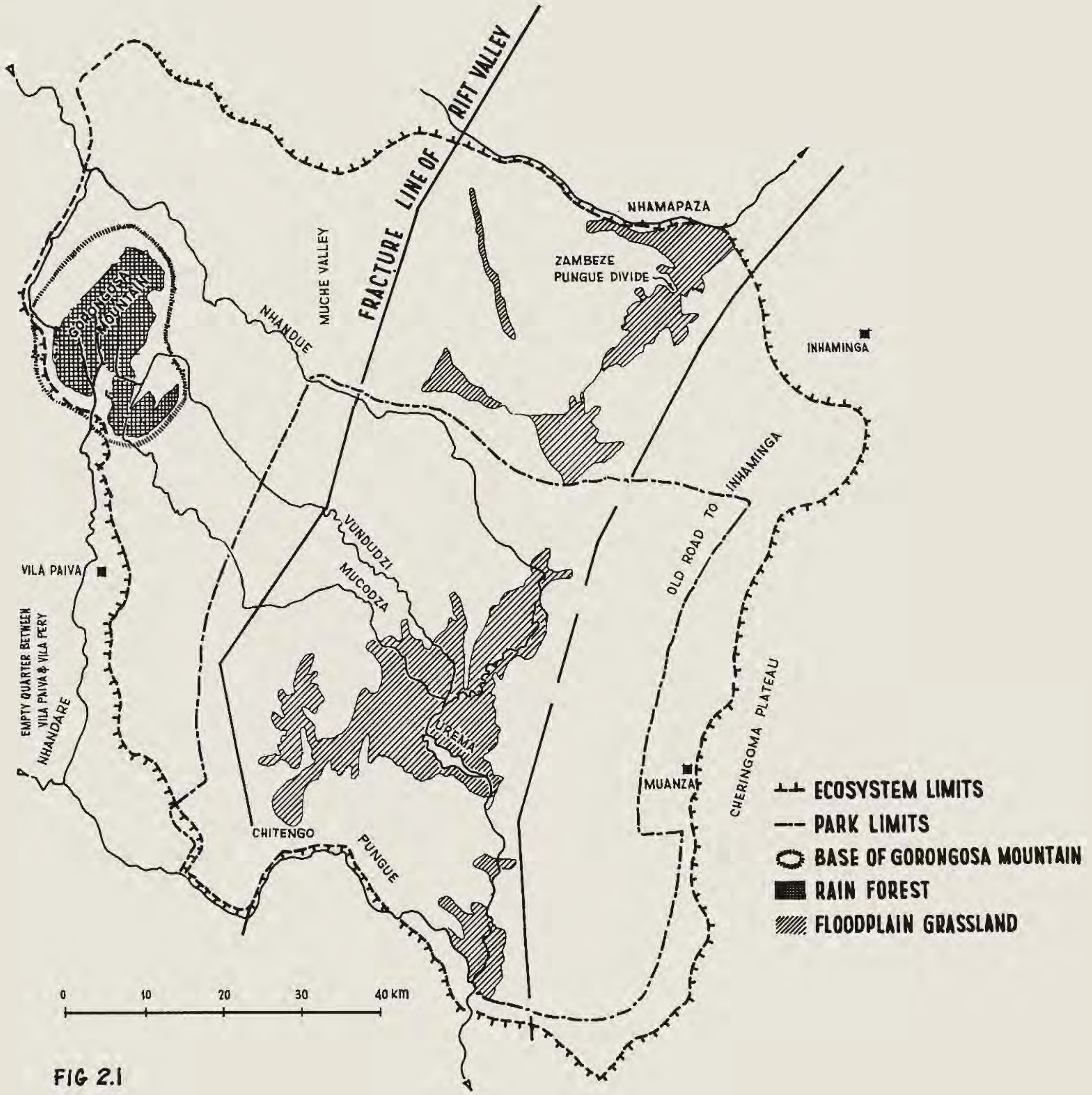


FIG 2.1

LEFT: Figure 2.1

Boundaries of the Park and the greater ecosystem.

The reduction of the national park area in 1966 marked the beginning of a political and conservationist defeatest attitude mollifying invasion of park area by tribal cultivators, and pressure from timber and safari companies to exploit as-yet undamaged natural resources within the park. Contraction of park boundaries meant that tribal cultivators who had invaded from the margins or had remained from the earlier cotton plantation days would, with each contraction, be conveniently 'left outside' the new limits. The land hunger of the surrounding cultivators was said to be a valid demand for this and other boundary reductions were envisaged. The truth, however, is that vast uninhabited areas of well-watered, high rainfall, miombo woodlands are and were available all around the park, especially in the midlands between the mountain and Chimoio (Vila Pery) area to the south-west—but there was a lack of game as it has been exterminated. The sole reason why the park area of low and unpredictable rainfall is called for by cultivators (or those behind them desiring ivory) is to get at the last meat resource—their hunger is for protein not land. Instead of authorities protecting this resource for rational utilization leading toward maximum benefit for the regional economy, it was politically expedient to rather give up these resources for eventual total elimination.

Until the present (1976), the 1966 boundaries have been maintained though there are constant pressures for its further reduction for exploitation. Since independence the Mozambique authorities have forbidden cultivation of Gorongosa Mountain above the 600 m contour around its base.

2.2 STUDY AREA

The Gorongosa ecosystem is that area delimited by almost all the drainage caught by the Urema Trough. The one exception is a seasonal 'sand river', the Nhandue, which enters the park in the north-west after rising far to the

Key features of the Gorongosa Ecosystem. Late summer rains aspect.

RIGHT:

A Mountain catchment,
B Urema Lake & floodplains,
C In the foreground the sill (alluvial plug) responsible for B formed by Muaredzi stream deposits from the right.

Key features of the Gorongosa Ecosystem. Dry season aspect four to five months later of part of the same area shown in the photo opposite, (page 10).

LEFT:

C Sill formed by alluvial plug clearly exposed by low-water conditions, displaying its key role in pinching off the Rift Valley drainage at this point.

High floodwaters inundating the Dingedinge Slacks at the Urema–Pungue confluence in midsummer (Jan. 1970).

RIGHT:

In the foreground, termite hill islands in various stages of development and erosion.

west on the Midlands near the base of the Great Escarpment. Apart from this river which rises outside the Gorongosa area, all the drainage into the Urema Lake is local from both sides of the Rift Trough. This Rift floor lake is a partial internal drainage basin which, when filled, overflows into the Pungue River.

Rightly, the study area should be referred to as the Urema ecosystem, but the region as a whole and the national park are named after Gorongosa Mountain. In addition the perennial water born on the mountain is the key to human and animal life in the whole region (Tinley 1969, 1971). The mountain was named after the first chief to settle there in the history of the tribes. Further south, between the Buzi and Save Rivers, is a small river which rises on the Buzi Coastal Plateau referred to as Gorongose (spelt with an *e* ending).

The Gorongosa ecosystem, therefore, comprises the entire park area plus the terrain west to include Gorongosa

LEFT:

The Dingedinge Slacks in the dry season. The same area shown on the left of the photo opposite (page 12), seven months later. The different green and brown grass tones indicate different soil moisture and salinity levels.

Mountain and its radial drainage, and eastwards to the divide on the Cheringoma Plateau separating the seaward and Riftward drainage. On the Rift floor the limit of the ecosystem in the north is the seasonal ‘sand river’, the Nhamapaza, close to which is the faint convex surface forming the divide between the Zambezi and Pungue drainage. In the south the perennial Pungue River is the limit as the convexities separating it from the Urema depression are formed by the alluvial deposits of this river.

From the divide along the crest of the Cheringoma Plateau, which is a cuesta in profile, the seashore is just under 100 km distant. On the white podsolized sands of the seaward dipslope is a mosaic of unique ecosystems comprising forests, heath, extensive grassy dambos and systems of forested streams with oval pans. Large estuaries are covered in some of the finest mangrove forests (containing nine species) on the

Mozambique coast. Some of these systems are not represented, or only fragmentarily so, elsewhere in Mozambique.

Presented with this unique montane to mangrove ecocline transect across a stepped landscape and climatic sequence parallel to the coast, I included the seaward sector as an extension of my study area, for comparative purposes, quite as much as for its distinctiveness.

RIGHT:

Cheringoma Coast with eroding inlet.

PART 1

PERSPECTIVE

Chapter 3

Approach

Approach

The observer must empty his mind and be
receptive only of the deer and the signs of the country.

Frank Fraser Darling 1937

A holistic ecological approach is used in this study. Emphasis is on the salient reciprocal relations and succession of the important biotic communities or their components with landscape processes. In many regions large changes in habitat structure, relative plant and animal biomass, species composition, and complete community replacement are wrought over contemporary time (Iet alone in geologic time) by normal geomorphic succession without any change in the local or regional climate. This succession is either due to factors which alter the soil water balance, or to the spatial replacement of land surfaces by erosion and sedimentation. It can also be due to within-habitat changes due to selection and influence of biotic competition and the activities of animals including man.

As correlations of these relationships and processes require both a total interacting framework and the details of the main components of that framework, presentation is divided into three sections. Part I titled PERSPECTIVE provides the essence of the Gorongosa ecosystem and the approach by which the details of Part II CORRELATION are built. Part III KALEIDOSCOPE attempts to relate the salient features of processes and correlations into an evolutionary whole caught at that particular stage in space and time by the study. Such an appreciation of ecosystem dynamics at the salient factor level, supported by detailed data, will then allow prediction of past, present, and future changes or tendencies. These criteria are central to the realisation of significant conservation management based on causes. The effects are, however, important for determining many of the causes.

3.1 ECOSYSTEMS

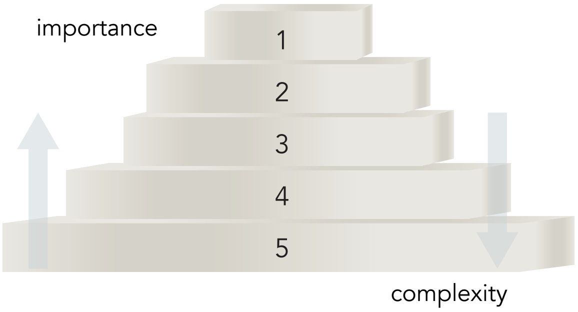
Ecosystems are of inordinate complexity. This feature is emphasized repeatedly in the literature, in the training process and by field experience. It is well known that disturbance to one part of an ecosystem can set up a chain reaction affecting many other components, the result of which are hard to imagine let alone predict. But each ecosystem is in fact governed by a few relatively simple *salient factors,* a feature of ecosystems rarely mentioned anywhere. The identification and protection of the salient factors holding an ecosystem together ensures survival of its components and processes over the long-term in a human temporal scale. In the geologic time scale, however, it would merely act as a damper to the tempo of inexorable landscape change. The method I have used over the years, with some success, for analysis of natural ecosystems is shown in Table 1, using the terms 'key' and 'master factors'. The most lucid exponent of salient factors analysis is by Ian McHarg (1969), whose entire approach to landscape planning is determined by the salient factors governing each ecosystem. His chapter titled 'Processes as values' is a masterly treatment of the method, and in three words synthesizes a main criterion of analysis. McHarg's methodology and terminology is more elegant and refined than my own although the same results can be obtained. I have, therefore, used his term 'salient' in preference to 'key and master factors'.

3.2 SALIENT FACTORS

Salient factors are the keystone elements holding an ecosystem together as a viable dynamic system. The loss of any one of these factors would cause perturbations (multidirectional shifts in trends) and replacement of the system or its component parts. The salient factors important at any one time are replaced by others through changes imposed by natural processes. Ecosystems are of various kinds and sizes and the salient factors controlling the viability of each will vary accordingly. In addition, not only is it usually impossible to study all the details and complexities of an ecosystem in a life time, it is also unnecessary, as once the salient factors have been determined further indepth study will not change their key importance.

TABLE 3.1
Hierarchy of Salience
(or of key and master factors)

LEVEL	LOCATION
1st Level:	Regional Ecosystem e.g. ocean, continent, island, desert, mountain, river basin. Natural processes of landscape evolution, climate, hydrography, geomorphic and edaphic controls. Extremes, opportunities and limitations expressed by the intrinsic features, and their controls.
2nd Level:	Major Elements (elements with the greatest impact, most importance or largest space requirements). Examples: 1. Man (hunter-gatherer, fisherman, pastoralist, cultivator, beekeeper, technological man). 2. Large wild ungulate migrations (seasonal limits and episodic occurrence: substrate controls in each sector). 3. Representation of the full spectrum of ecosystems. 4. Unique elements (e.g. scenery, aquifers, endemics, rare or endangered species).
3rd Level:	Individual Ecosystems (and Communities)
4th Level:	Macrobiotic Components (e.g. ungulates)



In each ecosystem there is a hierarchy of salience. This depends on the dimension of the ecosystem under study and on the components identified as requiring priority attention. The salient factors form a pyramid composed of five levels of salience (Table 3.1). In each level the factors are evaluated in a gradient of values from most to least. Either the maximum condition or the minimum can be the most important for different ecosystems. For example, a forest may require high soil moisture with good drainage, a swamp also requires high soil moisture but with poor drainage. What are the salient factors maintaining these two requirements and what are the implications? In certain circumstances fifth level components (microbiotic), such as tsetse-fly or *Anopheles* mosquito that are disease carriers, are moved up to the second level (Major Components) because of their impact.

These features require to be mapped at intervals to provide templates of the changing importance of various key and master factors to anticipate or predict what will result from their influences. In this way planning and management (protection and utilization) is causes-based on the salient processes and interactions governing a particular system or situation. The ecological study thus passes through the following cycle: (1) synopsis (salient factor analysis), (2) correlation, (3) synthesis, (4) application, (5) response monitoring, (6) re-assessment and back to (1). Most situations can, however, be adequately handled by going directly from (1) to (4) to (6) and back to (1) again. As most management programmes are biologically biased, they typically start and stop at (2) or leap to (4), setting in train a bewildering new series of interactions superimposed over the natural ones that have not been identified. Management at all levels thus requires a rational, explicit and replicate method (McHarg 1969) from which to work out from and back to. Another value of the method is that it enables studies to get to the root causes rather than attempt protection and control by dealing with the effects.

As natural processes are dynamic, it is necessary to identify and evaluate those operating under present circumstances. In addition, it is vital to identify the tendencies exhibited by the present processes toward future changes. Many of these tendencies are successional and are thus part of an inexorable change which can only be slowed or ameliorated. Without the last data, no valid evaluation or interpretation can be made with the other information for predictive purposes and management action.

The five levels of salience show a pyramid of increasing complexity from top to bottom and increasing importance from bottom to top (Table 3.1). The gradient of importance is based on the precept that if the ecosystem as a whole is maintained, survival of its components is ensured, at least in a human time scale.

Ecosystems study requires the worker's complete immersion and empathy with the subject to 'feel' in the Taoist philosophic sense by becoming the ecosystem oneself—I am the inselberg, the plains and the totality of the elements and life at play on them. Such a sixth sense or 'bump' of ecology is similar to that possessed by some individuals for direction. Primitive man confronted with a landscape can assess its qualities as his bump of ecology is probably honed to maximal awareness by survival of the multiplicity of experiences that he has been exposed to since birth. His search for food, particularly, educates him into ecological awareness; his stomach is, therefore, the master tutor.

This total identification with, and joy in, their habitat is a feature of most hunter-gatherer peoples of the world, particularly the American Indian of North America (Grey Owl 1931; Mails 1974, pp. 18–19); The Australian Aborigine (McCarthy 1957); the Mbuti Pygmies of the equatorial rain forest (Turnbull 1961); the Bushmen and members of pastoral and cultivating tribes that still practice hunting and gathering; and some modern naturalists. Bushman claim they have a telepathic system which enables them to feel the presence of springbok on the far side of a hill, as they are so keenly aware of the wind blowing through the dark hair on the animals flanks, or the presence of strangers long before they have arrived (Bleek & Lloyd 1911; van der Post 1961; Eve Palmer 1966 p. 74; p. 138). Turnbull (1961) describes how, on returning to their forest home after an excursion to neighbouring tribal cultivators, pygmies became more and more animated and excited until they spontaneously shouted greetings to the forest, expressing the sheer joy they felt in the completeness of life.

Despite the fact that students attracted to research are probably those with more than usual curiosity, this personification of the subject in the imagination is vital to modern man in producing original research as it enables him to picture in his mind how the processes work (Beveridge 1950). It allows the subconscious to absorb the total make up of the subject and its unique features; the conscious acquisition of the details can then be worked on in a context which allows the mind to use creative thinking to attain orginality or new ways of seeing the same subject. The tools for forward moving creative thinking are by the use of (1) stepping-stone (intermediate impossible), (2) random juxtaposition of ideas, and (3) reappraisal of ideas reckoned to be perfectly right and absolute (challenge for change) (De Bono 1973).

The trained ecologist entering fieldwork for the first time has to learn how to identify completely, and attain the telepathic awareness of the hunter-gatherer, with the ecosystem. As even the unique rapport primitive people have with their environment is unable to develop intellectually as it is restricted by superstitions and beliefs, and day to day survival; likewise, modern education conditions individuals and traps cultures into accepted ways of doing things, channeling ideas and disciplines to the specialised subservience of ideological, technological and economic values (Reich 1970; Tinley 1974). Only by integrating disciplines and ideas through lateral thinking (De Bono 1973) can modern man transcend all these conditioning processes to restore material values as the tools of men, and human and environmental values as the determinants of life.

It is thus not enough to recapture the ecstasy of wonder and curiosity at the spiritual and intellectual level and identify completely with one's environment without extracting the mind from conditioned thinking. Combining these as part of the evolution of the self realises the core of existence. What is required is the kind of empathy obtained by some unorthodox experimenters with their living plant subjects (Tompkins & Bird 1974).

The diversity of natural systems and habitats in a region means an increased array of choice (plasticity) for organisms under changing environmental conditions, as many kinds of systems each have different responses and potentials to these changes. Evolutionary success can in one sense be defined as the maintenance or increase of reproductive fitness by opportunistic response to changing conditions. This response can be by migration, a change in habitat use, or by organic change.

Consider the relatively poor array (brittleness) of habitat variety expressed by a pure grassland as opposed to a compound habitat such as a savanna. These differences in variety are intrinsic expressions of brittle as against plastic ecosystems. In the same way, fullness of the human condition can be defined by the old saying 'variety is the spice of life'. In ecology a good grounding in earth and life sciences is in vain without its maturation through a diversity of field experience. Total identification with one's subject is required on the one hand, whilst exposure to other biomes and life ways is as vital for comparison, stimulation and new approaches. A balance is required so that the worker neither becomes desensitized by staying too long in one site, growing with the changes and thus not able to 'see' them, nor merely occupying the superficial role of visiting scientist.

Those who have maintained a balance of in-depth studies correlated with salient analyses in other systems, for example, have the opportunity to cross-correlate disciplines and attain originality and meaningful expression by a freshness maintained through the stimulation of variety. This faculty is well exemplified by a Professor Theodore Monod or Fraser Darling who in one week can lucidly assess the co-relations and their limiting factors in an ecosystem or region where local scientists have spent 20 years of effort without seeing the wood for the trees. My most unforgettable experience of looking at something and not recognizing it was in my late teens, when I was out in the veld with friends one day, and casually turned over a loose stone at my feet. When it was pointed out to me that the object was a prehistoric hand-axe, in a blaze of enlightenment I was suddenly able to recognize stone-age implements everywhere. My earlier 'blindness' had been in spite of growing up amongst primitive tribes on a farm where sharpness of eye was honed every day by playing and hunting in the veld. Thus evolution of the self, too, comprises lifting as many of these 'blinds' as possible by exposure to variety and by striving for versatility. Like other animals we need to undergo periodic change or migration. It can thus be said that the maintenance of diversity is fundamental for the evolutionary success of both ecosystems and individuals— variety is life, as this thesis plans to show.

REFERENCES / PERSPECTIVE

Beveridge, W.I.B. 1950. *The art of scientific investigation.* Heinemann, London.

Bleek, W.H.L. & Lloyd, L.C. 1911. *Bushman folklore.* Allen and Unwin, London.

Darling, F. Fraser 1937. *A herd of red deer.* University Press, Oxford.

De Bono, E. 1973. *Po: Beyond yes and no.* Penguin Books.

Grey Owl 1931. *The men of the last frontier.* Country Life, London.

Mails, T.E. 1974. *The people called Apache.* Prentice-Hall, New York, pp.18-19.

McCarthy, F.D. 1957. *Australia's aborigines: their life and culture.* Colorgravure Publications, Melbourne and Adelaide.

McHarg, I.L. 1969. *Design with nature.* The Natural History Press, New York.

Palmer, Eve 1966. *The plains of Camdeboo.* Collins, London.

Reich, C.A. 1970. *The greening of America*. Random House Inc., New York.

Tinley, K.L .1969. *The ecological Iimits of Gorongosa National Park, Mozambique: and the maintenance of wilderness.* Report to the Mozambique Government. (bilingual English/ Portuguese).
—1971. 'Sketch of Gorongosa National Park' in *Nature conservation as a form of land use.* Proceedings SARCCUS Symposium, Govt. Printer, Pretoria, pp. 163-172
—1974. 'The study of the "incomprehensible" by the "incompetent"' in *Training in environmental sciences at South African universities*. Symposium Proceedings, CSIR.

Tompkins, P. & Bird, C. 1974. *The secret life of plants.* Allen Lane, England.

Turnbull, C.M. 1961. *The forest people.* Chatto & Windus, London.
—1963. *The peoples of Africa.* Rockhampton Press, London.

Van Der Post, L. 1961. *The heart of the hunter.* Hogarth Press, London.

PART 2

CORRELATION

Chapter 4

Climate

OPPOSITE:

Orographic thunderstorm over Gorongosa Mountain.

Climate

4.1 INTRODUCTION

Central Mozambique is situated 19° south of the equator on the east coast of Africa at about 34° east longitude, and lies due west of Madagascar Island, from which it is separated by a 400 to 850 km wide strait, the Mozambique Channel. Madagascar Island is about 1,600 km in length and with a high mountain spine along its east coast it effectively blocks off the direct influences of the Indian Ocean. Almost the full length of Mozambique thus lies in the lee or shadow of Madagascar which causes far reaching climatic implications.

Apart from the local and regional climatic data personally collected, or recorded by stations, these notes on climatic processes are obtained mostly from Thompson (1965), Tyson (1969) and Griffiths (1972). Due to its geographical position, Central Mozambique, though lying directly in the path of the southeast trade wind belt, is close to the southern limits reached by the northeast monsoon in summer. The major determinants of climate in this region are, therefore, the zonal wind systems of both the Southern and Northern Hemispheres. The southeast trades are air masses blowing from the semi-permanent tropical high pressure centres of the South Indian Ocean. The monsoon system is an alternating macroscale air stream flow blowing in opposite directions in summer and winter. During the boreal winter, some of the air streams emanating from the Asian Continent traverse the northwestern Indian Ocean to the east coast of Africa and pass south of the equator to Mozambique and Madagascar, where they contribute to precipitation processes or drying, depending on their trajectory. During the boreal summer the air streams are reversed. The southwest monsoon, of recurved Southern Hemisphere southeast trades, blows towards the Asian landmass from the equator and forms the major air mass contribution to Arabia, India and Burma at this time (see Fig. 4.5).

In midsummer, tropical cyclones (hurricanes) move from east to west and are mostly intercepted by Madagascar. As the hurricane tracks re-curve southwards, chiefly along the west coast of Madagascar or in mid-channel, drought conditions occur in Mozambique over the months of their greatest frequency (Fig. 4.6 and personal data). Conversely a hurricane track which approaches or crosses the Mozambique Coast causes floods.

Interrupting the interplay between two major zonal air flows are invasions of temperate depressions moving from west to east and up the southern coast. In addition to these polar low pressure centres are equatorial low pressure troughs formed by recurved South Atlantic Anticyclone air, known as Congo air. This low pressure trough system penetrates southwards during the austral summer over the interior plateau of the subcontinent.

The tropical anticyclone centres do not occur vertically from ground level upward but are inclined westward with increasing height. Thus, at a height of 6 km the east coast cell is centred over South West Africa. This displacement causes an opposing flow of easterlies at the surface and of westerlies at 6 km. The persistence of the upper westerly geostrophic air stream is made conspicuous by the northeasterly anvil spread of cumulonimbus which develop on Gorongosa Mountain (Fig. 4.9). Beneath these major wind systems are tertiary surface, diurnal air reversals of sea and land breeze circulations between the Eastern Great Escarpment and the Mozambique Channel, which are probably linked with similar centripetal flow form the western slopes of Madagascar. The nocturnal katabatic land breeze component is strongly developed throughout the year whenever clear skies occur. The sea breeze, or anabatic component, is due to deepening of the trade wind ground-wards, from above the cold air drainage flow, as the surface of the land heats up in the mornings.

The interaction of the above air masses and their streamlines produce a moving pattern of interacting anticyclone and cyclone centres which are responsible for either precipitation, or alternatively, drought.

4.2 SEASONAL CLIMATIC CONTROLS

Summer

In the southern summer the major determinants of climate in Central Mozambique are two anticyclone systems and two low pressure areas. The high pressure cells are those over the Asian landmass, and the other is situated midway between Africa and Australia and is known as the South Indian Ocean high. A low pressure cell (heat low) occurs over the interior of the sub-continent, or is associated with the Zambezi Valley. A persistent low pressure cell occurs over the Zambezi Delta, or seaward of it, extending at times from Beira to Pebane (as plotted on synoptic charts).

Part of the Asian air masses flowing south, as the northeast monsoon, maintain an oceanic trajectory and are thus moist. Another branch curves over the East Africa interior via Somalia and the Rift Valley heat lows to Central Mozambique, where they are very dry winds.

The northeast monsoon reaches its southern geographical limit in midsummer at about 16^0 to 17°S, and the southeast trades are then confined mostly south of the 18° latitude. The interface between these two air masses along an east-west trough is generally regarded as being the southern position of the Inter-Tropical Convergence Zone (ITCZ).

Winter

In the winter dry season the ITCZ moves north, with a northward shift in the South Indian Ocean anticyclone, resulting in a deepening and freshening southeast trade wind as its air masses are re-curved past the equator to form the southwest monsoon bringing the rains to Asia.

4.3 CLIMATIC CLASSIFICATlON

The sector of Central Mozambique forming the study area all falls within Köppen's Tropical Savanna Climate (AW), with the exception of a small island of Warm Temperate Rainy Climate (CW) formed by Gorongosa Mountain (Faria & Goncalves 1968). Köppen's Steppe Climate (BS) is noted by these authors on either side of the study area in the Zambezi Valley and from the Save Valley southwards (Gazaland). However, analysis of Rift Valley data recorded at Chitengo since the publication of the above authors shows that the Urema Trough experiences a BS climate in six years out of eight.

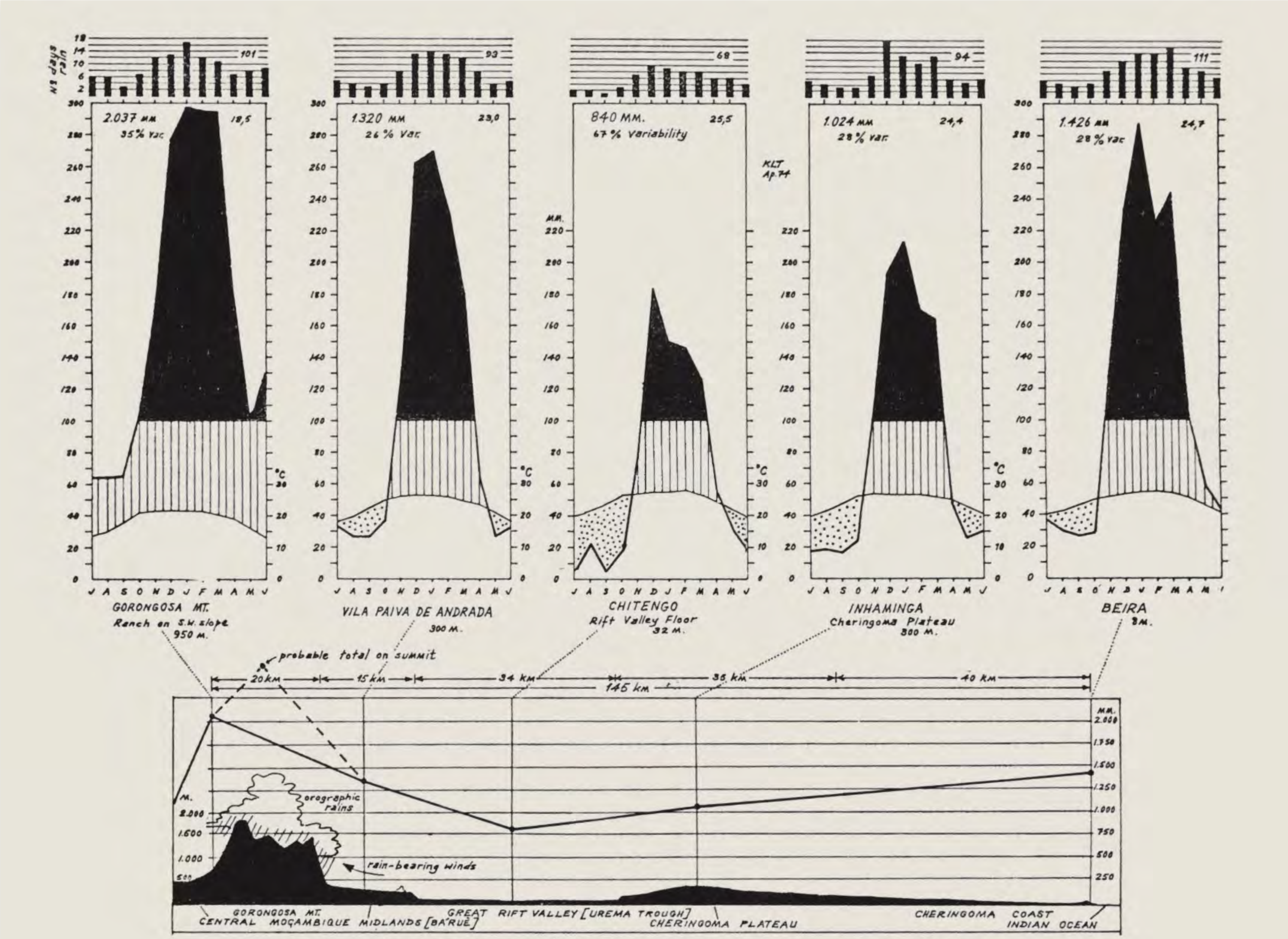


FIG 4.1 OROGRAPHIC & MARITIME CONTROL OF RAINFALL REGIMES IN THE GORONGOSA - CHERINGOMA REGION.

LEFT: Figure 4.1

Orographic and maritime control of rainfall regimes in the Gorongosa–Cheringoma Region.

De Martonne's Index of Aridity—P/ (T + 10)—separates the four main physiographic regions of the Gorongosa–Cheringoma transect into: (1) Mountain (90%), (2) Midlands (41 %), Rift Valley (23%), Coast Plateau (30%), and land-sea junction (41 %). The high Aridity Index for the Urema Trough is of the same order as those in the Zambezi Valley and Gazaland areas.

4.4 CLIMATIC PARAMETERS

As the various climatic components are summarized in diagrammatic form the relevant data and their seasonal relationships can be read from these. The longterm climatic features of the physiographic units in the Gorongosa–Cheringoma transect are depicted by comparative (Gaussen 1955) climatograms in Fig. 4.1.

Radiation, Insolation and Day length

see Fig. 4.2

Temperature

see Figs. 4.3 and 4.13

Humidity

see Table 4.1

Cloud Cover and Cloud Types

see Fig. 4.4

Wind

see Fig. 4.5 for regional airstreams, and Figs. 4.7 A and B for frequency of direction of winds in the Rift Valley. Hurricane tracks are plotted in Fig. 4.6

Rainfall

The mean annual isohyets for the whole territory are depicted in Fig. 4.8. The trigger effect of the Gorongosa orographic high on cumulonimbus thunderstorm development, or instability rains (*guti* drizzle), is shown by a series of sketches, drawn at intervals on one day, of the growth of a thunderstorm (Fig. 4.9). The importance of this feature on all life surrounding the mountain is highlighted by a variety of examples throughout the thesis. Its key position in the water cycle of the Gorongosa ecosystem is emphasized by the contrasting precipitation regimes of the adjacent Urema Rift Valley 15 km distant (Fig. 4.1, 4.10 and 4.11). Nevertheless, dry months in the orographic rain forest climate are experienced at intervals (Table 4.2).

TABLE 4.1
Relative Humidity % (Means)

		MONTHS											
LOCATION		Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
1	Vila Paiva de Andrada	75	71	66	63	65	71	75	76	78	76	74	74
2	Vila Machado	68	69	66	65	66	74	72	74	74	71	69	70
3	Inhaminga	66	65	64	63	67	70	72	72	74	72	68	67
4	Beira	81	80	77	76	76	77	77	78	78	78	78	80

KEY
1 = Midlands
2 = Rift Valley Floor
3 = Cheringoma Plateau crest
4 = Land-sea junction (Cheringoma Coast)

TABLE 4.2
Occurrence of dry months (<50 mm) in an orographic rainforest climate.
Recorded on the windward S slopes of Gorongosa Mountain (950 m alt.).

	MONTHS												
YEAR	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total P mm
Mean No. days rain	17	14	13	9	7	9	6	4	3	7	13	15	=117
1963										33	31		2 469
1964									20	38			1 985
1965				5		13							1 983
1966					38		36						2 022
1967													2 550
1968							43						1 804
1969							13		18		20		2 182
1970								13	20				1 970
1971				31			28	10	20				1 949
1972						50	45	12					1 871
1973									19				2 473
Occurence				2	1	2	5	3	5	2	2		

KEY
April 1965 = lowest rainfall recorded
July 1971 = end of month fire burnt out greater part of summit

LEFT: Figure 4.2

Radiation and temperature.

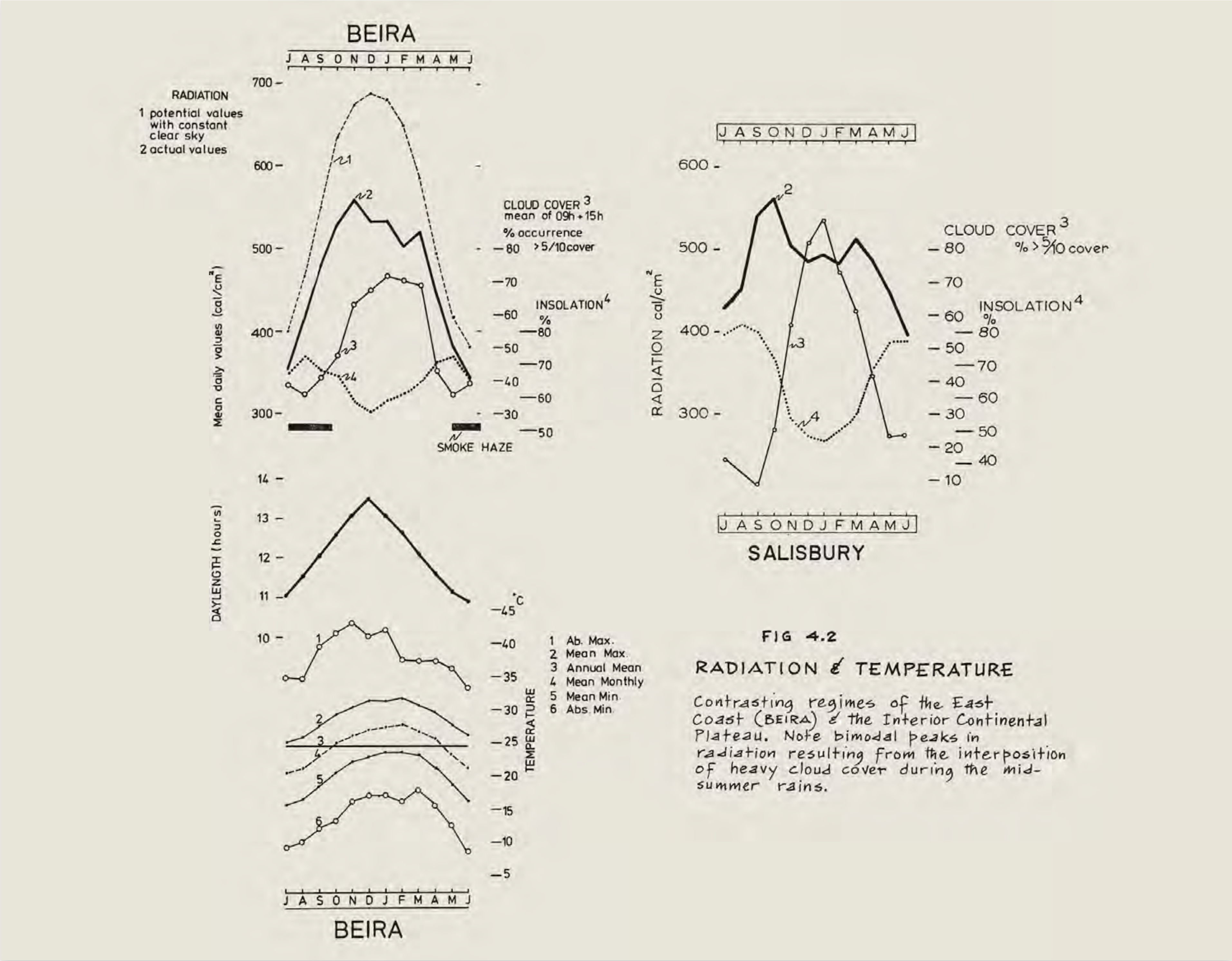


FIG 4.2

RADIATION & TEMPERATURE

Contrasting regimes of the East Coast (BEIRA) & the Interior Continental Plateau. Note bimodal peaks in radiation resulting from the interposition of heavy cloud cover during the mid-summer rains.

OPPOSITE:

Lake Urema with Gorongosa Mountain in the background.

A characteristic feature of precipitation along the coast and interior of Central Mozambique is the occurrence of rain, from congestus and cumulonimbus, being carried inland by the southeast trade on the interface with the underlying cool, saturated wedge of land breeze air flowing seawards (Tinley 1971). The processes involved appear to be similar to those described for the land breeze associated rainfall in Natal (Preston-Whyte 1970).

Fog

Two quite different kinds of fog occur in the ecosystem. An anabatic orographic fog or drizzle, which is known locally as *guti* along the Great Escarpment, or *chiperoni* in Zambezia and Malawi, and a low level nocturnal cool air, land breeze from the uplands to the sea (Fig. 4.12). The katabatic fog is carried by the land breeze far out to sea over the Mozambique Channel, and often clears at Beira only in midmorning during winter (Tinley 1971).

Guttation and Dew

A notable feature in all physiographic units is the occurrence of heavy dews. As can be ascertained by direct observation, however, most of this 'dew' is in fact guttation, that moisture exuded by plants at specialized pores termed hydathodes. This occurs when soil moisture is near field capacity at night or in the early morning when no evapotranspiration is taking place. The conditions under which guttation takes place are generally favourable for dew formation, but guttation continues in conditions unfavourable to the formation of dew.

It is significant that the abrupt termination of valley fog occurrence in September (Fig. 4.12) is associated with the termination of guttation (soil moisture depletion). The spring thermal changes and wind intensity patterns may also be contributing factors, but light valley fog occurs again in midsummer on cloudless nights, thus the pumping out of soil moisture by plants may be of more than local significance and may contribute directly to katabatic fog development.

Frost

No frost is recorded from the Rift Valley, and only rarely from the Midlands. There are no records of its incidence on the summit areas of Gorongosa Mountain. At Inyanga (Rhodes Estate), at a comparable altitude and latitude 120 km inland, frosts are recorded only in June and July.

Evaporation

Actual and potential evapotranspiration data for the transect (excluding the mountain) are presented in Table 4.3.

The Seasons

Fig. 4.13 summarizes the march of the seasons in each physiographic unit. Due to cold air drainage of the nocturnal land breeze component, the Rift Valley trough, which lies at right angles to the flow, is a cold air sink and thus experiences a mild midwinter period. The coast plateau and land-sea junction experience torrid or hot thermal conditions throughout the year.

TABLE 4.3

Evapotranspiration (mean values mm), (from Conçalves & Soares 1972, p. 485).

		MONTHS												
Location		Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Year
1	Vila Paiva de Andrada	41	58	95	131	170	171	174	146	130	103	71	42	1332●
		37	*42*	*47*	*53*	*129*	*171*	*174*	*146*	*130*	*100*	*50*	*37*	*1124#*
2	Vila Machado	67	9	127	118	192	202	207	175	176	145	93	63	1655
		10	*17*	*8*	*32*	*95*	*176*	*174*	*139*	*116*	*48*	*17*	*15*	*847*
3	Inhaminga	63	82	114	148	191	197	196	165	167	132	99	63	1617
		23	*23*	*20*	*22*	*100*	*179*	*196*	*165*	*166*	*81*	*43*	*34*	*1052*
4	Beira	93	121	150	186	189	202	189	174	171	138	109	87	1809
		56	*53*	*37*	*33*	*128*	*202*	*189*	*174*	*171*	*136*	*97*	*66*	*1342*

KEY

1 = Midlands

2 = Rift Valley Floor

3 = Cheringoma Plateau crest

4 = Land-sea junction (Cheringoma Coast)

● Potential

Actual

RIGHT: Figure 4.3

Temperature regimes of each physiographic unit.

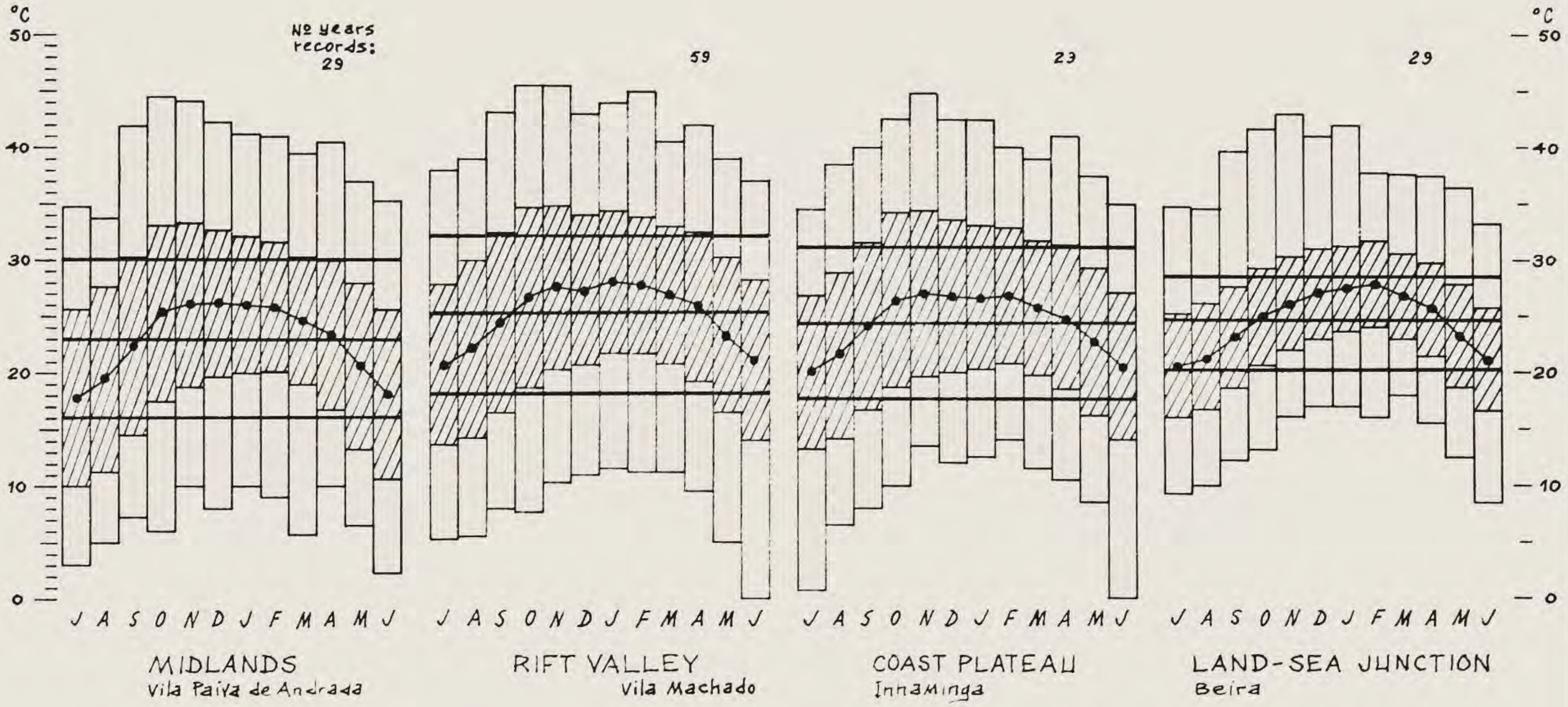
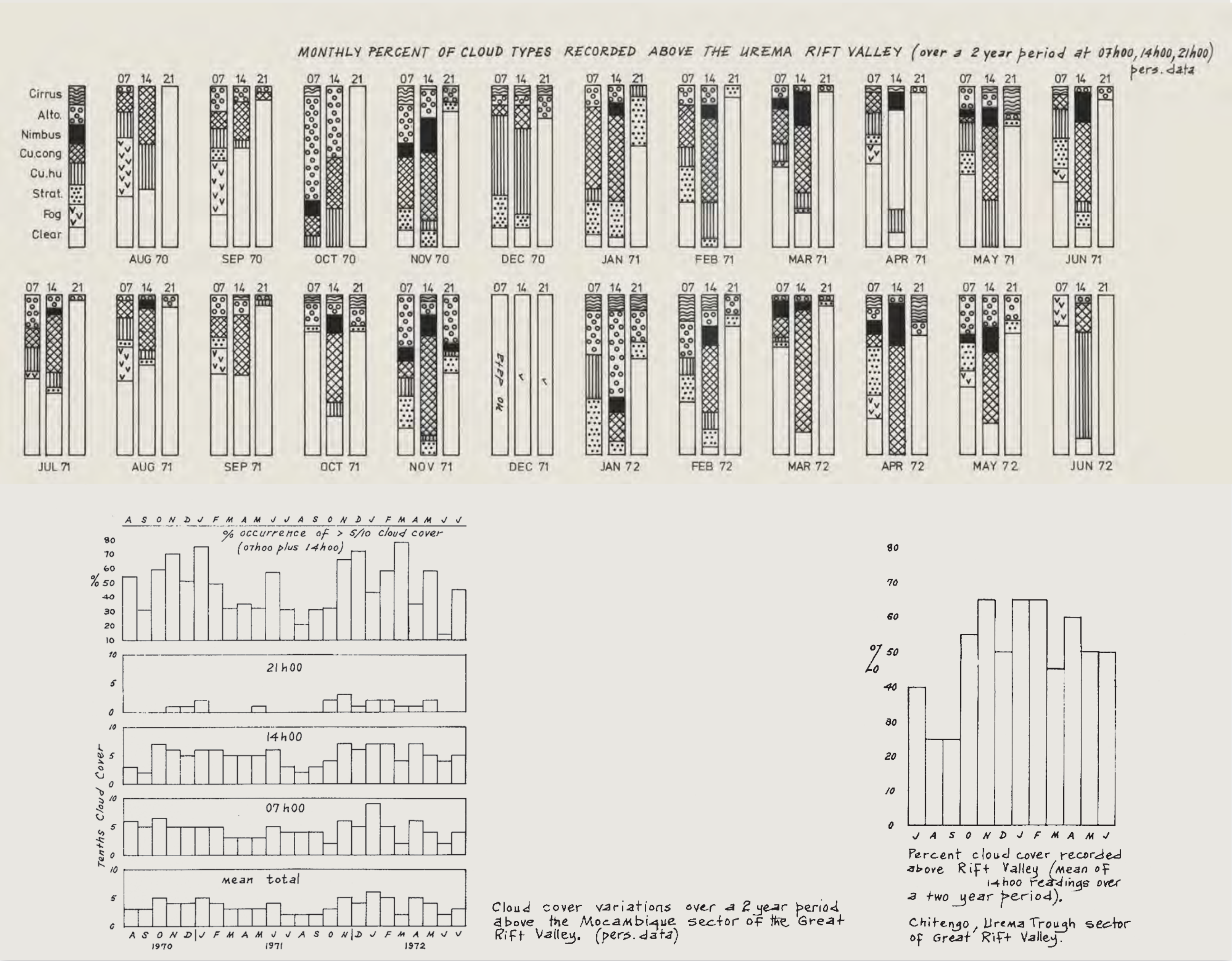


FIG 4.3 TEMPERATURE REGIMES OF EACH PHYSIOGRAPHIC UNIT °C



MONTHLY PERCENT OF CLOUD TYPES RECORDED ABOVE THE UREMA RIFT VALLEY (over a 2 year period at 07h00, 14h00, 21h00) pers. data

Cloud cover variations over a 2 year period above the Mocambique sector of the Great Rift Valley. (pers. data)

Percent cloud cover recorded above Rift Valley (mean of 14h00 readings over a two year period).

Chitengo, Urema Trough sector of Great Rift Valley.

LEFT: Figure 4.4

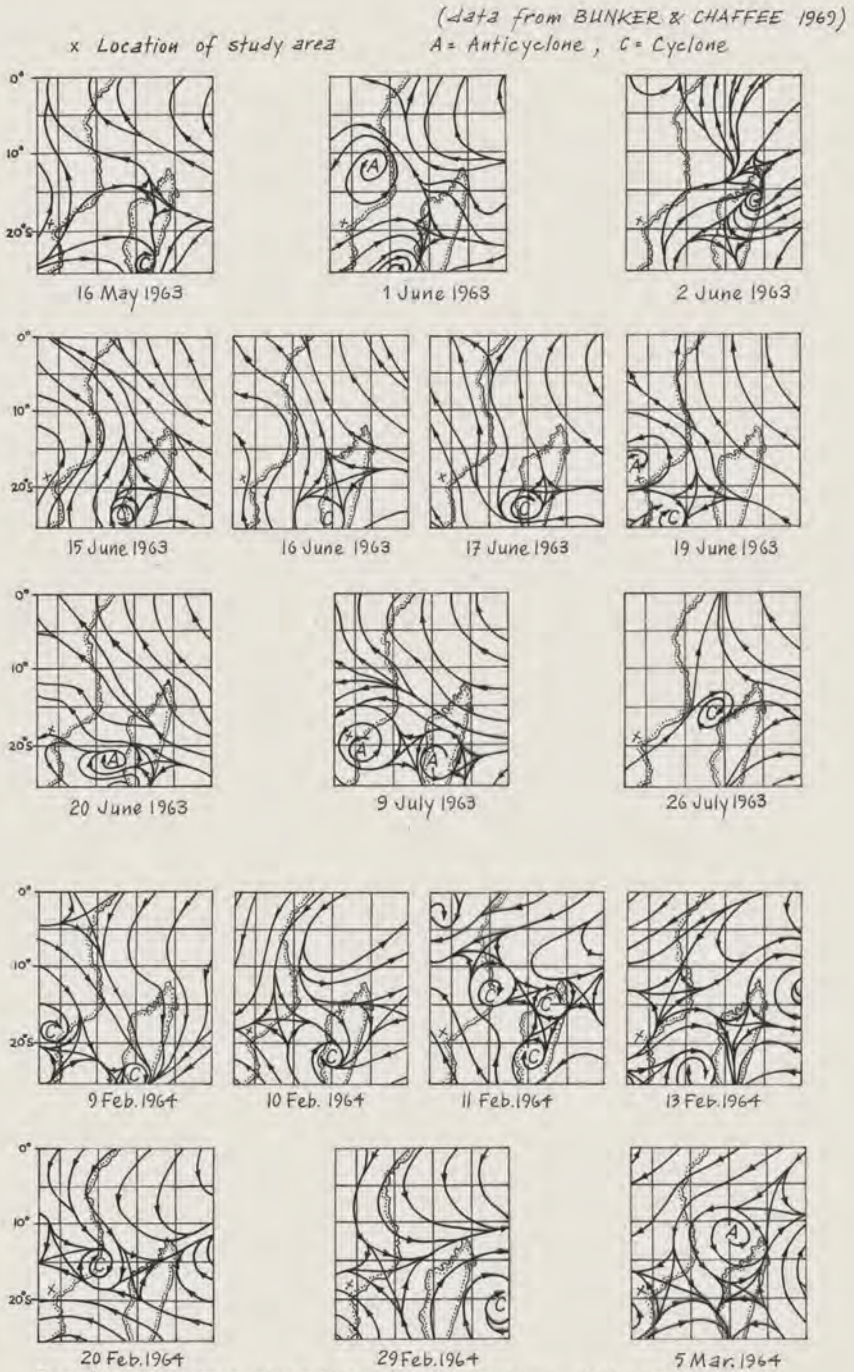
Cloud cover sequences over the Rift Valley.

RIGHT: Figure 4.5

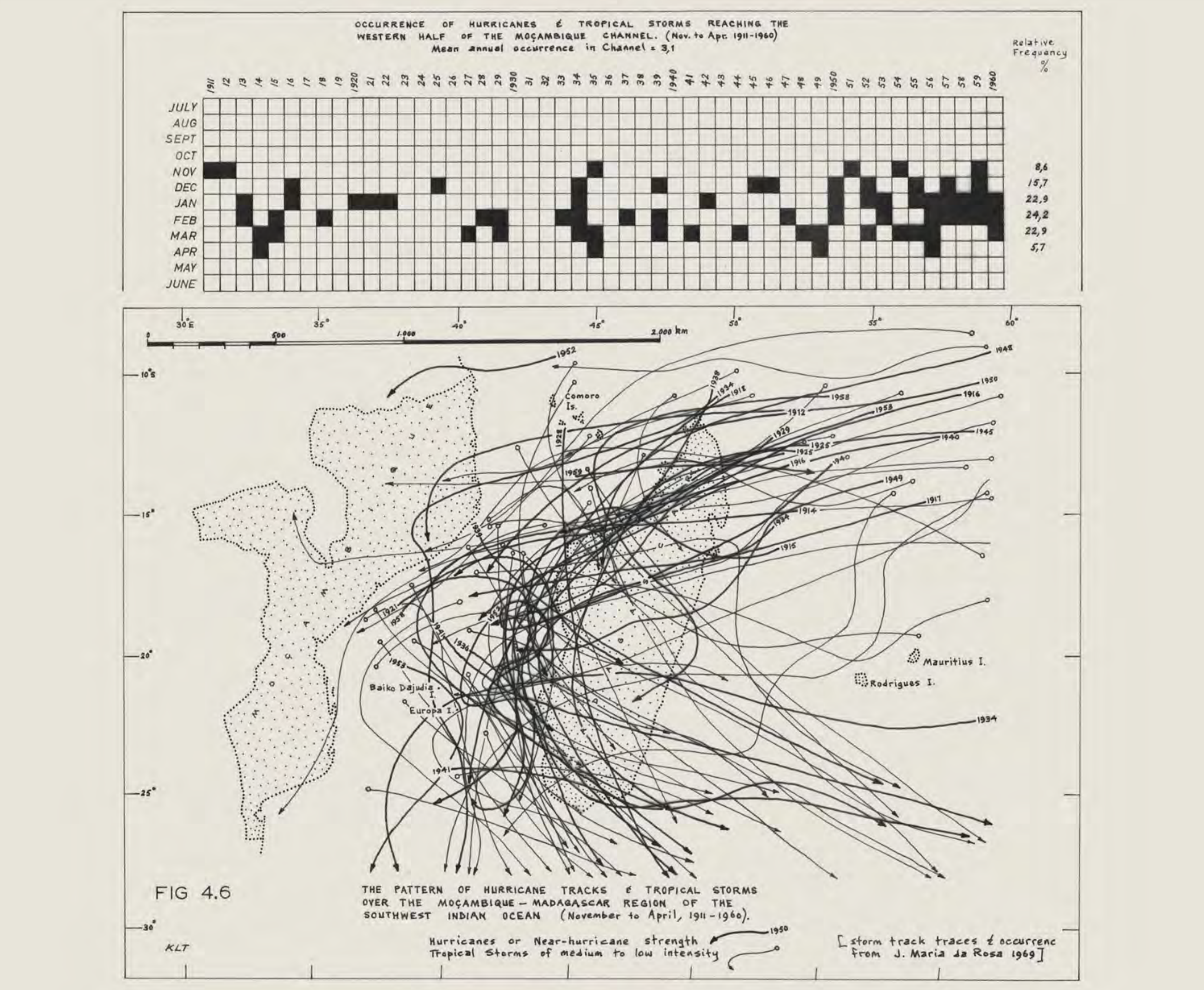
Examples of surface streamlines over Mozambique and Madagascar.

FAR RIGHT:

A surfboard proved to be a useful tool for studying coastal dynamics.



Examples of surface streamlines over Mocambique & Madagascar.
These show the close interplay of the macroscale air masses across the equator in the development & movement of anticyclonic & cyclonic processes.



LEFT: Figure 4.6

The pattern of hurricane tracks and tropical storms over the Mozambique–Madagascar region of the southwest Indian Ocean.

RIGHT: Figure 4.7A

Wind direction frequencies for the Rift Valley (Urema Trough).

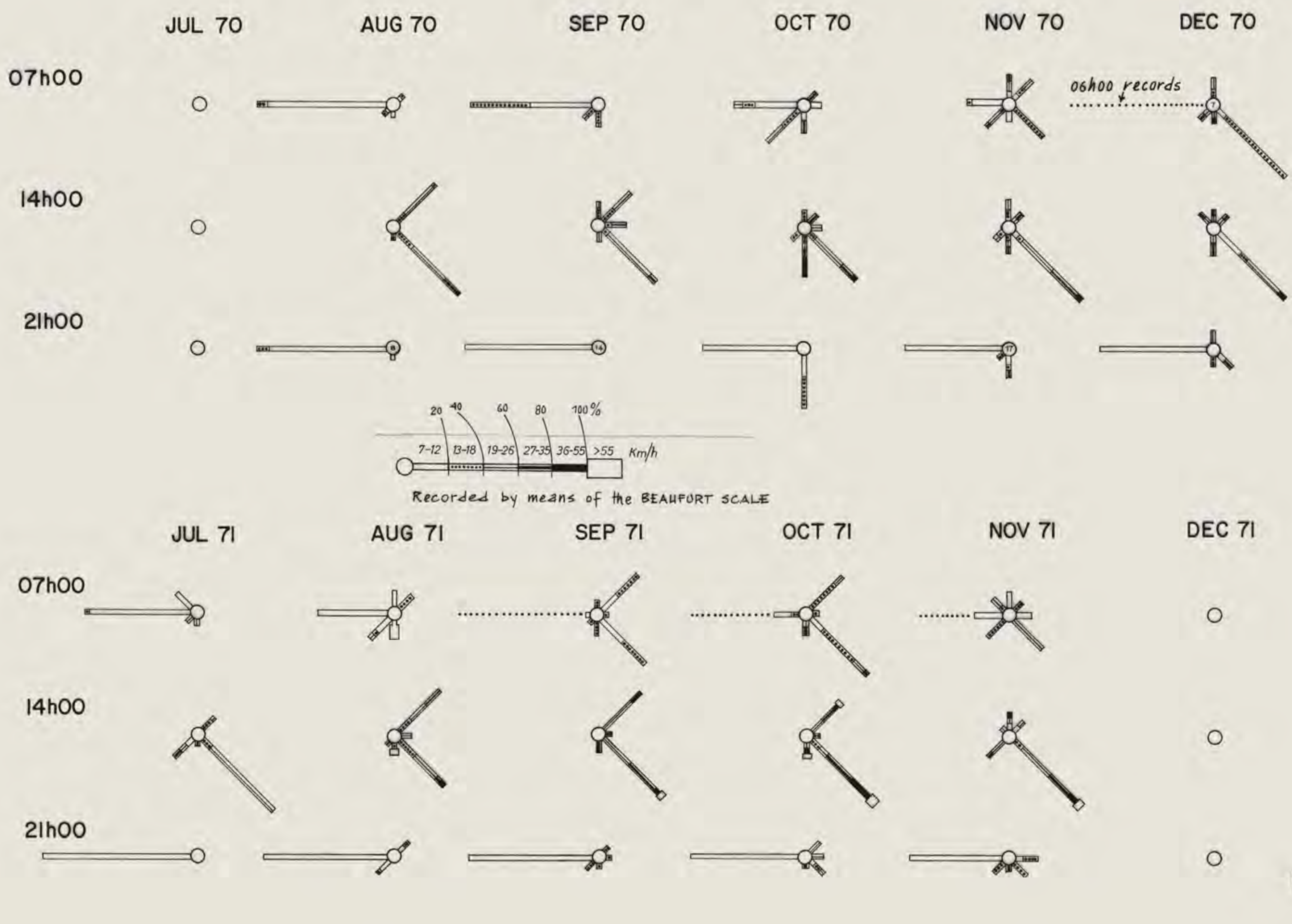
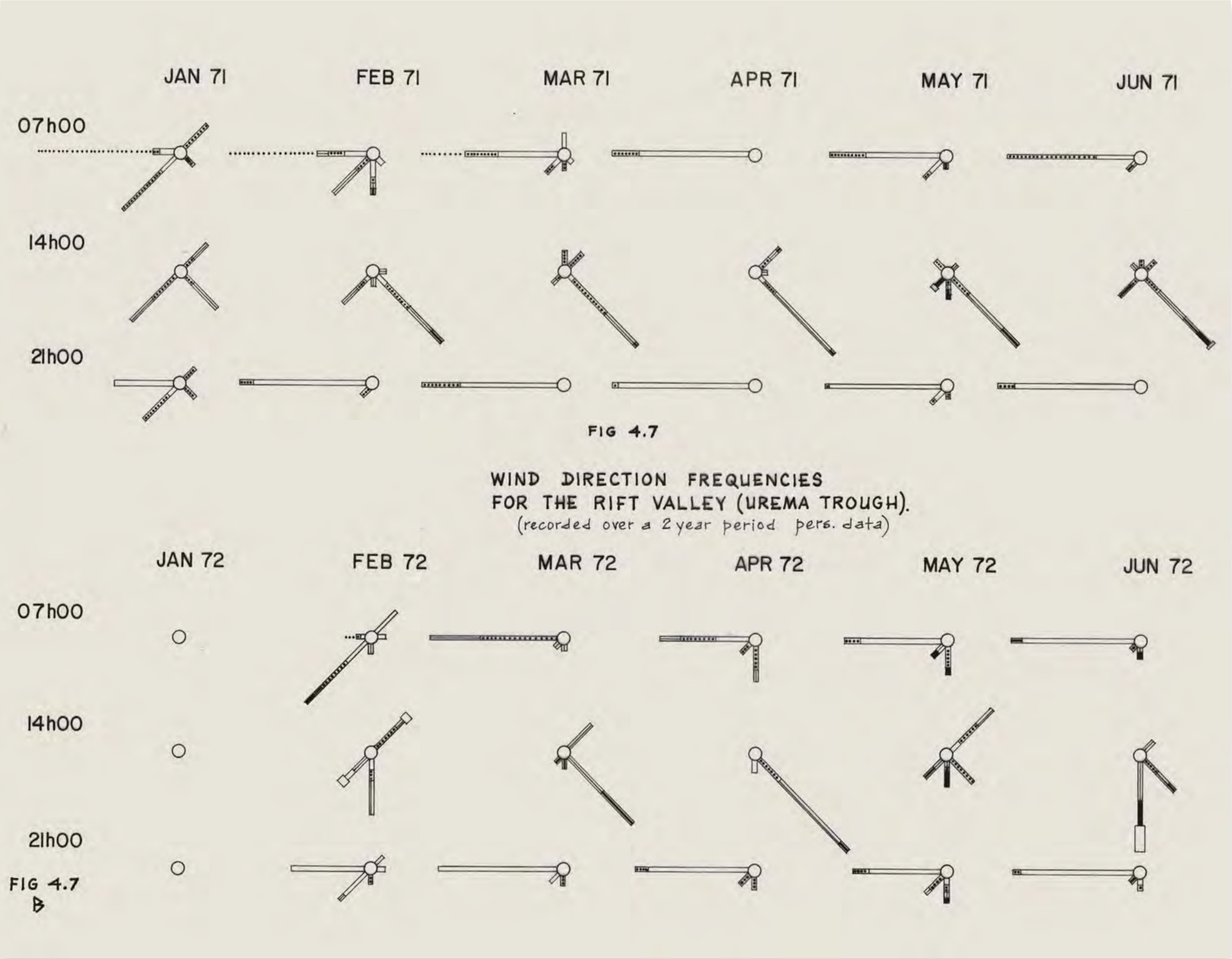


FIG 4.7
A

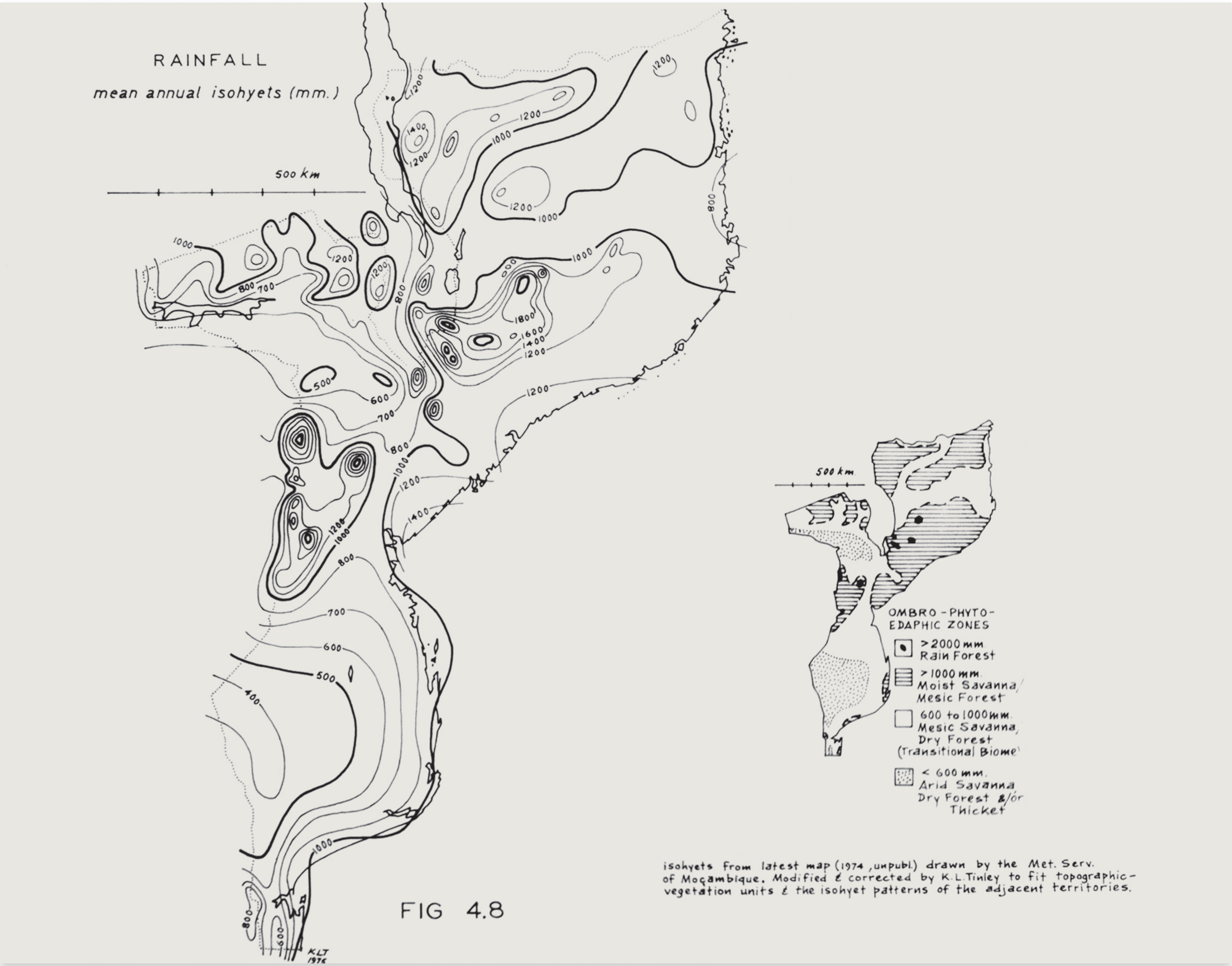


LEFT: Figure 4.7B

Wind direction frequencies for the Rift Valley (Urema Trough).

RIGHT: Figure 4.8

Rainfall over Mozambique.



isohyets from latest map (1974, unpubl.) drawn by the Met. Serv. of Moçambique. Modified & corrected by K.L.Tinley to fit topographic-vegetation units & the isohyet patterns of the adjacent territories.

FIG 4.8

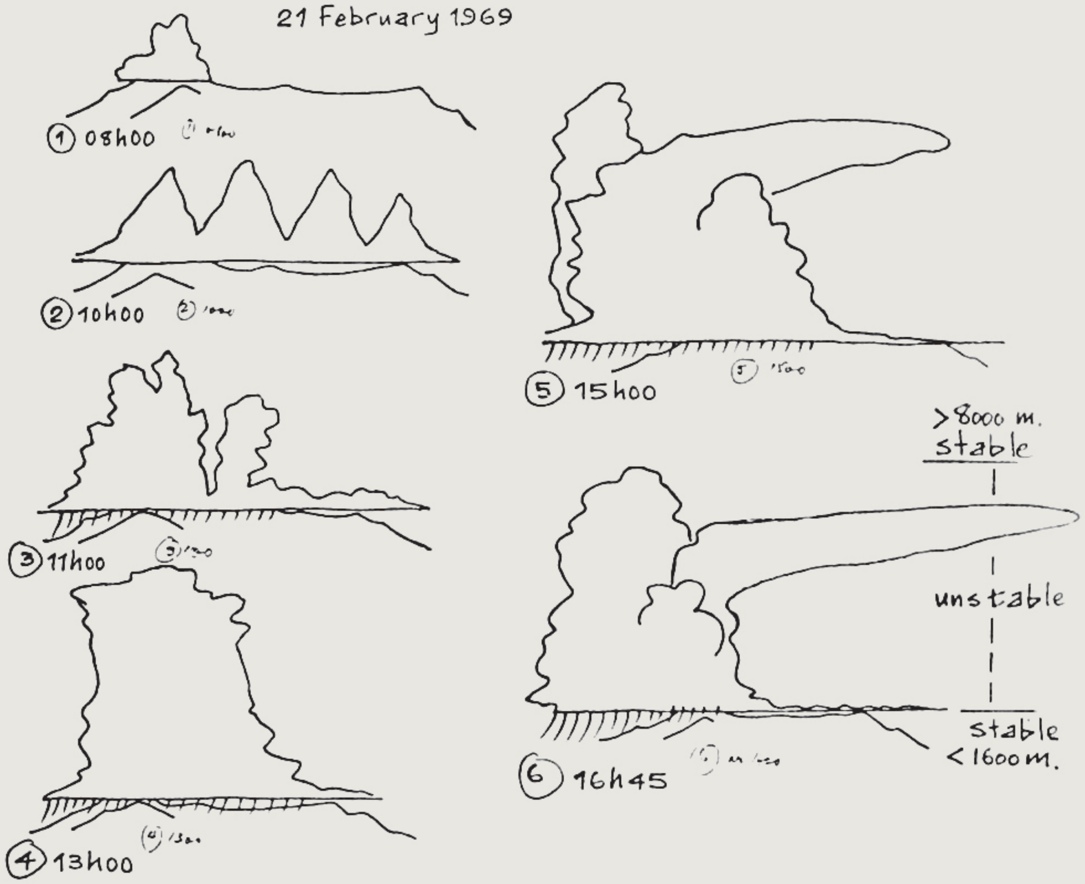


FIG 4.9 A typical example of orographic cumulonimbus rain development over the isolated massif of Gorongosa Mt. (1863 m. asl.) on the western edge of the Rift Valley in Mocambique.

The groundlevel wind . was from the SE Trades off the sea (from the observer toward the mountain) with a condensation level at c.1.600 m. Above this at about 6000 – 8000 m was the opposing SW/W geostrophic flow from the upper level of the same anticyclone system centred over the Kunene at the 6 km level.

LEFT: Figure 4.9

A typical example of orographic cumulonimbus rain development over the isolated massif of Gorongosa Mountain.

RIGHT: Figure 4.10

Daily summer rainfall comparisons between Gorongosa Mountain and the adjacent Urema Rift Valley.

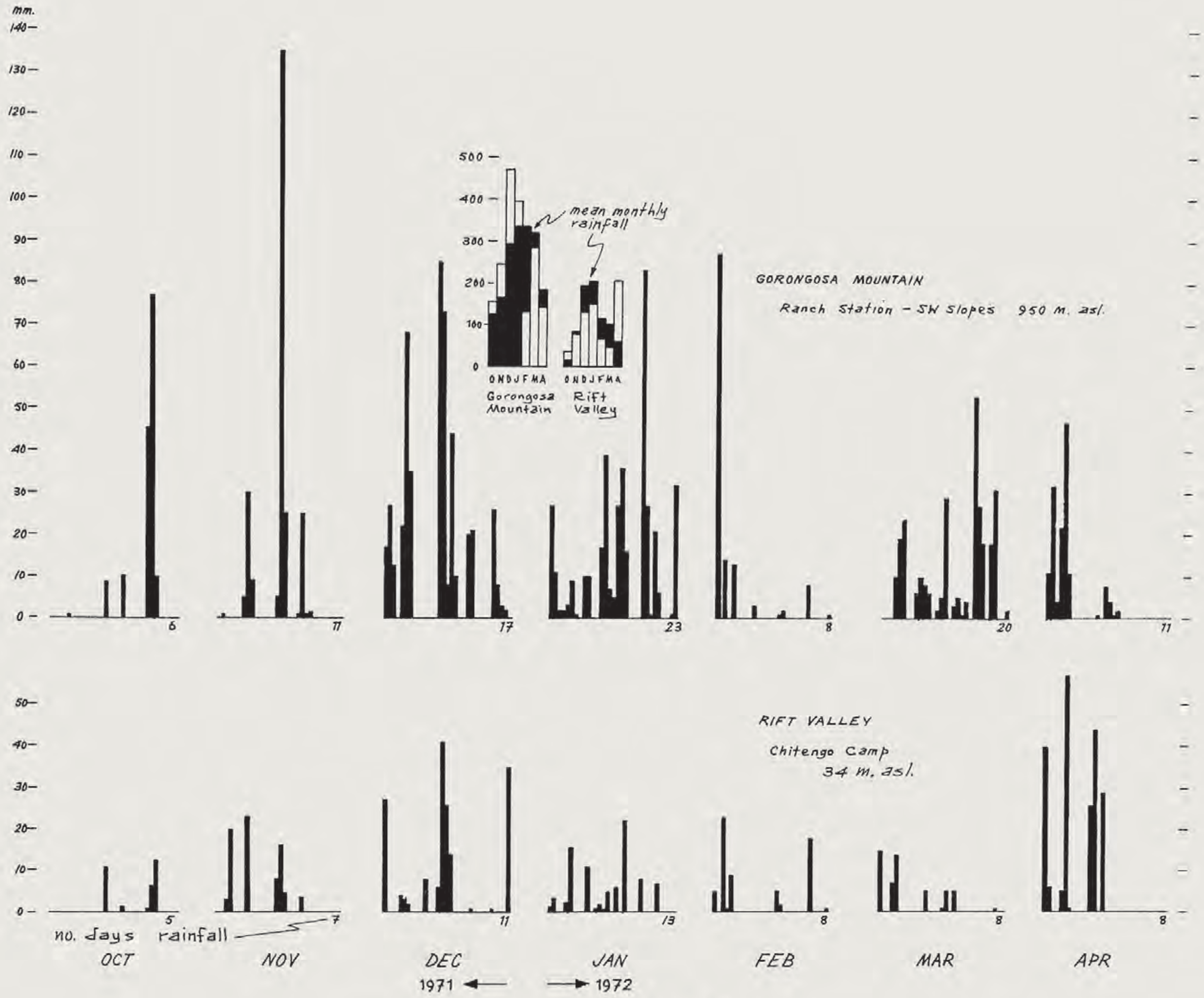


FIG 4.10

DAILY SUMMER RAINFALL COMPARISONS BETWEEN GORONGOSA MOUNTAIN & THE ADJACENT UREMA RIFT VALLEY.

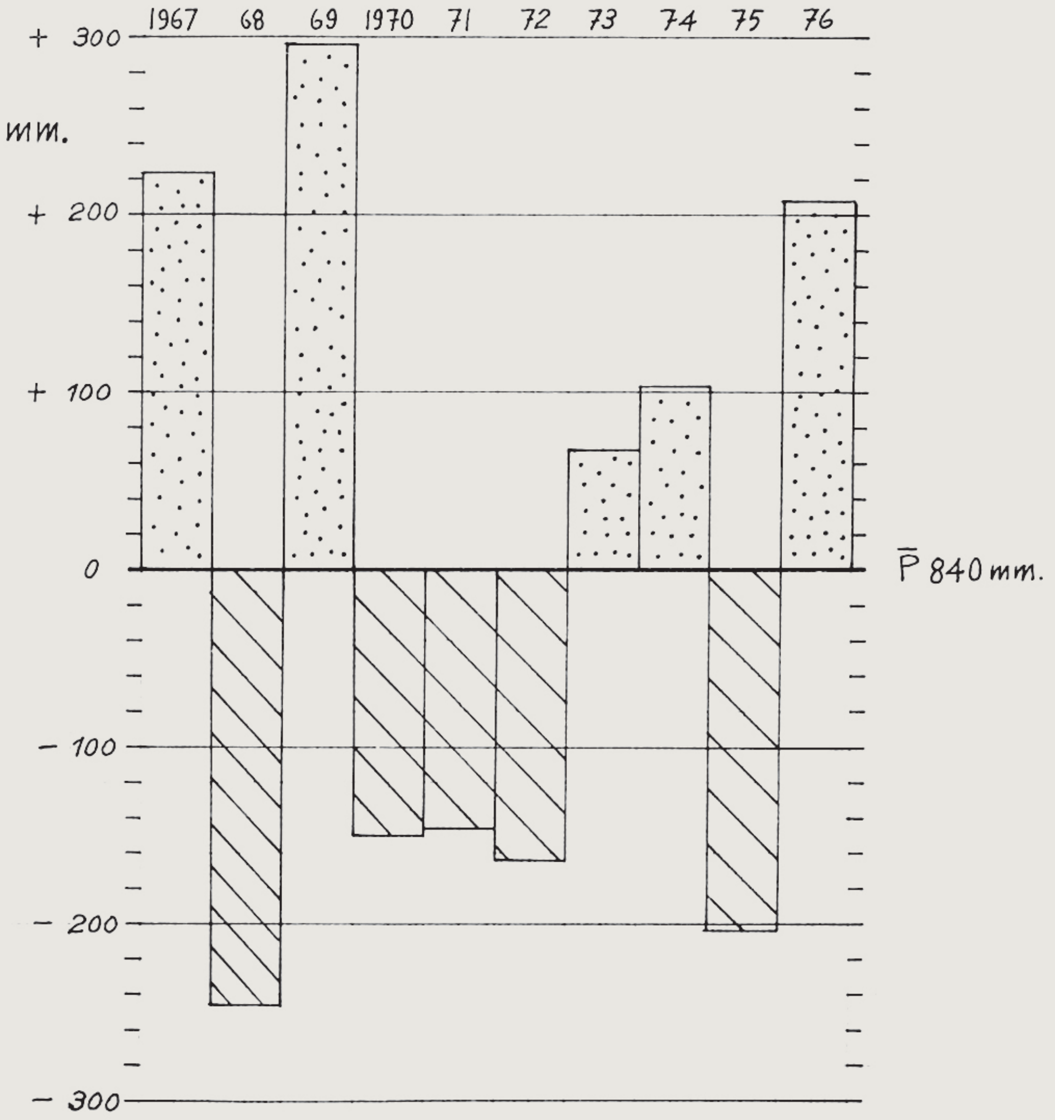


FIG 4.II

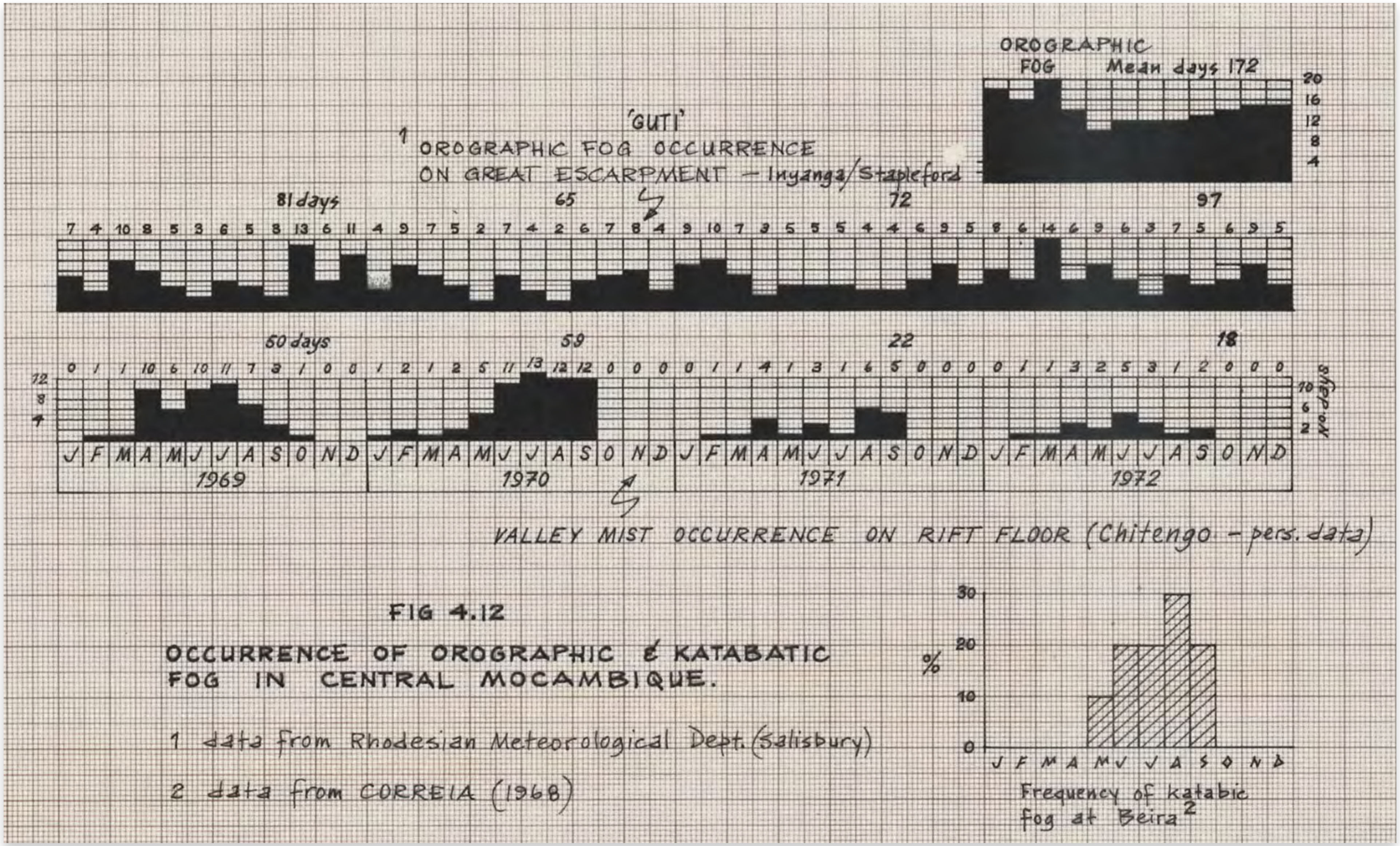
RAINFALL DEPARTURES FROM THE MEAN
IN THE UREMA RIFT VALLEY.
(as recorded at Chitengo Camp)

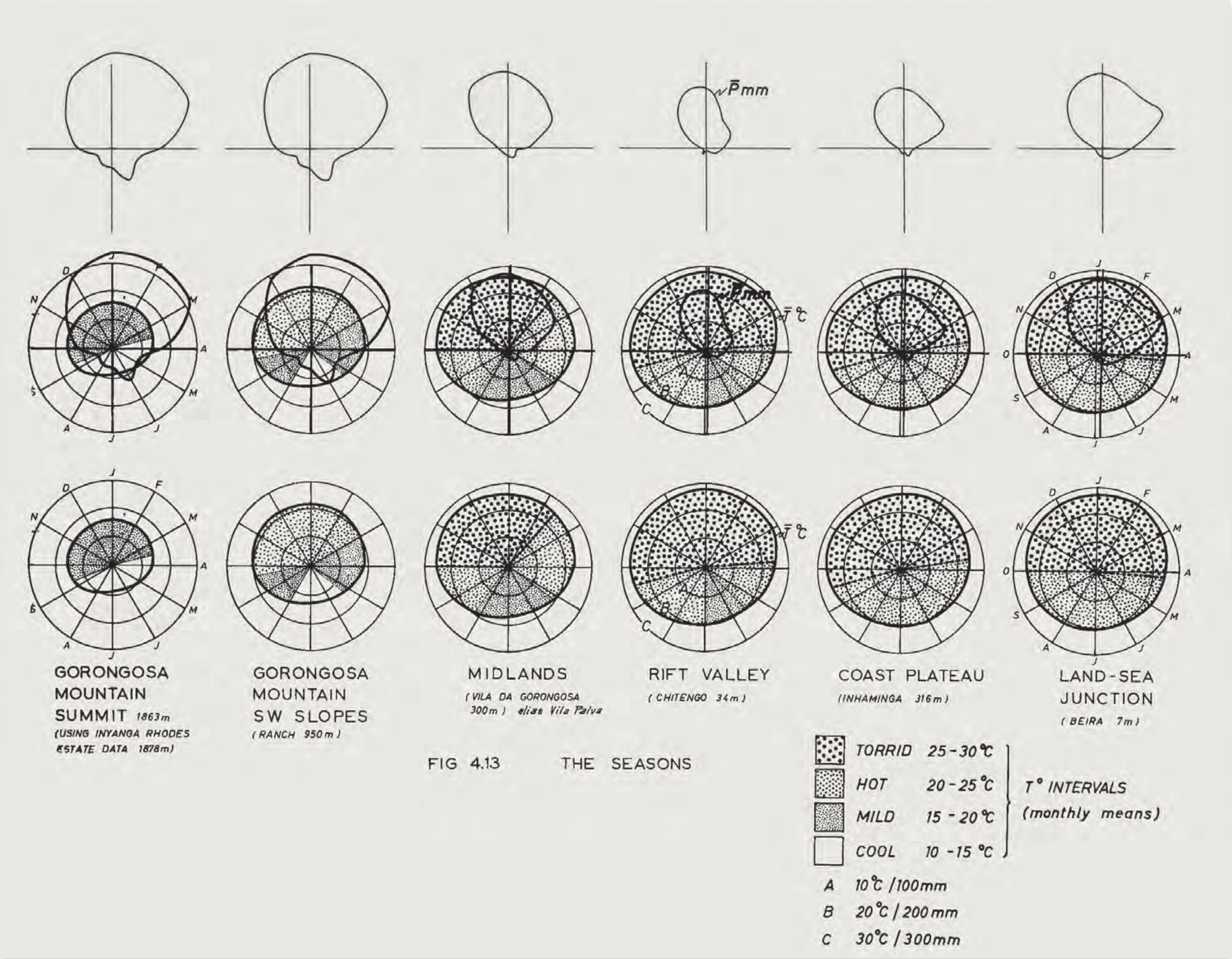
LEFT: Figure 4.11

Rainfall departures from the mean in the Urema Rift Valley.

RIGHT: Figure 4.12

Occurrence of orographic and katabatic fog in Central Mozambique.

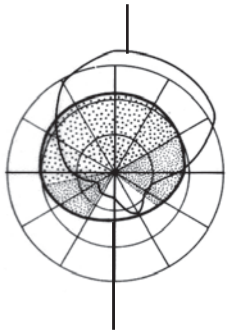




LEFT: Figure 4.13

The seasons.

Mean annual rainfall Pmm



Mean annual temperature T°C

REFERENCES / CORRELATION
CLIMATE

Bunker, A.F. & Chaffee M. 1969. *Tropical Indian Ocean clouds*. Indian Ocean Expedition Meteorological Monographs No 4, Honolulu, East-West International Indian Ocean Expedition, Honolulu.

Correia M.M. 1968. *Aspectos aeronauticos das condições climéticas do Aeroporto de Saca dura Cabral (Beira).* Serv, Meteor. de Moç., SMM 44, Mem. 42.
—1970. *Nebulosidade total na Beira.* Serv. Meteor. de Moç., SMM 65, Mem. 60.

Gaussen H. 1955. *Expression des milieux par des formules écologiques leur representation cartographique.* Coll. Int. Nat. Rech. Sci. 59, pp. 257-269.

Goncalves, C.A. & Soares, H. 1972. *Actualizaçáo do estudo climático e definiçáo de zonas de sequeiro e de regadio no Vale do Zambeze.* Fomento, 10 (4), pp. 313-491.

Griffiths, J.F. (ed) 1972. *Climates of Africa.* World Survey of Climatology, Vol. 10, Elsevier.

Mata, L.A. Da 1966. *Caracteristicas da incidencia da radiação solar em Moçambique*. Serv. Meteor. de Moç., SMM 23 , Mem. 21.

Preston-Whyte, R.A. 1970. *Land breezes and rainfall on the Natal Coast.* S. Afr. Geog. J. vol. 52, pp.38-43.

Rocha Faria, J.M. Da & Goncalves, C.A. 1968. *Cartas de isopletas dos valores médios de alguns elementos climáticos e da classificação de Köppen em Mocambique.* Serv. Meteor. de Moç., SMM 38, Mem 36.

Rosa, J. Maria Da, 1969. *Ciclones e depressões tropicais do Canal de Moçambique.* Serv . Meteor. de Moç., SMM 54, Mem 52.

Thompson, B.W. 1965. *The climate of Africa*. Oxford University Press, London.

Tinley, K.L. 1971. ‘Determinants of coastal conservation: dynamics and diversity of the environment as exemplified by the Moçambique Coast’ in *Nature Conservation as a form of land use.* Proceedings SARCCUS Symposium, Govt. Printer, Pretoria. pp. 125-163.

Tyson, P.D. 1969. *Atmospheric circulation and precipitation over South Africa.* University of the Witwatersrand. Environ. Studies Occ. Paper, No.2, University of the Witwatersrand.

PART 2

CORRELATION

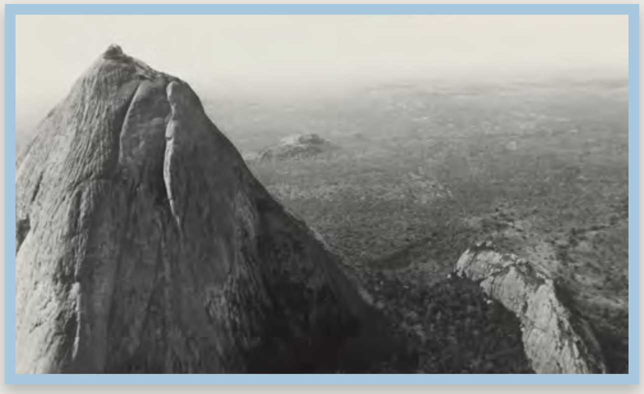
Chapter 5

Structure and Surface

OPPOSITE:

Mhanda Inselberg
(1,423 m.)

Structure and Surface



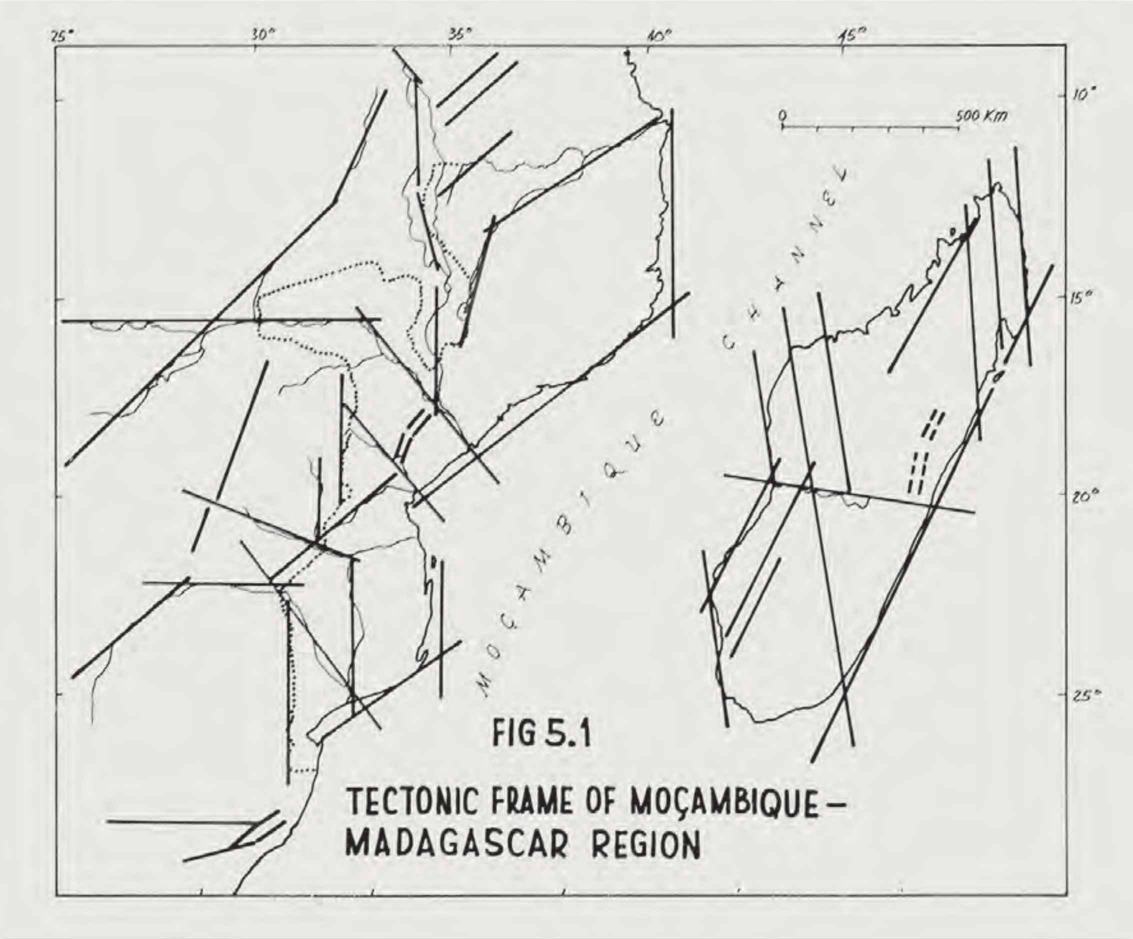
5.1 PHYSIOGRAPHY

The physiography of Central Mozambique comprises a stepped topography rising inland to the Eastern Great Escarpment some 250 km from a low coastline which is fronted by a broad shallow continental shelf of 120 km width. Almost bisecting this plan on a north–south rectilinear curve is the southern end of the Great Rift Valley system of Africa, the Urema Trough, which extends south of the Niassa–Shire Trough for 280 km from the Zambezi–Shire Junction to the sea at Beira and Sofala. At its southern end the Rift bifurcates just south of the main road and rail route which traverses the Rift floor to Beira. The western branch forms the Buzi Trough which in turn is linked to the Limpopo Trough and the Lebombo monocline in the south. The eastern branch joins the fracture system of the Mozambique Channel down the continental shelf front of the southern coast as evinced by the seismo-tectonic record (Fig. 5.1 and 5.2).

The Urema Trough is bound on the east by a remnant seaward inclined block cuesta of Cretaceous and Tertiary sediments, forming the Cheringoma Plateau. This block once formed the coast plain to the Midlands, with which it forms an even convex profile, prior to the downthrow of a 40 km broad strip of land by rifting which formed the Urema Trough. The western side is formed by midlands of Precambrian migmatitic gneiss which rise inland to the base of the north–south trending Great Escarpment at 600 to 900 m altitude. The midland zone of Central Mozambique is also known as the Manhica Platform (Wellington 1955). The Great Escarpment rises abruptly from the midlands in rugged and precipitous scenery to over 2,000 m elevation. The crest is relatively narrow and descends more gently west of Inyanga to meet the Interior Continental Plateau of Zimbabwe at 1,800 m descending gently westwards to 1,200 m towards the Kalahari Basin in the centre of the subcontinent. In contrast, the southern sector of the Great Escarpment, from Vumba to Mt. Selinda, descends steeply on the west to the deep north–south valley gouged out by the Sabi River.

RIGHT: Figure 5.1

Tectonic frame of Mozambique-Madagascar region (Dixey 1956, Gabao 1969, Flores 1970, Darrcott 1974).

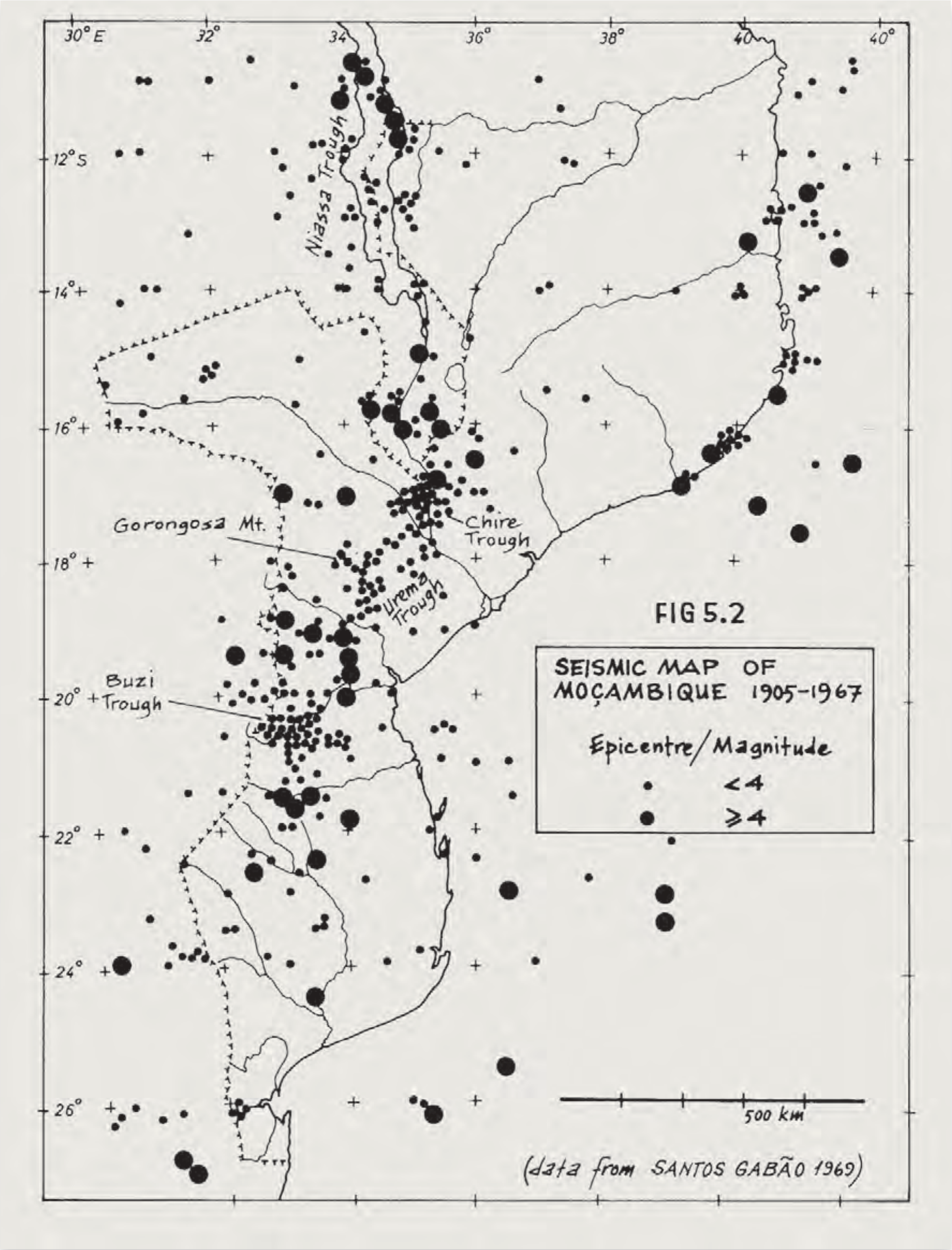


The Great Escarpment on the Mozambique–Rhodesia frontier is composed chiefly of Precambrian metamorphosed sediments, chiefly quartzites of the Frontier Formation. Umkondo schists and quartzites, small areas of Manhica talc schists, chlorite schists, quartzites, serpentines, banded ironstones and greenstones. In the central part these metamorphic outcrops are interrupted by granite-gneiss of the Basement Complex. The Frontier Formation forming the escarpment crest was overthrust along a north–south fracture by Precambrian earth movements from the east. This fracture line extends for more than 300 km between latitudes 19^{o} and 20^{0}, interrupted at both ends by the transverse fractures of the Lower Zambezi in the north and the oblique fracture of the Buzi Trough in the south (Teale & Wilson 1915).

The broad coast plain of southern Mozambique is linked to the Zambezi and Niassa lowlands by the southern end of the Rift Valley and the low, flat coastal margin of the Cheringoma Plateau. The plains of the seaward margin are formed in part by the Zambezi Delta alluvium which together form a northeast trending shoreline, the delta front alone comprising nearly 250 km in length. South of Beira the coast changes to a southerly trend, the indent forming the Bight of Sofala. At this point the sea is only 155 km from the Chimanimani Massif of the Great Escarpment.

The geology of Central Mozambique is complex, providing a great heterogenity of rock structure and textures, many of which have undergone repeated tectonic fractures and earth movements since the Precambrian. Major dislocations and warping occurred with the breakup of Gondwanaland in the Jura-Cretaceous, followed by moderate movements in the later Cretaceous and Miocene, culminating in the early Pleistocene, in a major episode of uplift and warping. The uplift formed the rim of the escarpment zone and elevated the interior plains of a continental plateau. The coast margins of the subcontinent were tilted downward to the sea with the formation of the Mozambique Channel and contemporaneous Rift Valley faulting on the crests of the downbent crust (Dixey 1955, 1956; King 1962).

The result of these tectonic movements was to impose a strongly developed fracture system on the landscape which controlled hydrographic development and thus the main lines of erosion and deposition by water. Close to the escarpment the fracture lines are chiefly north–south, and at right angles to this in the north is the east–west fracture line of the Kafue and Mid-Zambezi. The remainder of the country is dominated by strongly developed northeast–southwest and northwest–southeast tectonic lines superimposed on the older north–south lines (Teale & Wilson 1915); well illustrated by the trends of the coastline, Rift Valley, Midland drainage and especially the Lower Zambezi, Pungue and Buzi Rivers. These tectonic lines accord with the major fracture system of the continent (see Furon 1963, Fig. 3). Sets of faults and fractures oblique to these, on north-north-east to south-south-west and north-north-west to south-south-east



LEFT: Figure 5.2

Seismic map of Mozambique.

trends, are responsible for the Urema Trough and adjacent highground on either side, exemplified by the dyke swarms north and south of Gorongosa Mountain and the Inhaminga fault.

The physiography of the Gorongosa ecosystem is boldly defined by the 40 km broad Rift Valley trough, the sloping sides of which are formed by 300 m high plateaux, and the isolated massif of Gorongosa Mountain which rises abruptly from the crest of the western side to over 1,800 m. These features clearly divide the ecosystem into four physiographic units:

(1) Gorongosa Mountain
(2) Midlands (Báruê or Manhica Platform)
(3) Rift Valley
(4) Cheringoma Coast Plateau

The ecosystem, defined by the limits of the Urema catchment basin, is 7,850 km^2. If the entire mountain and the south bank of the Nhampaza River is included, as suggested for the new park boundaries (Tinley 1969), the area is 8,200 km^2. Within these latter limits the mountain massif comprises 550 km^2 (7% of the area), the Midlands 2,100 km^2 (26%), the Rift Valley 3,650 km^2 (45%), and the riftward catchment of the Cheringoma Plateau 1,900 km^2 (23%). Separated into altitudinal limits these features comprise: mountain land 550 km^2 (7%) between 600 m and 1,863 m, midlands 4,000 km^2 (48%) between 100 and 600 m, and lowlands 3,650 km^2 (45%) less than 100 m (Fig. 5.3).

Gorongosa Mountain

The oval mountain massif rises in bold and picturesque scenery to over 1,200 m above the surrounding Midlands. The eastern precipitous escarpment is formed by bare granite bornhardts interspersed with forested ravines whilst the steep western flanks are deeply ribbed by radial drainage. The northeast and southern flanks have been breached by deeply incised headward erosion of the

Gorongosa Mountain landscape

TOP RIGHT:

Gogogo summit area, the highest point (1,863 m) against the skyline on the extreme left. Light areas are montaine grassland and/or rock outcrops. Dark fine-textured canopyin foreground is *Philippia benguellensis* fynbos thicket surrounded by rainforest canopy.

BOTTOM RIGHT:

The western rim looking toward the southeast source of the perennial Vundudzi (valley on left), Nhandare (valley on right) and Muera (foreground slopes). Vundudzi flows southeast then turns east (left) into a second catchment basin below the line of cloud on its way to the Urema Lake. Note beheading of Vundudzi and Nhandare headwaters by Muera.

Vundudzi and Nhandare Rivers respectively. The western rim of the mountain remains unbreached.

Four main rivers, the Nhandare, Chitunga, Muera and Vundudzi, drain the massif in an annular pattern, contributed to by lesser streams in a radial pattern. The first two of these rivers join below the mountain and flow south along a strongly developed north–south fracture line in the Midlands to join the Pungue River. The latter two flow east and traverse the Rift Valley floor to the Urema Lake. The Nhandare and Vundudzi Rivers rise on the western rim of the mountain and traverse the entire summit area southward in deep V-shaped valleys below the 1,400 m contour. Above this contour the catchments are of open-concave to poly-concave relief. These upper valley areas have lightly meandered stream courses separated from the lower gorges by nick points with falls or rapids between the 800 and 1,000 m contours. The drainage density on the mountain is high to very high.

The drainage of the summit area is aligned along the major north-south and east-west fractures in the mountain, and these form a zigzag pattern in the Vundudzi Valley on the eastern side where different sets intersect. Although the mountain drainage is controlled by the weak lines of the fracture system, both first and second order streams can either be meandered or coarsely reticulate. The streams rising on the northeast and west of the mountain have etched deep amphitheatre catchments into the outer slopes.

The deeply incised drainage on the south and east of the mountain and the persistence of an unbreached divide forming a rim on its western side indicates that the upper mountain drainage was initiated on a planation surface inclined to the southeast, and the south and east were possibly more easily erodable due to the well developed fractures. The cross-fracture system appears to have been a major factor facilitating river capture of one of the upper Nhandare valleys by the Vundudzi, which drains to the Urema Lake on the Rift Valley floor.

The valley capture point lies close to the main Nhandare Valley and is separated by a narrow saddle. The Vundudzi has thus effectively eaten back into the overall oval of the mountain to form an assymetric figure of eight shape, and comprises an upper catchment above 1,200 m and a lower basin between 500 and 1,200 m. Viewed from the southwest or northeast the massif has a higher western block with steep scarp faces. A similar shape and proportion is replicated by the higher pluton of Mlanje Mountain in Malawi (see Dixey 1927, Fig. 7).

Although rapids are abundant there are only three major falls on the mountain. Two of the highest, some 100 m in height, occur on the Murombodzi stream at the 900 m contour and at the 700 m contour and are associated with a broad bench or step formed on the gabbro outcropping on the southwest of the massif. A series of falls occur in close sequence on the Vundudzi River near the 1,000 m contour in the ravine just below the site of river capture.

Viewed from the Rift Valley (Fig. 5.4) the mountain top comprises three main summit areas above 1,700 m on the western block, attaining 1,863 m at the highest point of Gogogo Peak in the southwest. The largest summit area above 1,700 m (4 km^2) is that in the southwest which has the second highest peak Nhandohue (1,858 m) at its southern end. The second highest summit area is Zombue (1,845 m) followed by the northernmost peak of Inhantete (1,762 m) overlooking the Nhandue River valley. The summit areas are grasslands on gently undulating to steeply rounded slopes with small areas of flat ground. Large, deeply fissured granite outcrops occur on the summits, supporting thicket, forest or patches of arborescent *Strelitzia*. Springs, bogs and oozes are common on the summit areas, and one isolated seasonal tarn occurs on the plateau spur east of Zombue summit. The eastern block nearest the Rift Valley is surmounted by the forest-covered Nhansocossa Peak of 1,478 m height. The remnants of related planation surfaces on the mountain summits correspond to Gondwana and Post-Gondwana bevels, and the disposition of lower summit bevels and benches on the flanks of the mountain is shown in Fig. 5.8. The most important benches or steps occur between 800 and 1,200 m (Figs. 5.3 and 5.13).

Although the scarp faces are erosional and not due to recent faulting, earth tremors are frequent (Fig. 5.2). Only one area of vertical cliffs occurs, on the northwest corner of the massif which appear to be used for nesting by birds of prey, and possibly vultures, as evinced by the white streaked cliff faces. The greater part of the mountain is covered in rainforest and this clothes the magnificent deep gorges cut by the Nhandare and Vundudzi Rivers on the south and east flanks. The Vundudzi River forms a second deep gorge where it leaves the mountain and enters the Midlands near Cavalo.

Midlands

The Midlands, which begins abruptly in the east at the fall line against the Rift Valley, and rises inland westwards to the Great Escarpment, is a maturely dissected former planation surface. Remnants of the former southeast inclined surface is shown by the accordance of the interfluves and relic dambo (mature) drainage not yet incised by the lesser tributaries of the main rivers. Deep, steeply sloping V-shaped valleys alternate with narrow steeply rounded interfluves.

The fall line is delimited by an abrupt, or gradual, drop to the Rift floor. In parts, the crystalline hills rise to over 300 m within 2 km of the Rift floor which is at 80 m, e.g. near Rerembe where the Mucodza River meets the Rift. In general the rise is much less abrupt attaining 300 to 400 m altitude over a 5 to 10 km distance as exemplified by the rise to the north–south interfluve separating the Nhandare Valley from riftward drainage south of Gorongosa Mountain.

The Midlands have been gouged out along two sets of strongly developed fracture lines southeast–northwest

Gorongosa Mountain landscape

TOP LEFT:

The seasonal tarn or pan on the plateau bench below Zombue summit in the centre of the massif. Montane grassland surrounded by rainforest and *Widdringtonia nodiflora* woodland (slopes on left of bench).

BOTTOM LEFT:

Eastern escarpment of mountain with bare rockfaces of exfoliating granite and rainforest in the ravines.

Midland inselberg and hill miombo landscape

TOP RIGHT:

Mhanda Inselberg (1,423 m) surrounded by a set of Midland hill-miombo savanna. Mesic forest forming an apron around the outcrop base is a typical feature. Light areas in the miombo are relic dambos, incised and being invaded by savanna trees. Clumps are termitaria thickets. The dambo areas are remnants of the Midland late tertiary planation surface.

BOTTOM RIGHT:

Dry forest on the sands of an aggraded valley floor in dry *Julbernardia-Pterocarpus brenanii* miombo northwest of Gorongosa mountain (Nhamacapinda River).

and north–south, thus the deeply cut valley and spur topography trends along these lines. Although the lesser tributaries of first, second and third order generally show a dendritic pattern, all orders including the Pungue, Nhandare and Nhandue Rivers have incised meanders and river capture has probably been of common occurrence (e.g. Nhandue drainage). In many parts, these meanders may be superimposed from the original planation surface, but in others, meanders appear to have been formed by intersecting sets of opposing fracture lines. The Midlands has a high to very high drainage density.

The deepest gorges in the system area are formed by the Nhandare and Pungue Rivers at their confluence. The Nhandare joins the Pungue along a major north-south fracture parallel to the Rift line nearby. The perennial Nhandare River which drains the southwest part of Gorongosa Mountain is joined from the west by a large 'sand river', the Vunduzi (not to be confused with the Vundudzi draining the eastern sector of Gorongosa Mountain to the Rift Valley), which rises on the Midlands and is thus a 'sand river', strongly seasonal in flow. The Nhandue and Nhamapaza are the other two large 'sand rivers', which rise on the Midlands and drain into the Rift. The Nhandue reaches the Urema Lake, and thus the Pungue, only during the rains. The seasonal Nhamapaza River has a wide braided riverbed which traverses the Rift Valley maintaining a southeast course to meet the Zangue, a small tightly meandering subsequent course draining the Urema Trough north towards the Zambezi River. In the northwest of the system is a broad north–south valley formed by the Muche River which meets the Nhandue at the Rift Junction. This valley appears to be a major fault related to the Rift dislocations. A range of rounded lava hills, known as Panda, mark the confluence area of the Muche and Nhandue. In the northwest of the system the large tributaries of both the Nhandue and Nhamapaza are also 'sand rivers'. All the rivers entering the Rift from inland across the crystalline Midlands are rejuvenated in their lower courses and descend to the Rift through deep rocky gorges over rock bars, rapids and small falls, and flood to over 10m in their gorge tracts. However, those rivers such as the Nhamapaza which enter the Rift across the Continental Cretaceous meet the floor in broad valleys with braided courses.

Rising above the Midland interfluves are many inselbergs of various dimensions (Fig. 5.5). Only Mhanda (1,423 m), which lies 60 km northwest of Gorongosa Mountain, and Cudzo (805 m), 20 km southwest of the massif, are of large size. These, and the smaller koppies west of the mountain, are exfoliated domes of granite cores also known as Bornhardts. Those in the eastern quadrant from the mountain are either composed of quartz breccia (Siciri, Xivulo), trachyte (Bunga trio and Panda) or basalt (Cuncue). Extending for nearly 30 km north of Gorongosa Mountain, like root outgrowths, is a series of four parallel ridges formed by composite dykes of granophyre and dolerite. The east and west faces of these ridges support different woody plant cover. Less conspicuous are dykes of granophyre forming outcrops and interfluve surfaces southwest of the mountain. Lying 40 km southwest of the park are the Xiluvo Inselbergs formed by the breached rim of a carbonatite volcano now covered in forest.

Rift Valley

The Urema Trough sector of the Great Rift Valley is shallow with relatively low sloped sides, unlike northern sectors of the Rift which have high and steep escarpment sides. The width of the Rift here averages 40 km, the same order of width recorded throughout the Rift system, and is indicative of the thickness of the continental crust below the trough (Holmes 1965, p. 1061). The Urema Lake and its outlet to the Pungue forms the lowest part of the Rift occuring within the study area, this is approximately 12 m above sea level. The margins of the lake are at the 15 m contour and from this basin the contours of the valley floor rise to 80 m at the margins. South of the Zambezi River the Rift Valley is faulted on both sides in a rectilinear curve beginning with a north-north-east to south-south-west trend and changing to north–south near the Pungue River and thence northwest–southeast where it bifurcates and joins the Mozambique Channel.

The western faults probably predate Juarassic times and have been refractured along the same lines. In contrast the eastern faults are much younger, of Tertiary age, and these resulted in a stepped downthrow of strata on the inface of the Cheringoma block. The western side of the Rift is eroded to a gentler slope than that on the eastern Cheringoma side where there are geologically recent fault line scarps, particularly near Inhaminga.

The even seaward dip of the Continental Cretaceous north of the Nhamapaza River implies that the fractures shown on maps are without throw, the dip of strata continuing beneath the Rift Valley alluvium and faulted with displacement only on the inface of the Cheringoma noted above; that is single-sided (trap) block faulting on the Cheringoma side only. This Cretaceous (Ksm) and associated Stormberg Basalt is totalIy absent on the western side of the Rift between the Nhandue River and Vila Machado in the south. This and the occurrence of the small horst inlier of Precambrian metamorphic rock in the southwest of the system suggest that this sector underwent trough faulting (see Section 5.2).

A three to five degree seaward dip is typical of the whole region, including the Karoo and Precambrian below the Meso-tertiary cover (data from explanatory notes of Geological Sheets of Mozambique 1:250,000, 1968). The original incline between the Midlands, the remnant Cheringoma block and the lip of the continental shelf has been maintained, despite the large scale trough faulting of the Rift which separated the inland and coastal areas. As the Buzi block shows a similar profile relationship with its immediate hinterland, it is probable that they are islanded remnants left behind by a general widespread lowering of the continental margins, and not uplifted blocks as usually defined (e.g. Wellington 1955; Flores 1964; et al.), an interpretation agreed with by Professor L.C. King (pers. comm. 1977). These releases of crustal tensions appear to have resulted from the gigantic downbowing of the faulted syncline forming the strait between Mozambique and Madagascar (Dixey 1956) (see section 5.3). The seismic map of Mozambique shows the repeated occurrence of earth tremors recorded along the fracture line of the Rift (Fig. 5.2).

Additional evidence that the eastern edge of the crystalline Midlands was faulted in pre-Jurassic time is shown by the extended consequent drainage, now dislocated, of the major rivers on a southeast trend across the original single coast plain. This major plain was formed by the present Rift Valley floor together with the backslope

RIGHT: Figure 5.3

Relief and drainage.

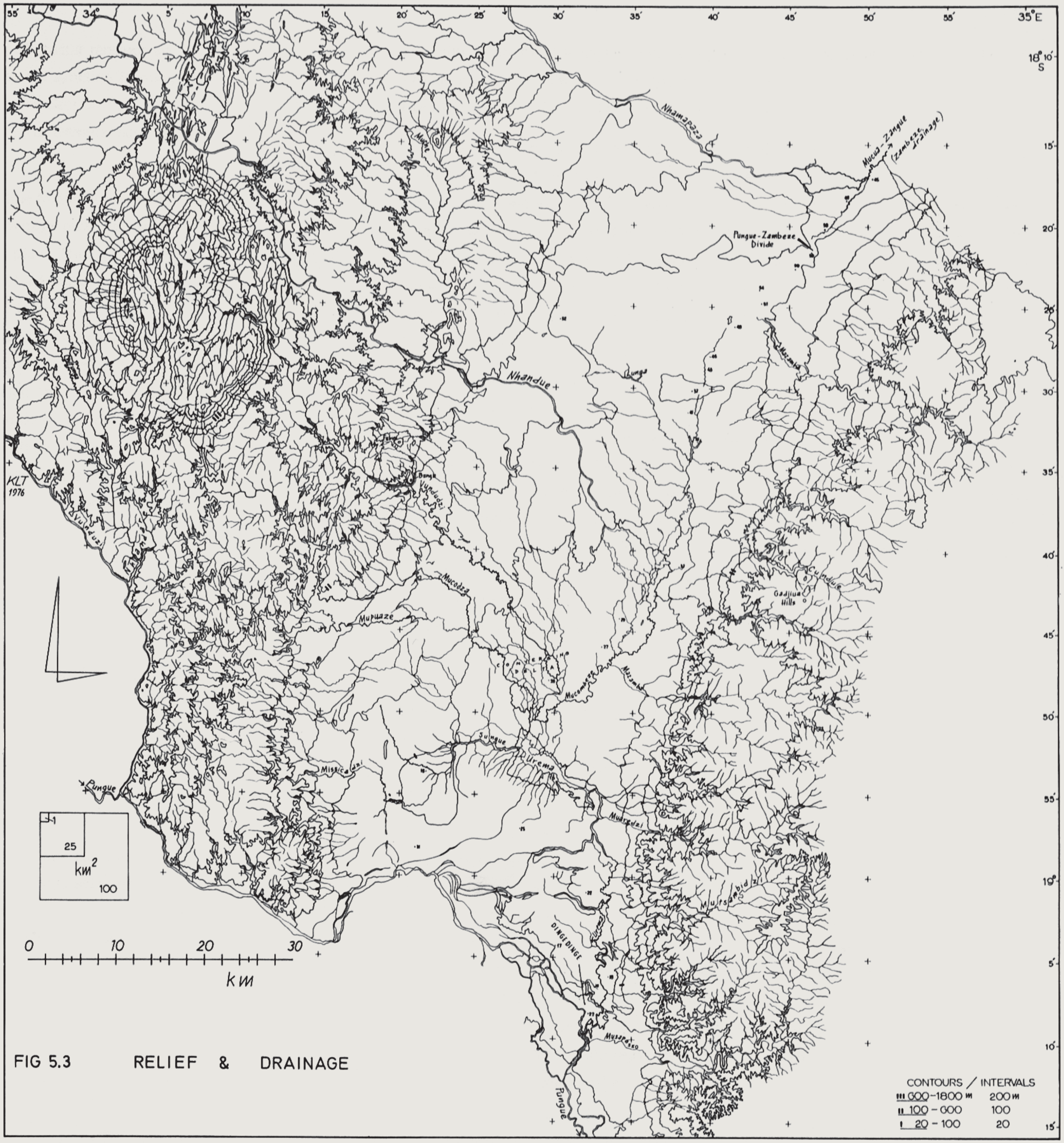


FIG 5.3 RELIEF & DRAINAGE

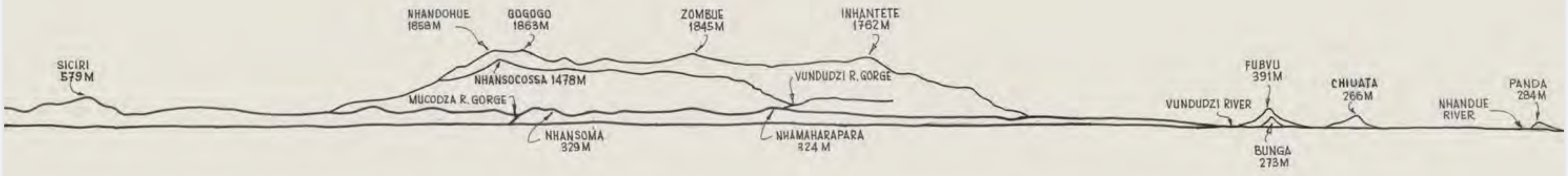


FIG 5.4 GORONGOSA MOUNTAIN & THE WESTERN SIDE OF THE RIFT VALLEY VIEWED FROM THE S.E. ON THE UREMA PLAINS

LEFT: Figure 5.4

Gorongosa Mountain and the western side of the Rift Valley viewed from the southeast on the Urema Plains.

of the Cheringoma cuesta. The extended consequent drainage on the southeast fracture line has been maintained only by the Zambezi River. With separation of the Cheringoma sector of the coast plain by downthrow of the Rift trough, the other rivers were severed in the middle and formed subsequent drainage on the Rift floor. A singular feature of the Rift drainage pointed out by Mouta (1956) is the continued southeast trend of all the major rivers crossing the Rift floor from inland, as well as Urema Lake which lies on the same axis. Thus, despite the large series of alluvial fans and shifting river courses formed during accumulation of sediment, the shallowness of the underlying hardrock fracture system and its seaward dip continued to be an underlying control of drainage development. Due to these influences, the Rift floor is asymmetrical in profile with the lowest basins of subsequent drainage closer to the foot of the Cheringoma inface. The incline from these basins up to the 100 m contour is over 20 km long on the western side and half, or less than half, this distance on the Cheringoma side.

With separation of the Cheringoma from the immediate hinterland by the rift trough, the beheaded rivers retained their seaward courses on the dipslope (i.e. they became resequent). If the inland southeast drainage patterns are followed seaward the original extended consequent drainage can be paired, for example, the Nhamapaza with the Mupa; Nhandue and Vundudzi with the Chinzuia; Corone with the Sambazo; and the Pungue with the Sangussi.

A diversity of sediments has been deposited in the Rift, but generally the sandier detritus have formed alluvial fans of all dimensions whilst the finest sediments gave rise to slacks and basins (Fig. 6. 3). These basins are extremely flat with gently inclined margins and they occur as a necklace along the length of the Rift floor, pinched off at various intervals by the fan sand deposits which have grown out from both sides of the Rift. The close juxtaposition of two of these fans built by the Nhamapaza River from the west and the Mazamba River from the Cheringoma Plateau forms the divide at 59 m altitude between the Pungue and Zambezi drainage on the Rift floor. This site is on the Tengane dambo in the northeast of the ecosystem. Where the Urema Trough meets the Zambezi River, the altitude is about 25 m, at a distance of 170 km from the Zambezi mouth. The Rift Valley floor has a low drainage density.

Both perennial and seasonal streams which traverse the Rift floor are tightly meandered. The Mucombezi, Vundudzi, and Mucodza Rivers which flow into the Urema Lake have incised their courses from 7 to 10 m below the floodplain surfaces from which they originated. The Vundudzi and Urema Rivers in particular have incised deeply through alluvial deposits. The Urema River is now underfit as it no longer forms part of the course of the Pungue River, and only during exceptional flood years is a bankful condition reached when Pungue waters dam up the Urema's flow at their confluence.

Formed at the head of the Urema Lake is an extensive converging delta built by the confluence of deposits from the Nhandue–Mucombeze, Vundudzi, and Mucodza rivers. This type of delta, as opposed to the diverging delta type typical of certain river mouths where they meet the sea, is replicated in larger scale across the continent by the Upper Niger in Chad, Kunene–Kuvelai in Ovamboland where it meets the Etosha Basin, and the Okavango where it abuts on the Makarikari Basin. In

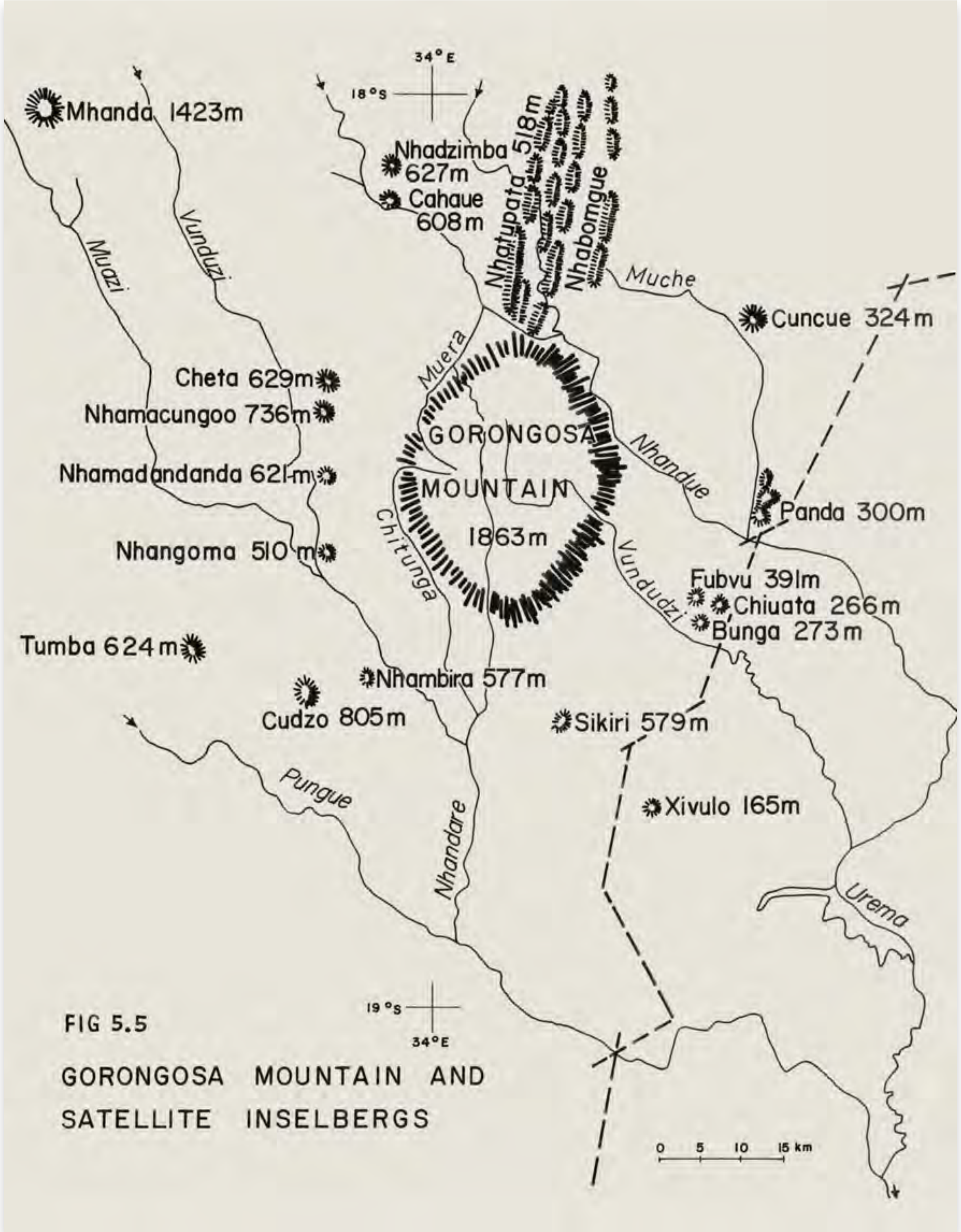
Mozambique the largest partial endoreic basin is represented by Banhine in Gazaland. Banhine is surrounded on its northern quadrant by an extensive converging delta of the fossil Save drainage, formed prior to its capture by headward erosion of direct drainage to the sea. This sequence is again replicated by river capture of the Kunene from Atlantic drainage, which resulted in the major hydrology responsible for the formation of the Ovambo Delta, the Etosha Pan and its overflow to the Okavango River via the Omuramba Omaheke (pers. data). The junction of this Omaramba with the Okavango River is 60 km west of Rundu, just upriver from the village of Mawewe. The evolution of such alluvial processes as they pertain specifically to the Gorongosa ecosystem will be dealt with in Chapter 6.

Unique on the floor of the Urema Trough are two outcrops, or inliers on the southwest side between the Vundudzi and Pungue Rivers. One, Xivulo, is a small inselberg of 165 m height formed by quartz breccia. The other, a low rounded horst block rising to 78 m, is of Precambrian migmatitic gneiss with dykes of granophyre (Gorongosa granite) and dolerite. Immediately east of this isolated block with parallel north–south faults is a major fracture line (Fig. 5.8) on the Rift floor, made conspicuous by the north–south drainage and series of small pans which formed part of the Pungue's original river course (Fig. 6.3). This north–south fracture reappears to form the Muche valley in the northwest of the park. Apart from these two outcrops, the remainder of the Rift Valley floor south of the Zambezi River is composed entirely of alluvial deposits.

Due to their flat open nature, the floodplains of the Rift floor emphasize the physiographic importance of termite hills in the landscape. These hills are especially conspicuous on open floodplain areas where their bare conical shapes dominate the relief. In other areas the hills are covered in tall dense thicket, which form islands in a

RIGHT: Figure 5.5

Gorongosa Mountain and satellite inselbergs.



sea of seasonally flooded grasslands. Most of the termite hills average 3 m in height with a diameter of 20 m, and these conical surfaces produced by biotic activity have enormous influence on the appearance and dynamics of plainsland. The highest density of termitaria occur on levees and splay deposits or on convex surfaces of the plains (see Section 6.3).

Cheringoma Plateau

As the plateau is in fact a cuesta in profile with a slight tilt of 3^0 to 5^0 to the south-east, this has profound influences on the rate and degree of erosion and depositional processes resulting in quite different physiography on the riftward scarp inface and the seaward backslope. They are thus discussed separately. The Cheringoma's surface has been eroded mainly from two sides, by riftward and seaward drainage, which now meet along a narrow north–south watershed formed by erosion of the inface scarp. As scarps retreat by erosion the crest moves in the direction in which the strata dip. This phenomenon is known as homoclinal shifting of watersheds (King 1963, p. 62). The significance of the reduction in catchment area by this and other processes is dealt with in Chapter 6.

Erosion, especially of the riftward slopes, has been greatest in the central and southern part of the block. Thus the oldest intact surfaces remaining are most extensive in the north of the cuesta, the lnhamitanga area, and on the seaward interfluves. Three areas above the 300 m contour remain. The largest is in the Inhaminga area with the highest point of 379 m on a sand rise close to the cliffed scarp overlooking the Rift Valley. The other areas above 300 m are small and occur on the watershed south of Inhaminga near Cundue.

Piercing the Cretaceous and Tertiary deposits are two isolated volcanic necks of basalt, the larger of which form the Gadjiua Hills of 346 m altitude near the Cundue ravine. Both occur on the heavily faulted inface of the cuesta.

Riftward slopes

The inface rises in a series of steps related to the alternation of hard and soft strata and their differential erosion. The rise from the Rift is generally steep at first, then flattening out with a much gentler rise between steps. The central part is characterised by deep cliff-sided ravines incised more than l00 m deep into the softer, Cretaceous, Grudja Formation. The dense system of parallel, oblique and normal faults and fractures characteristic of the inface has greatly favoured erosion processes. Five streams have cut these canyons, which are either narrow (Muanza) or wide (Nhandindi–Nhamfici), and headward erosion stops abruptly at nickpoints in the harder sandstone exposed at the surface. The most spectacular ravines have been cut by the Mazamba and Cundue streams. The yellowish-white calcareous sandstone cliffs and caves, formed by the Cheringoma Formation, weather in a similar manner to the Cave Sandstone in the Drakensberg, by basal sapping. Erosion is along the strongly jointed and fractured lines of weakness where subterranean limestone weathering also occurs. Truncation of the strata overlying the Cheringoma Formation has given rise to extensive tablelands with skeletal soils and conspicuous jointing.

All the present day streams of the riftward drainage are small and the majority are perennial, if only in their central courses. Where they meet the footslopes there is no running surface water as this disappears into sands. The streams pass through the stepped topography by means of falls and rapids separated by long pools. Where the riftward streams meet the alluvial toeslope, an apron of coalesced alluvial fans has been built out onto the Rift floor with the sediments derived from erosion of the inface (Fig. 6.3).

Headward erosion of the northern and central riftward slopes is damped by exposure of hard calcareous sandstone strata, but the southern sector has no such barrier and active slump and donga erosion of deeply weathered argillaceous sandstone of the Mazamba Formation is occurring, especially conspicuous in the Musapasso stream.

The crest of the cuesta comprises deep red sandy latosols alternating with high water table pallid to white sands. Dambo remnants form the headwater catchments of most of the riftward drainage; others have been eliminated by headward incision which has reached the divide itself. The drainage density of the riftward slopes is medium to high.

Seaward slopes

The drainage of the Cheringoma Coast is now composite in nature due to truncation of the overlying sands over the major part of the central and upper catchment. Thus an original coarse-grained parallel and rectangular drainage related to the cross-fracture system of the cuesta is typical of the main rivers and the dambo

The Cheringoma Ravines of the riftward drainage.

drainage on the remaining areas of sands, and this has been replaced by a fine-grained dentritic drainage on exhumed subsoil sandy clays. The main rivers such as the Mupa, Chinizuia and Sambazo have broadly meandered courses deeply incised into the middle to upper dipslope. These fifth order rivers also have wide braided channels enlarging by lateral erosion.

Where the underlying clays, formed by deeply weathered calcicargillaceous sandstones of the Mazamba Formation, have been exposed, the headwater tributaries are deeply incised giving rise to a highly eroded polyconvex landscape, replicating the situation in the Musapasso River and other riftward drainage to the south. Rapid erosion of these friable clays has resulted in numerous river captures and beheading of drainage as streams cut back laterally in the upper reaches. Thus a large part of the dambo drainage on the remaining duplex sands is in the process of extinction due to drying out and nickpoint migration from the coast.

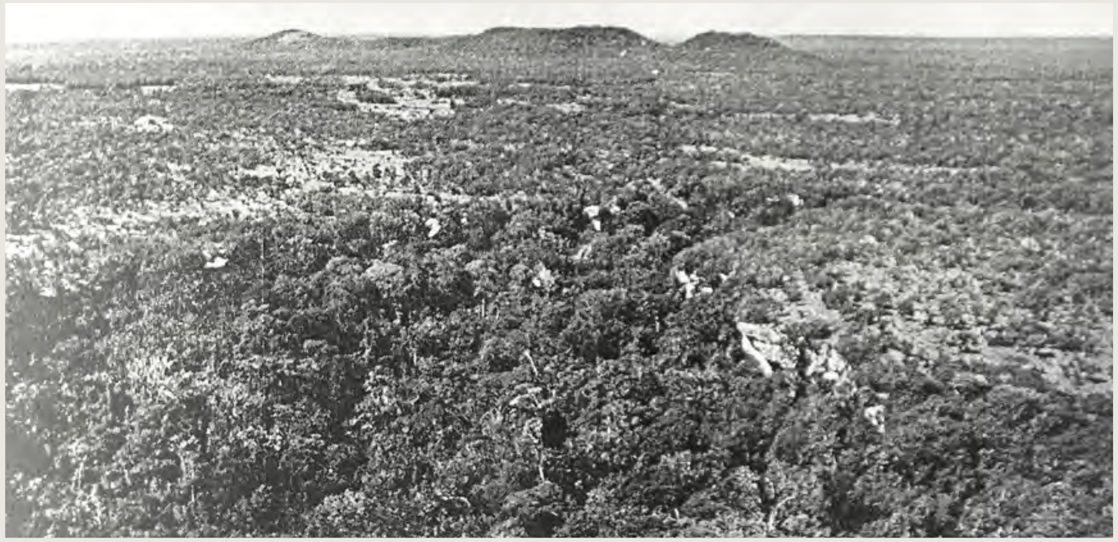
A unique feature of the dambo drainage on the eluvial sands (leached sands) of the seaward slopes is the large numbers of oval pans originating from the broader and deeper permanent vlei areas in the dambos. The largest area of these pans is in the north of the cuesta between Inhamitanga and Marromeu. This area has also the largest areic sand area on the Cheringoma. Similar pan systems in Mozambique occur near the coast in the extreme north, inland of Mocimboa da Praia, and near Dombe below the Chimanimani Mountains. In all three areas the oval pans occur on duplex sands. Elsewhere in the subcontinent similar pans occur: in the southern Kalahari (Kalahari Bult), eastern Transvaal, Western (Orange) Free State and Northern Cape (Wellington 1955; Boocock & Van Straten 1962; Grove 1969; De Bruiyn 1971).

Complementary to the massive erosion of the coast plateau hinterland by the main rivers, is the apron of coalesced alluvial fans formed between the 100 m contour and the alluvial front of the Zambezi Delta floodplains. Some of these fans measure 25 to 30 km in length (apex to front), and the abandoned aggraded distributaries are indicated by forest cover. The intervening slacks form part of a younger dambo system of drainage with oval pans and vleis.

The wearing back of the major river valleys has eliminated the overlying duplex sands on some interfluves resulting in a rounded, eroded topography, but in other situations the sands form valley-side scarps. In the latter situation interfluves remain flat to faintly undulating with dambo drainage.

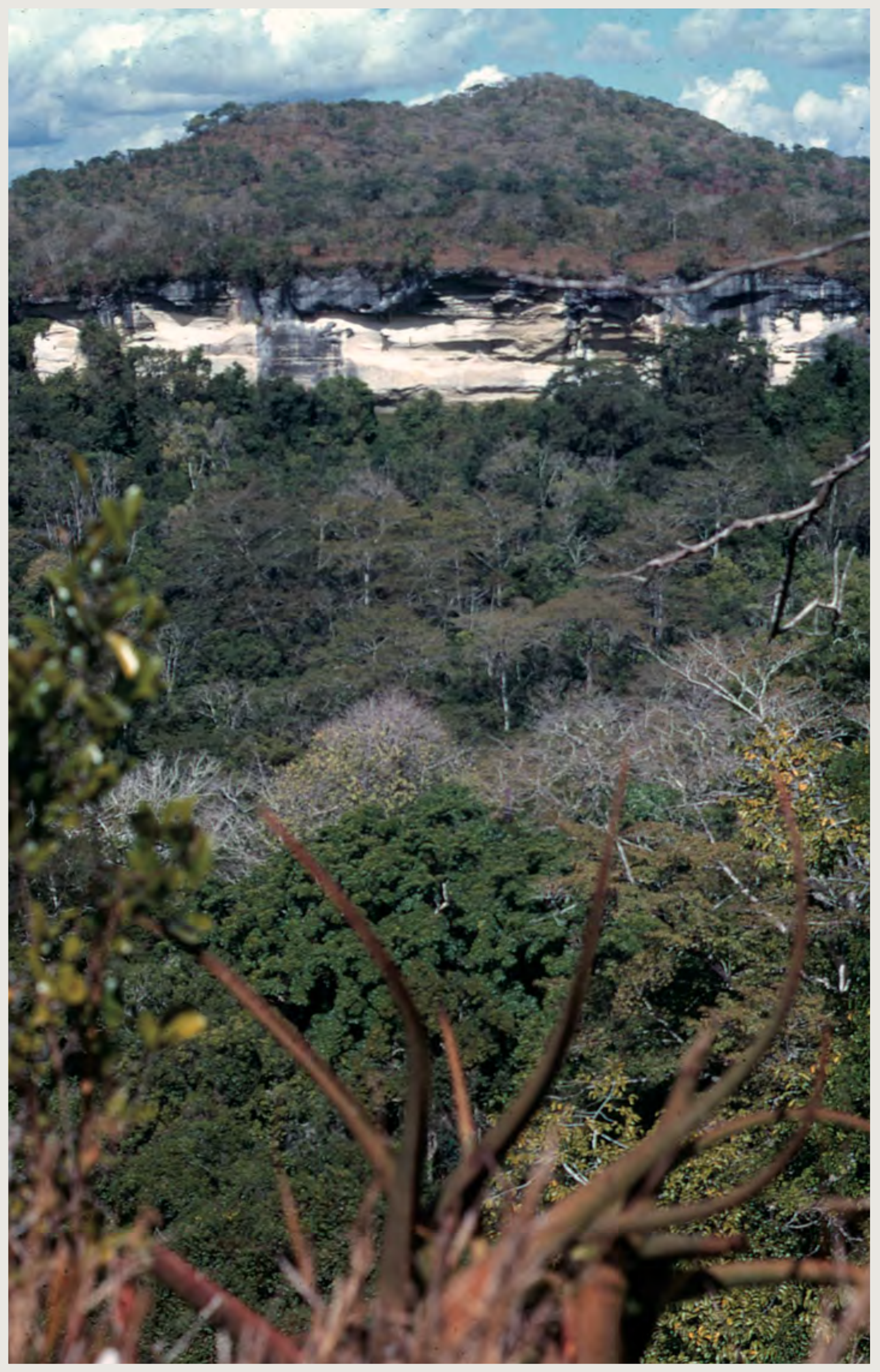
The dipslope drainage patterns meet a longitudinal floodplain meander drainage abruptly near the coast. The complex of distributary meander belts, meander cutoffs, meander scrolls, and swamp slacks extend in a narrowing front from its origin at the Zambezi River to half the length of the Cheringoma Coast, that is petering out near the Chinizuia River mouth. The larger resequent rivers have crossed this alluvial plain to form estuarine deltas covered in mangroves.

The Cheringoma Coast is classified as a barrier and swamp coast with estuarine deltas and linear beaches (Tinley 1971). Although the Cheringoma block was islanded in the Plio-Pleistocene, it is essentially a coastline of submergence (vide Holmes 1965, p. 828). The shallow and broad continental shelf extends to 120 km off the present coastline, and the continental slope descends abruptly at the 100 m isobath to over 2,000 m depth (see Tinley 1971 b, Fig. 6.). Recent research on this shelf has shown the existence of dune rock near the break in slope, thus the 120 km now under water was part of the Cheringoma land mass and the edge of the shelf was the old coastline.



BELOW RIGHT:

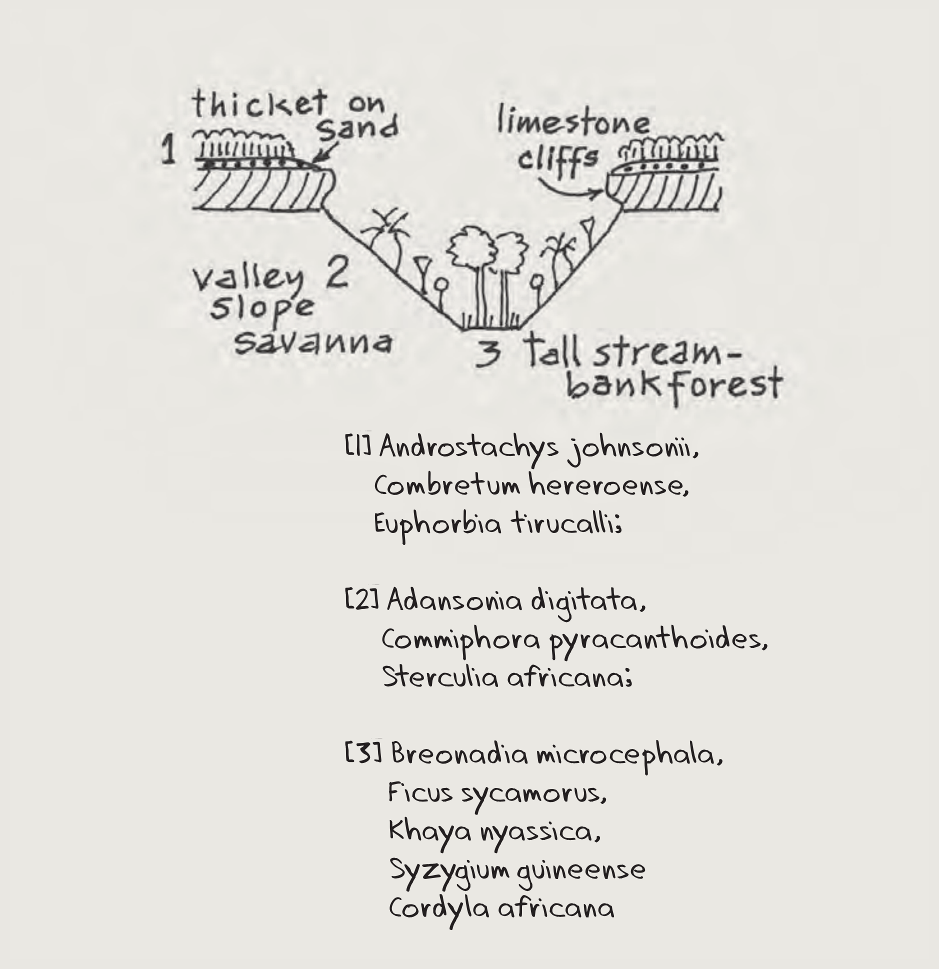
Oblique air view of the forested Maciguadzi Ravine looking north-east with the Gadjiua Hills formed by volcanic plugs of nepheline basalt on the crest of the Cheringoma Plateau. Limestone cliffs in right foreground.



© Paul Dutton

FAR LEFT:

The Cheringoma Ravines of the riftward drainage.



LEFT: Figure 5.6

Vegetation profile of the Cheringoma Ravines.

Continued coastal erosion is shown by truncated estuaries with new sand spits and active beach erosion (Tinley 1971b).

The estuary deltas are formed by fluvio-marine processes and these are protected by sand spits at their mouths. Only at the actual river or distributary mouths is there accretion of sediments. The linear beaches show two upper berms related to an equinox spring tide bevel and normal high tide bevel. In profile, the beaches show a steep upper slope and a long shallow lower slope. Separating the beach from the alluvial plains is a narrow barrier of low dunes of parabolic and hummock form. The highest attain only 14 m altitude as compared to the high parabolic dunes of the southern Mozambique Plain which attain 187 m at their highest (St Lucia Lighthouse). The parabolic dunes are formed by southerly

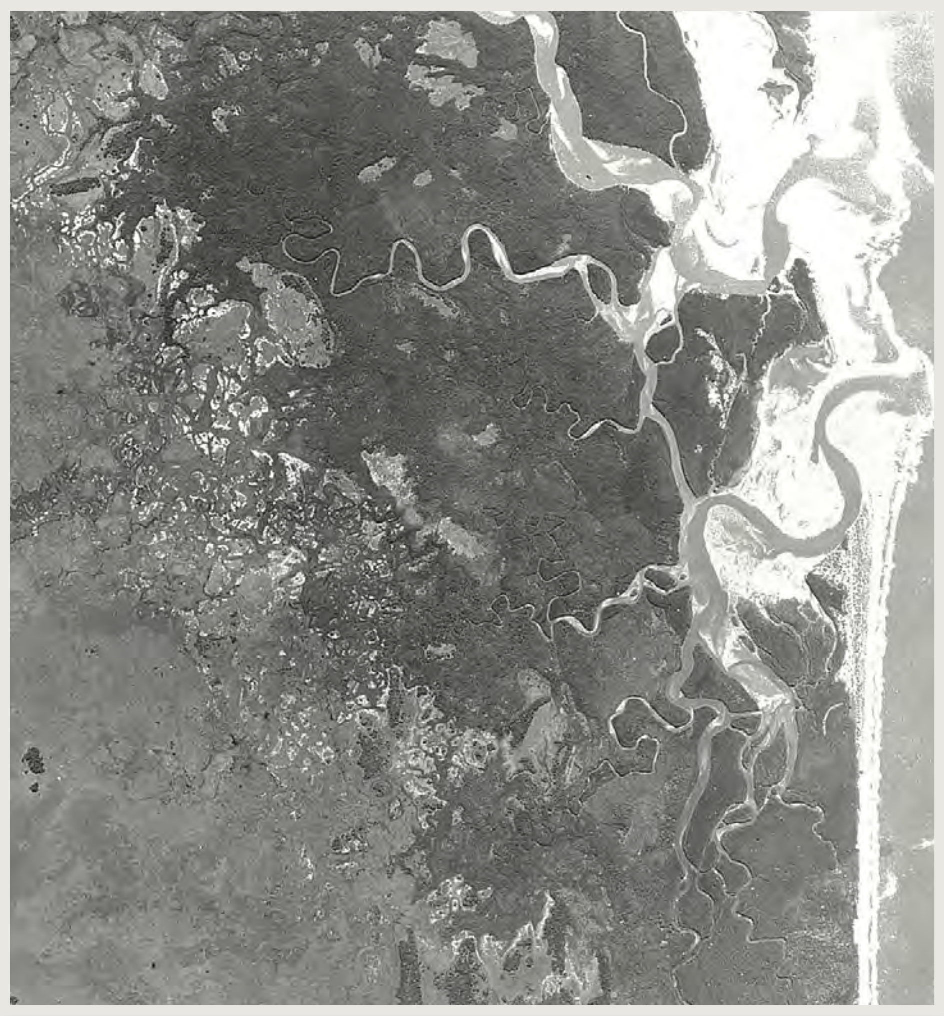
Alluvial fans and estuarine mangrove forests of the Cheringoma Coast.

RIGHT:

Aggraded distributary courses (convex surfaces) colonised by miombo and evergreen forest alternating with acid dambo grass slacks on duplex podsolized sands. The existing perennial blackwater streams have incised the slacks and these cuts are colonized by various kinds of hygrophilous forest. White dots are 'drowned' and eroded termitaria, dark dots are living termitaria covered in thicket.

FAR RIGHT:

Southern tip of Zambezi Delta organic alluvial clays interposed between the estuarine mangrove (right) and the duplex sand fans of the dipslope river (left). White patches are salinas. Receding coastline clearly illustrated by truncated estuary mouth and mangrove creeks.



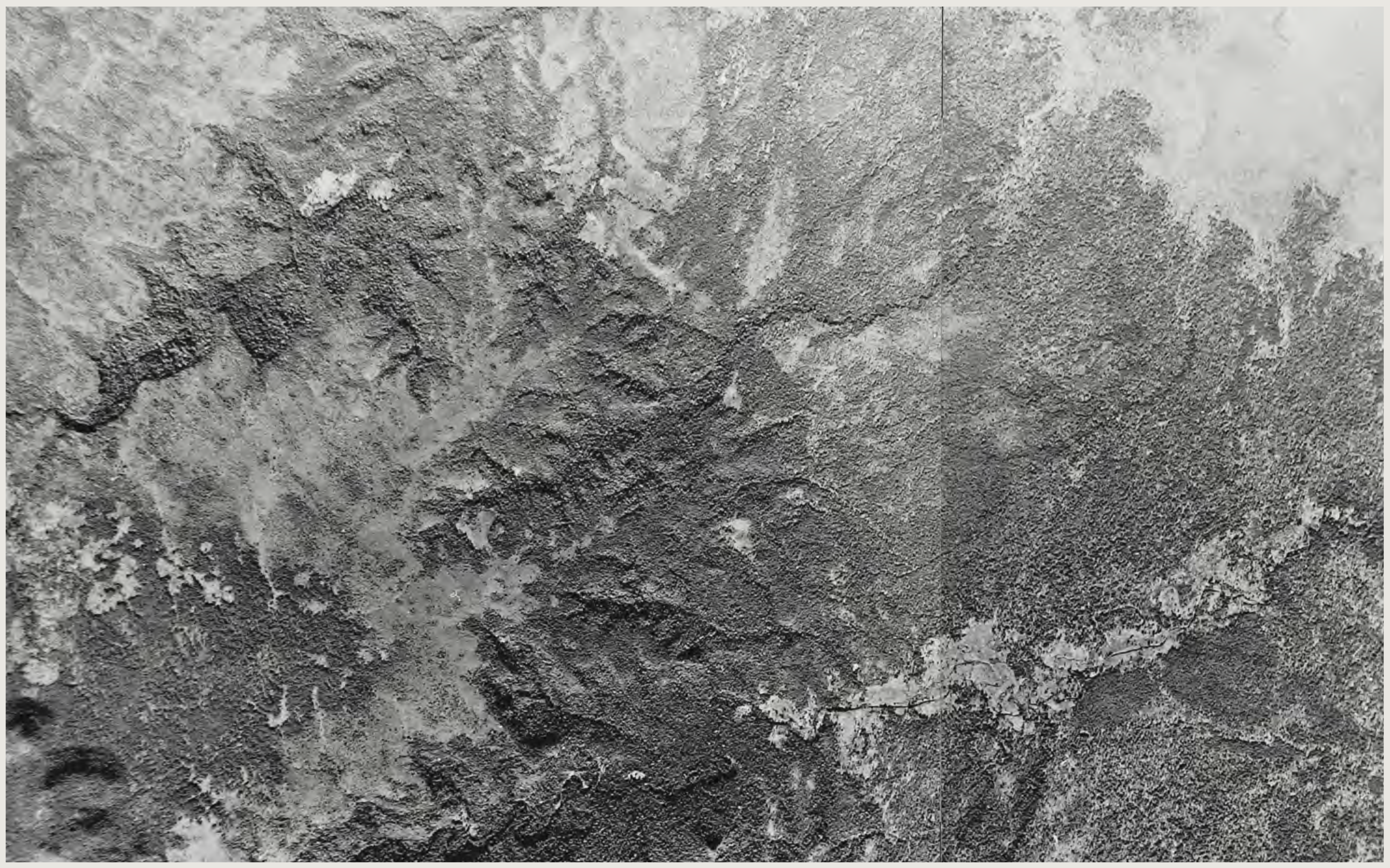
gale winds. Near the Nhandaze and Mungari distributary mouths of the Zambezi Delta are large areas of alternating dune and slack relief which occur in parallel or curved lines empathetic with the shape of the coast. The largest parallel dune area extends 5 km inland from the beach and older groups, now isolated, occur nearly 30 km inland from the delta coast. The inland groups are separated by slack vlei areas or mangrove swamps. The Zambezi Delta is of the arcuate type and three large distributaries are active all year—the Chinde, Cuama and Mucelo. The Cuama is actually a continuation of the main Zambezi course.

As in the Rift Valley, termite hills are a major feature of the Cheringoma coast plains. The hills formed here are much broader than those on the Rift floor and their influence on geomorphology, hydrology and ecology is considerable (see Sections 5.7 and 6.3).

5.2 GENESIS OF THE PRESENT LANDSCAPE

Except where otherwise indicated, this section is derived almost entirely from King (1962). Many of the regional and local events are fitted to his treatment by reference to the Mozambique 1:250,000 geological sheets revised in 1968 and the 1: 2 million map of the entire territory (Oberholzer 1968).

The implications of these landscape changes on the climate and its reciprocal role are personal interpretations except where otherwise noted. Central Mozambique, in



The Cheringoma Ravines of the riftward drainage.

LEFT:

The Cundue and Maciguadzi Ravines from the air with the Gadjiua Hills on the right (east) and Rift Valley floodplain on the left (west). Note: (1) forested ravines; (2) closed savanna-thicket mosaic on incised fan aprons in front of the ravines; (3) relic 'mesa grasslands' on impervious glauconitic clays (top centre of photo) being replaced by forest; (4) present aggraded floodplain now incised of Cundue Stream (and cultivated); (5) white patches around the hills are cultivation clearings; (6) sparse savanna cover on stripped horizontal limestone strata between the two ravines.

keeping with the remainder of the east coast of Africa (King 1972a, 1972b), took part in the diastrophic, sedimentary and volcanic history of the Gondwana super-continent. In the early Jurassic, basalt lavas, extruded from fissure swarms, formed vast lava plains blanketing the low relief formed by Karoo desertic formations.

The denudation and sedimentary processes, aided in part by the above horizontal structural control, cut across many geological formations and by the end of the Jurassic had reduced the landscape to a vast planation surface. Today the remnants of this Jurassic planation ('Gondwana') form the accordant summits of the highest parts of Africa's mountains and represent the oldest extant planations in the modern landscape (King 1962).

At the end of the Jurassic and in the early Cretaceous the incredible breakup of Gondwanaland took place, separating the southern continents and giving birth to new coastlines. The desertic continental climate of the super-continent was concurrently transformed to marine, coastal and interior climatic systems as the ocean areas grew in dimension between the separating continents. The first marine deposits of the Indian and Atlantic Oceans were laid down along the new outlines forming the African continent.

In Kenya, Tanzania and on the west of Madagascar, Permian marine deposits overlie the tillite and coal measures of the Karoo (Furon 1963), indicating that splitting of continental masses with marine transgressions took place from the north, in a gulf or a possible proto-Mozambique Channel. For this reason many authorities (Du Toit 1937; King 1962; Hallam 1973) suggest that Madagascar lay against East Africa and not Mozambique, as present outlines would suggest, having moved south to its present position. On the other hand Wellington, (1955, pp. 460-473) supported more recently by Flores (1970), suggests that Madagascar fitted against Mozambique if the Jurassic volcanics on both sides are matched. In addition the presence of Tertiary volcanics on the Mozambique coast are matched on the west coast of Madagascar, and are absent from the East African coast. Wellington also points out that the Precambrian metamorphic rocks of Cap St Andre of northwest Madagascar fits into the Lower Zambezi trough ('Lupata Gulf') where similar rocks would fit on either side. The sector where Cap St Andre would have fitted, is now occupied by Cretaceous alkaline lavas at the tip and a large area of continental Cretaceous sediments 3,000 m thick. The southeast part of this extraordinary thick deposit is now faulted by the Urema Trough and enters the Gorongosa region in the north. Flores (1970) fits Madagascar in a lower position with Cap St Andre against the Bight of Sofala (see Section 5.3).

The outpouring of early Jurassic volcanics was related to the increasing crustal tension which led to the final dismemberment of Gondwanaland; the lava emissions occurring along many fissures related to the main fracture system of the continent such as those of the Lebombo and Buzi, and between Lupata and Gorongosa which formed the edges of the Cretaceous sea. Prior to the Gondwana breakup there were also post-Karoo troughs formed in the Luangua, mid and lower Zambezi, and the Limpopo.

Wellington (1955, pp. 460-473) suggests that prior to the break up of Gondwanaland the drainage derived from the land mass east of the present coast (Madagascar in his thesis) and flowed westward along the Middle Zambezi and Limpopo into an interior continental basin as far as the Congo and Orange river areas. It is also possible that these sediments filled the west branch of the southern end of the Rift Valley, lying beneath the Okavango Delta front if it was faulted down in post-Karoo times. The break up of Gondwanaland truncated these drainage systems and downward bowing of the coastal margins reversed the drainage and initiated headward erosion toward the interior from the new ocean base level. This new cycle of erosion (Post Gondwana), which began dissection of the Gondwana planation surface, formed broad open valleys towards the crest of the convex warp and completely stripped off the remainder closer to the Cretaceous coastline by headward retreat of giant erosion scarps (e.g. Figs. 10-13 in King 1972a). King (1962, p. 158) reckons that the rate of retreat of such continental erosion scarps is about 30 cm in a 100 years, as evidenced by the Great Escarpment in Southern Africa and other parts of the world.

It was probably during the break up of Gondwanaland or just before, in the late Jurassic, that the younger syenite and granite intrusions (plutons) were emplaced, which today form the island massifs of Mulanje in Malawi (Dixey 1927) and Gorongosa, Morrumbala, Derre and Chiperoni in Central Mozambique (Oberholzer 1968). The last three inselbergs occur in the Zambezia District against the Shire Trough. Depending on the time of their emplacement, their summits were bevelled either by the last part of the Gondwana planation just before break up of the continents, or by the Post Gondwana erosion of the early Cretaceous.

In the Late Cretaceous further uplift with outward tilting of east and west coasts was repeated which initiated a fresh cycle of erosion lasting until the mid-Tertiary (Oligocene). This cycle of planation, the 'African', reduced the whole continent to an extremely smooth plain the remnants of which today form the South African High-veld, the watershed of Zimbabwe and the Serengeti Plains amongst other areas (see King 1962, Fig. 119). In Central Mozambique remnants of the 'African' surface are found on the highest slopes of the interfluves joining the base of the great escarpment. The most extensive is that of the Chimoio interfluve between the Pungue and Revue valleys which leads up to the saddle in the escarpment at Umtali.

At the end of the Oligocene and in the late Miocene, moderate uplift created fresh base levels for a late Tertiary dicyclic erosion cycle which cut back widely spaced broad valleys into the extremely smooth 'African' landscape left as remnants on the interfluves. By the end of the Tertiary, therefore, the greater part of Africa was reduced to a rolling lowland with vast plains and widespread formation of duricrusts indicating a phase of extreme stability in the landscape. To accentuate the far reaching effects of the coming diastrophism of the Plio-Pleistocene, it is important to emphasize that the lowland form of the subcontinent at the end of the Tertiary meant the interior was only 300-500 m above sea level (King 1962, p. 243).

The importance of these events, culminating in the late Tertiary duricrusted plains of continental dimensions, implies seasonal waterlogging on a vast scale which has important biogeographic implications as judged by present day spatial control of grass and woody vegetation by soil moisture balance. These aspects will be dealt with in Sections 5.7, 5.8 and Chapters 6 and 8.

If climatic patterns were similar to today over the 'low' southern Africa in the late Tertiary, the high rainfall (> 1,000 mm) would have been confined to orographic lines and to an extremely narrow belt along the coast, with isohyets decreasing parallel to the coast inland to less than 400 mm or 300 mm judging by the present Mozambique Plain area of Gazaland. The interior of the subcontinent would have been desertic with vast playas of alluvium, and islands of marshes and savanna strips extending along drainage lines. Judging by today's desert grassland substrate, a greater part of the continent could have been desert grassland where a sandy veneer covered the plains. In such circumstances it would have been possible for Pliocene gazelles, ancestral to the springbok, to have occurred from the Karoo to the Sahara (Pliocene fossil *Antidorcas* occur in the Marghreb: Cooke 1964).

This monotonous, and probably arid landscape was drastically changed in the Plio-Pleistocene by large scale land undulations and faulting. Intense upwarping elevated the interior to a plateau between 1,200 and 1,500 m and at the same time tilted the coastal margins strongly downward toward the ocean basins. These large crustal convexo-concave arches, called cymotogenes (King 1962— the 'undulating ogeny'), tilted the coastal hinterland upward and depressed the continental shelf zone.

Reference to King's (1962) Fig. 77, shows the outline of the cymatogenic arch through central Mozambique, from the Gondwana level at 2,400 m on the Frontier System summits of Inyanga to the same surface found in boreholes at 2,000 m below sea level at Inharrime forming the floor on which Cretaceous sediments accumulated. Where previous coastlines lay close to the hingeline of the arch, Iittle change occurred (as on the Natal Coast), but where the hingeline of the upwarp lay offshore broad coastal plains were added to the continent, as in southern Mozambique. Maximal uparching occurred inland as a rim over 2,000 m high, parallel to the coast and varying from 100 to 200 km distance from it. The uplifted and inclined planation surfaces of the late Tertiary then provided ideal conditions for massive headward and downward erosion by rivers, carving out great gorges, with rapids and waterfalls marking the inland invasion of erosion cycles. This marked diastrophic alteration took place slowly enough for the meandering drainage lines of the late Tertiary planation surface to incise their old-age form downward as they carved out youthful valleys in the slowly arching landscape.

Where faulting took place, as in the Rift Valley, dislocations were rapid. Judging from the presence of Mio-Pliocene littoral and fluvial sediments on the crest of the Cheringoma Plateau, when the sea level of that time was 300 m higher than the present, the cuesta was left as a relic by the receding sea level and downfaulting of the Urema Trough associated with the sinking of the remainder of the Mozambique Plain in the early Pleistocene. Relatively fresh fault scarps and ravines face the Urema Trough, and the south-east incline of the seaward plains enhanced headward erosion and incision of the fan distributaries formed originally by the inland rivers prior to rifting. The rifting on the western side of the Urema Trough was probably repeated along old fault lines of the Gondwana break up and earlier fractures. The western side of the Rift Valley is thus deeply eroded in comparison to the Cheringoma side.

As the rift valleys were trough faulted on the crests of tensional uparching, the old sedimentary formations would show least dip close to these dislocations. The upper Karoo sandstones, outcropping beneath Stormberg basalts in a narrow belt entering the north-west corner of the Gorongosa region, are only slightly inclined to the east and the overlying basalt flows are inclined to the southwest (Real 1966). However, cross faulting is abundant close to the Rift dislocations and the above disposal of strata may have no significant relation to the Plio-Pleistocene diastrophism. The younger granite plutons and the granite-gneiss cores which today form the Inselbergs of the Manhica Platform would have been exposed first by the Post-Gondwana and early Tertiary erosion and planation.

At the end of the Tertiary the vast 'low' continental plain was deformed into an undulation by the Plio-Pleistocene land movements which bowed the coastlands downward as the hinterland was uparched to over 2,000 m, raising the continental interior to between 1,200 and 1,500 m. This change from a low continental plain with high rainfall probably confined to the coast (judging by the Mozambique Plain) with a desertic interior, to an interior plateau with a rim of over 2,000 m meant that a change in rainfall regimen to two highs (of about 2,000 mm) must have occurred—one associated with the coast as before, and the other with the orographic line formed by the rim. A high rainfall belt along the rim would then have carried the precipitation tail-off deeper into the interior than was possible from the coast, changing these lands from desert to savanna.

The massive erosion, consequent of this arching, gouged deep valleys with planation remnants of various dimensions left on the interfluve spurs, and reduced that vast rim catchment to relics. These landscape changes alone can account for the changes in climate, with rainfall highs confined to orographic remnants and low precipitation in the valleys and plains areas. In addition to river capture effects, these landscape processes alone can account for the underfit nature of most present day rivers relative to the size of the valleys they have carved in the past.

Headward erosion of the great escarpment from inland would have also been given greater impetus during and after uparching. The continental interior was depressed relative to the rim and became filled with further sediments. Over this vast network of marshlands, which could have stretched from Bushmanland to the Sudan River, capture and draining of marshes by headward erosion would have begun their separation and contraction in the earliest Pleistocene.

Although climatic changes related to glaciation or to long term oscillations of the westerlies and intertropical front are important, it seems to have been underestimated that the geomorphic processes associated with diastrophism alone be responsible for leaving a similar fossil record. Nick-point breaching of wetlands can convert large areas of alluvium to aridisols as exemplified by northern Botswana where mopane savanna covers 'fossil' floodplain surfaces. Such changes would have left a pluvial and interpluvial record from changes in drainage and runoff due to uplift and subsequent reduction of relief alone, without requiring any change in climate.

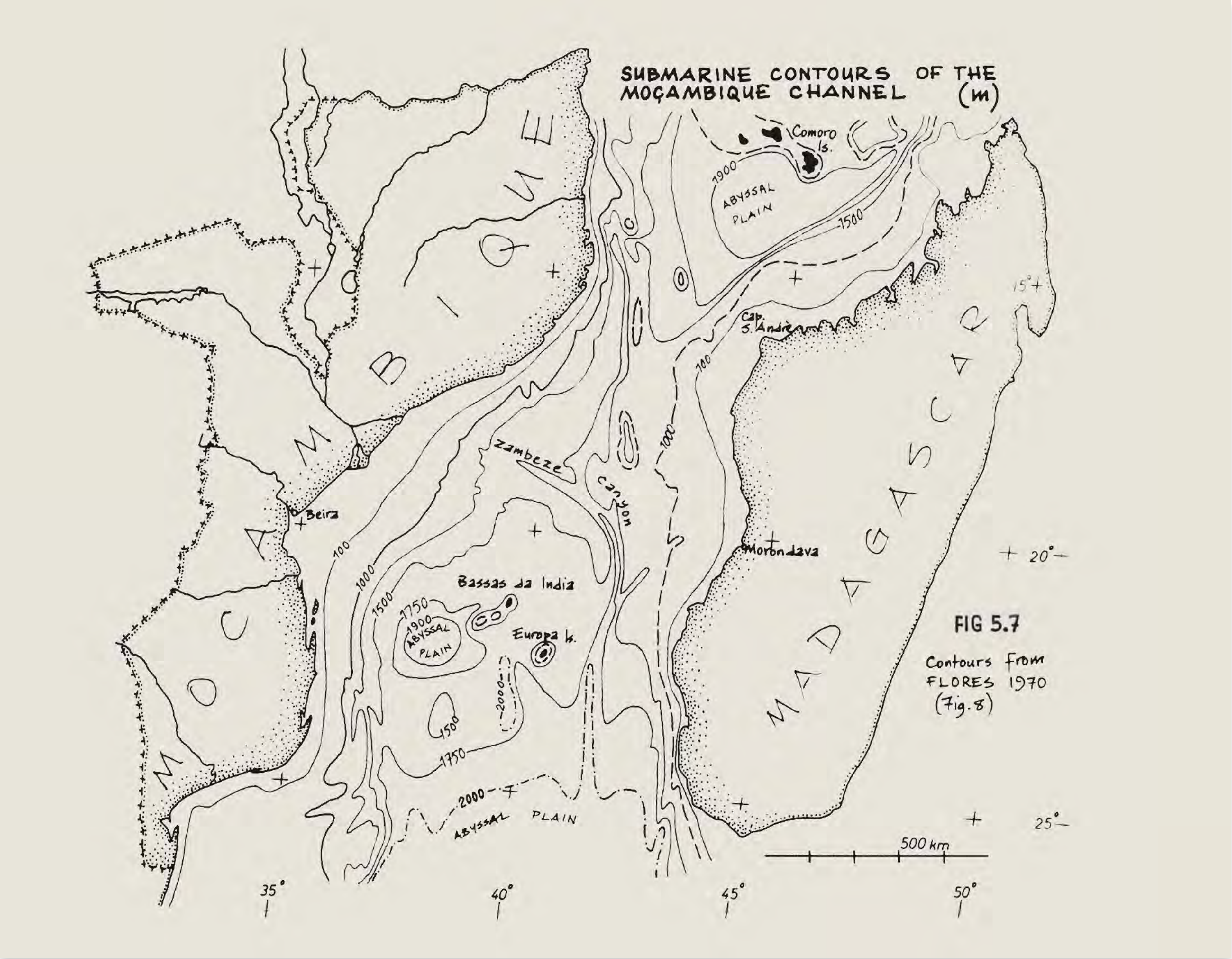
In sum, the Plio-Pleistocene deformations of the Tertiary landscape and consequent erosion and sedimentation is chiefly responsible for the face of modern Africa (King 1962), including its climatic and biome patterns.

5.3 MOZAMBIQUE AND MADAGASCAR

The presence of Madagascar Island, lying 400 km offshore at the closest point, and extending almost the full length of the Mozambique Coast, requires further explanation to elucidate landscape evolution and biogeographic relations in central Mozambique. Particularly as the position of Madagscar in the fit of Gondwana landmasses against the east coast of Africa has remained the most enigmatic part (Tarling 1971; Hallam 1973), giving rise to three contrasting theories.

The theory followed in this work is Dixey's (1956) interpretation of the geosynclinal nature of the Mozambique Channel and the permanence of Madagascar in its present or near-present position. Using new data, three recent publications augment this interpretation (Flower & Strong 1969; Darracott 1974; Kutina 1975). The other theories fit Madagascar either against the East African coast (Du Toit 1937; King 1962; Smith & Hallam 1970), or against Mozambique, in Gondwanaland times (Wellington 1955; Flores 1970; Wright & McCurry 1970). The biogeographic complications these theories raise are well exemplified by recent attempts to determine the possible position(s) of Madagascar relative to the mainland on the basis of its floral affinities (Wild 1975; Pocs 1975).

Kutina's (1975) studies of Madagascar support the suggestion by Fisher et al. (1967) and Fourmarier (1967) that the submarine Mascarene Plateau and Madagascar represent the uppermost remnants of a foundered or subsiding continental crust. This means a continuous area of Precambrian basement existed between the Mid-Oceanic Ridge and the present coast of Africa, of which the granitic Seychelles islands represent the easternmost exposures. Darracott (1974) shows that the Mozambique geosyncline and Madagascar submarine ridge are probably all composed of thinned continental or transition crust. The existence of the Mozambique geosyncline, the complex horst of Madagascar, and the submerged Mascarene Plateau are obstacles to the derivation of India from eastern Madagascar as propounded by Smith and Hallam (1970), for example, and contradict



LEFT: Figure 5.7

Submarine contours of the Mozambique Channel.

the available evidence from the floor of the Mozambique geosyncline (Darracott 1974). These data point rather to India's origin on a separate plate in the central part of the Indian Ocean from between the Chagos fracture zone and Ninetyeast Ridge (McKenzie & Sclater 1971; Kutina 1975).

The fracture system of Madagascar and the mainland are identical, and this, with stratigraphic similarities, is the major aid to the theory of Madagascar's origin against Mozambique. However, the intersection of these fractures and their exaggeration by downwarping and faulting has given rise to the sympathetic zigzag strike of Africa's east coast and the west coast of Madagascar. In addition the continuation of major fractures is expressed by bathymetric contours in the Mozambique Channel (Fig. 5.7). The most conspicuous of these is the continuation of the north–south strike of the northern Mozambique Coast southwards as the Zambezi Canyon (see Green 1972, Fig. 12; Flores 1970, Fig. 8). This canyon is separated by an oblique north-north-west to south-south-east rise above the 1,000 m isobath, which is the shallowest continuous link between the mainland and Madagascar at present. This rise marks the submarine divide between the Mozambique Basin in the south, into which the Zambezi Canyon empties, and the small Comoro Abyssal Plain immediately south of the islands.

Further evidence from this submarine ridge seems to be crucial for determining whether it lagged behind in the geosynclinal downwarping thus representing the last part of the geosyncline to be submerged. The Comoro Islands of volcanic origin rise from isolated 1,000 m deep platforms and are judged to be of Miocene age (Saint-Ours 1956; Besairie 1960). Completion of the separation of Madagascar from the mainland is judged to be at the Cretaceous-Tertiary time boundary 60 million years ago. Thus the relationship between the Mozambique mainland and Madagascar Island would seem to have been a gradual and continued sinking of the channel floor with intermittent faulting, possibly resulting in a gradually narrowing isthmus which remained into the Tertiary before final submergence, and 'stepping-stones' formed by the Comoro Archipelago in the middle to late Tertiary between the northernmost coasts of Mozambique and Madagascar.

5.4 PLANATION SURFACES

Section 5.2 outlined the possible changes in landscape responsible for the present day appearance of Central Mozambique. All denudational and aggradational surfaces are represented in the Gorongosa system (Fig. 5.8). Dixey's (e.g. 1956) work; King's morphologic map of Africa (1962, Fig. 119); and Real (1966, Fig. 1) who followed King's older work, provide a guide to differentiating the various surfaces. The surfaces are separated on the basis of landform development assisted by contour intervals, since surfaces of the same age on upwarped continental margins are tilted lower seaward and higher inland. As in other parts of Africa the oldest land surfaces in the present-day landscape are the planation remnants on the highest summits and watersheds. In the study area these Jura-Cretaceous bevels are confined to Gorongosa Mountain.

The African (Early Tertiary) planation surfaces survive only as steplike benches on the lower crests and sides of Gorongosa Mountain and elsewhere in the study area have been totally eliminated by erosion. Remnants of this surface occur again to the west on the highest parts of the midland interfluves which merge into the base of the Great Escarpment.

The accordant interfluve crests of the western midlands, deeply incised by the Congo Cycle, and the remnant flat crest along the top of the Cheringoma Plateau are Post-African (Late Tertiary) planation surfaces. The Post-African surface is interrupted by the Rift Valley whose floor is composed of Pleistocene (scarp alluvial fans) to recent sediments. Sediments of similar age form the plains of the Cheringoma Coast, the delta plains of the Zambezi, and the confluence of the Pungue and Buzi Rivers in the Bight of Sofala.

The sediments of the Mazamba Formation forming the Cheringoma crest are littoral facies at their base passing upward into continental fluvial fan material. The final sedimentary phase is probably due to coalescence of alluvial fans of the Zambezi and Pungue Rivers and the lesser rivers between them, such as the Nhandue and Nhamapaza, prior to rifting. This drainage was severed in the Early Pleistocene by downfaulting of the Urema Trough, resulting in reversed drainage on the inland side of the Cheringoma and beheading of the seaward drainage. The original seaward distributaries formed by the rivers from the hinterland became the main lines of river downcutting due to the 3^0-5^0 seaward incline, causing drainage rejuvenation superimposing the original distributary meanders. From their in situ exposure to eluvial pedogenic processes, a leached sand

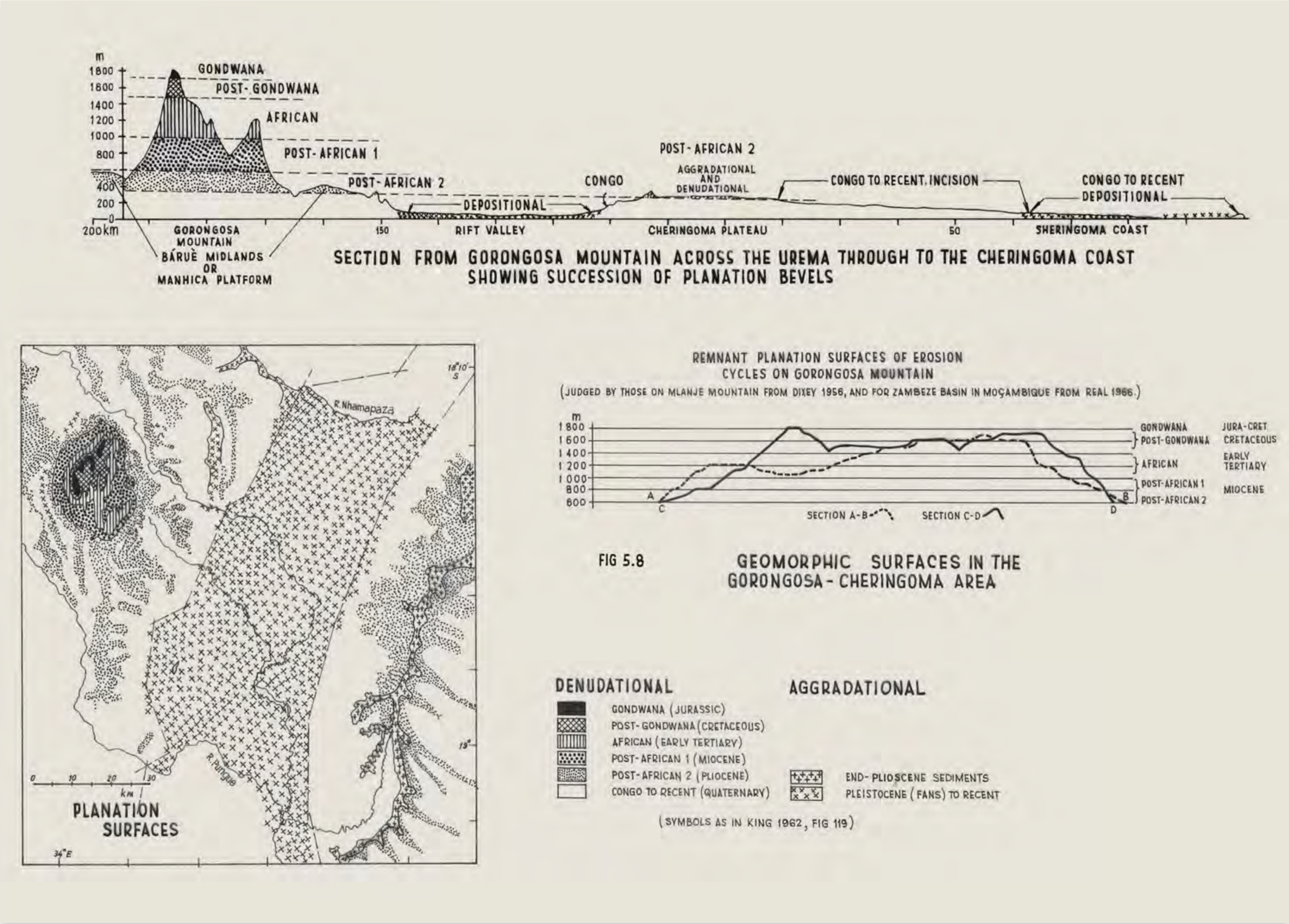


FIG 5.8 GEOMORPHIC SURFACES IN THE GORONGOSA-CHERINGOMA AREA

LEFT: Figure 5.8

Geomorphic surfaces in the Gorongosa-Cheringoma area.

OPPOSITE: Figure 5.9

Geology of the greater Gorongosa region.

surface of almost pure quartz was formed with an impermeable kaolin and iron-rich clay subsoil (C horizon), (data from Geological Sheet Sul-E-36/X of Mozambique, 1968). The development of such a profile ensures maximal capture of the relatively high rainfall, caused by proximity to the land-sea junction and a 300 m rise above sea level. Thus a highly efficient aquifer was formed which provides a perennial high water table flow. The sediments derived from active headward and valley incision were deposited as a broad plain of coalescing alluvial fan distributaries along the entire seaward margin of the now isolated plateau. The differentiation of the surfaces on the Cheringoma Plateau is a personal interpretation derived from ground and air study, based on the assumption that the plateau was exposed to aerial weathering in the Plio-Pleistocene by a retreating (dropping) sea level.

Cutting back from the Rift Valley, the Congo Cycle has gouged deep gorges and valleys far into the Midlands and into the foot of Gorongosa Mountain. Deep ravines of the same cycle have cut back from the Rift into the western fault scarps of the Cheringoma Plateau. In the northern and southern sectors of the plateau the Congo Cycle has consumed the Pliocene denudational surface and is now actively eroding back directly into the remnants of the Pliocene aggradational surface. On the seaward slope of the plateau Late-Tertiary denudational surfaces remain as interfluve fingers which extend seaward from the watershed.

5.5 GEOLOGY

The geology of the Gorongosa region is complex, but clearly defined (Figs 5.8 and 5.9). The Rift Valley plains of recent alluvia separate a western midland of Precambrian metamorphic crystalline rocks from an eastern cuesta block of Cretaceous to Recent sediments forming the Cheringoma Plateau. The crystalline rocks are intruded by a double igneous pluton, dyke swarms and volcanic necks of Jurassic to late Tertiary age, and these with granite-gneiss bornhardts form the isolated peaks, mountains and ridges on the Midlands. The eastern sediments are pierced by only two small nepheline basalt necks of Pliocene age.

The following data are obtained from Real (1966) and the geological maps of Mozambique (Oberholzer 1968) at a scale of 1: 250,000, and their accompanying explanatory notes (Geological Sheets Sul-E-36/R,Q,X,Z).

Precambrian (Age: >570 Ma)

The metamorphic crystalline Precambrian basement forming the Midlands and western edge of the Urema Trough are granitic and migmatitic gneisses. These metamorphic rocks belong to the Bárué Formation and are the oldest in the region. Abutting on the southwest of the study area, against the junction of the Pungue River with the Rift, is a large isolated outcrop of similarly aged metamorphics of the Manica System. This oval-shaped area of gneisses mixed with hornblendes, pyroxenes, quartzites and schists, is pierced through at the centre by a carbonatite volcano of Cretaceous age. An island of Precambrian with intruded Gorongosa granite, gabbro and trachyte occurs as a small horst, or foundered remnant, on the floor of the Rift Valley in the southwest of the park.

The Bárué Formation breaks down chiefly into sands of fine to coarse texture, but the associated mica contributes to the formation of layer-silicate clays such as montmorillonite. The crystalline Midlands are cut by abundant dyke swarms of dolerite, granophyre, quartz, pegmatite and the double pluton of gabbro pierced by micropegmatite granite which forms Gorongosa Mountain. The dyke swarms are aligned chiefly in a north–south rectilinear curve parallel to the Rift Valley fractures. Cores of granite gneiss form domed or bornhardt inselbergs of various dimensions south and west of Gorongosa Mountain. The highest of these, Mhanda, rises over 800 m from a flat interfluve to 1,423 m, midway between Gorongosa and the Great Escarpment. The dykes of basic rocks and areas of heavy mafic mineral content (e.g. biotite) weather into loamy textured latosols, providing the only fertile soils in the Midlands. The geology of the other dykes add to the predominantly sandy soils and sediments derived from the crystalline basement.

Triassic to Jurassic (Age: Karoo between 160 and 225 Ma)

Karoo

The Karoo is represented by a narrow longitudinal area in the northwest of the region comprising sandstone, basalt and rhyolite. The acid lava peters out just north of the study area, and all three components of the Stormberg Series lie at the junction of the crystalline basement with the Cretaceous sediments along the major tectonic line of the

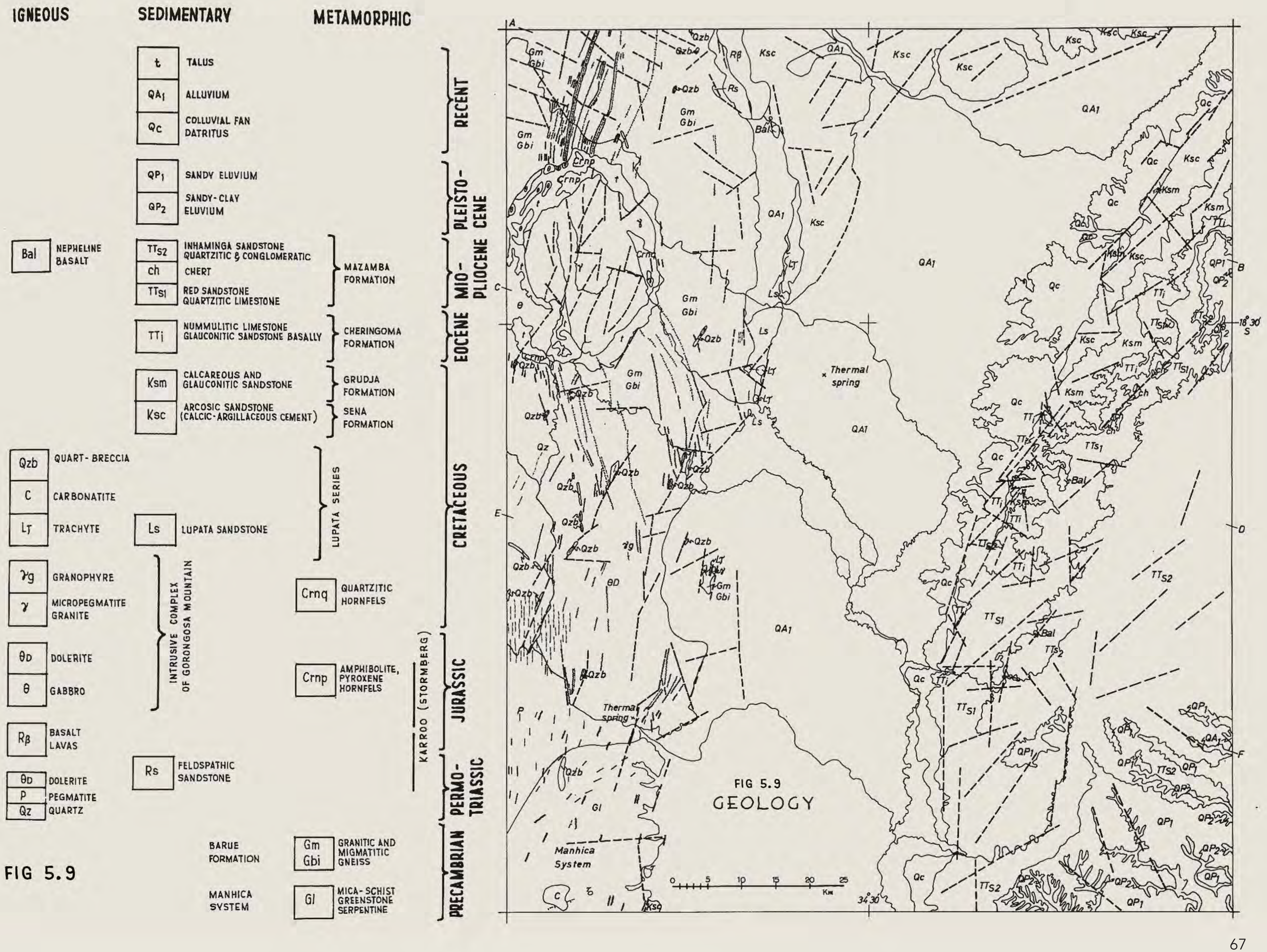

IGNEOUS
SEDIMENTARY
METAMORPHIC
t TALUS
QA1 ALLUVIUM
Qc COLLUVIAL FAN DATRITUS
RECENT
QP1 SANDY ELUVIUM
QP2 SANDY-CLAY ELUVIUM
PLEISTO-CENE
Bal NEPHELINE BASALT
TTS2 INHAMINGA SANDSTONE QUARTZITIC & CONGLOMERATIC
ch CHERT
TTS1 RED SANDSTONE QUARTZITIC LIMESTONE
MAZAMBA FORMATION
MIO-PLIOCENE
TTi NUMMULITIC LIMESTONE GLAUCONITIC SANDSTONE BASALLY
CHERINGOMA FORMATION
EOCENE
Ksm CALCAREOUS AND GLAUCONITIC SANDSTONE
GRUDJA FORMATION
Ksc ARCOSIC SANDSTONE (CALCIC-ARGILLACEOUS CEMENT)
SENA FORMATION
Qzb QUART-BRECCIA
C CARBONATITE
Lγ TRACHYTE
Ls LUPATA SANDSTONE
LUPATA SERIES
CRETACEOUS
γg GRANOPHYRE
γ MICROPEGMATITE GRANITE
θD DOLERITE
θ GABBRO
INTRUSIVE COMPLEX OF GORONGOSA MOUNTAIN
Crnq QUARTZITIC HORNFELS
Crnp AMPHIBOLITE, PYROXENE HORNFELS
KARROO (STORMBERG)
JURASSIC
Rβ BASALT LAVAS
Rs FELDSPATHIC SANDSTONE
PERMO-TRIASSIC
θD DOLERITE
P PEGMATITE
Qz QUARTZ
BARUE FORMATION
Gm Gbi GRANITIC AND MIGMATITIC GNEISS
MANHICA SYSTEM
Gl MICA-SCHIST GREENSTONE SERPENTINE
PRECAMBRIAN
A
B
C
D
E
F
18°30' S
34°30'
Thermal spring
Manhica System
0 5 10 15 20 25 Km
GEOLOGY

FIG 5.9

RIGHT: Figure 5.10

Geological sections across the Urema Rift.

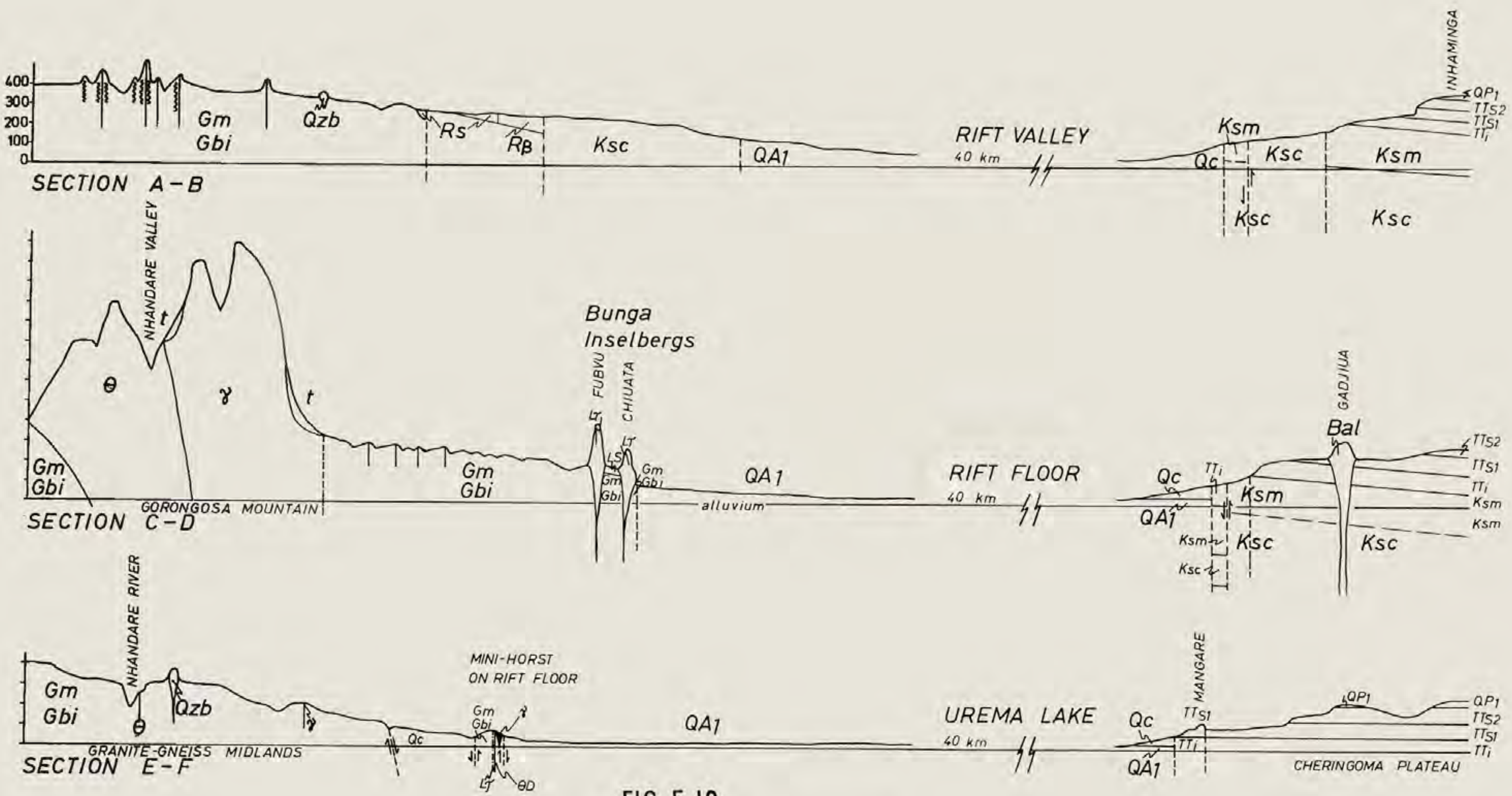


FIG 5.10

GEOLOGICAL SECTIONS ACROSS THE UREMA RIFT

Rift Valley and Lower Zambezi trough. A gap of 125 km on the western side of the Rift occurs, between their occurrence in the northwest of the region and the re-appearance of Karoo basalts in the south on the Buzi River fracture line.

The surface of the Karoo series forms low undulating terrain sloping evenly eastward from the crystalline surface to the Cretaceous sediments. The sandstone weathers into sands, and the feldspars produce sandy clay or clays; latosols and gritty clays are derived from the basalts.

Gorongosa Igneous Complex (Late Jurassic)

The sequence of basic and acid plutonic intrusion, forming Gorongosa Mountain, is judged to be of late Jurassic age to possibly early Cretaceous (Oberholzer 1968). The first intrusion was of gabbros and the contact with the crystalline gneisses produced pyroxene and amphibolite hornfels. The succeeding micropegmatite granite pluton, which forms the major body of the mountain, produced quartzitic hornfels on its contact with the Precambrian gneisses. Dyke swarms of dolerite and granophyre, associated with the main intrusions and having the same composition as them, pierced the surrounding gneisses on a north–south trend along the older lines of foliation or weakness in the crystalline rocks.

Latosols, gritty ferromagnesium-rich loamy clays are derived from the gabbros on the southwest slopes of the mountain. The central acid granite pluton produces mainly sandy and light ortho-ferrallitic soils, and humus-rich podsols with pipe drainage on the mountain summits.

Upper Jurassic to Cretaceous (Lupata series)

Upper Lupata Sandstone

These are Post-Karoo red sandstones and mudstones cemented by argillaceous calcareous and tuffaceous material. This polygenic sandstone also contains fragments of most of the surrounding intrusive rocks, and in its upper beds are intercalated tuffs and ignimbrites. Red sandy clays and clays are produced from the weathered products with a calcium-rich subsoil.

Alkaline lavas (Age: Ma)

Occurring as volcanic necks exemplified by the trio of Bunga lnselbergs or as fissure flows (Panda Ridge), these trachytes and phonolites are confined to the central western junction of the Rift Valley with the crystalline Midlands immediately east of Gorongosa Mountain.

Twenty five kilometres southwest of the ecosystem on the edge of the Rift is Mt. Xiluvo, a carbonatite volcanic neck with ring structure, containing calcite in the centre and volcanic breccias in the outer ring. The present day appearance is a breached volcanic crater covered in forest.

Cutting through all the above formations was a hydrothermal phase resulting in brecciated quartz dykes. One forms a small inselberg on the western margin of the Rift floor in the park known as Xivulo (not to be confused with Xiluvo above).

Continental Cretaceous (Lower to Mid-Cretaceous)

The oldest Cretaceous sediments are of continental origin, largely unfossiliferous and little stratified they attain a thickness of 3,000 m. These calcareous sandstones are known as the Sena Formation and are mainly of Albian to Senonian Age (Mid-Cretaceous). At the bottom, plant remains and scales of fish and arthropods with calcareous schists have been encountered (Real 1966, p. 69). The top of the formation passes without break into marine fossiliferous strata of the next formation. The Sena Formation comprises course to medium arcosic sandstone, cemented by calcic-argillaceous material, of beige, yellow-grey or sometimes reddish colours. The main area of Sena (Ksc) calcareous sandstones is in the north of the region, reappearing on the east side of the Rift on the inland side of the Cheringoma Plateau. Weathered products are sand and calcareous sandy clays.

Marine Cretaceous (Senonian to lowest Eocene)

Known as the Grudja Formation (Ksm), its initial strata on the previous formation is indicated by the presence of *Lopha ungulata* shell fossils in a matrix of yellowish-green glauconitic sandstone. Interbedded are highly fossiliferous arenaceous marls and limestone, the whole formation attaining about 200 m thickness. Other fossils include *Ostrea, Cardium, Cardita* and fragments of *Inoceramus* (Real 1966, p. 70). Higher in the formation, fossils of *Gryphea, Viniela, Babculites* and bryozoans, teeth of fish and ostracods appear. At its uppermost it passes without discordance into Eocene sediments characterised by the abundance of *Nummulites* foraminifera.

Tertiary Sediments and Volcanics

Cheringoma Formation (TTi) (Age: 54 Ma)

Eocene fossiliferous sediments of the Cheringoma Formation comprise a neritic, warm water facies of white to pinkish calcareous limestone of about 70 m thickness. This formation is characterised by the abundance of foraminiferan fossils (*Nummulites*). The sandstone weathers into overhangs and caves, and forms sheer cliffs in the deep ravines of the riftward drainage from the Cheringoma Plateau.

Mazamba Formation (TTS) (Age: between 7 and 26 Ma)

Mazamba Miocene (TTS1) to probably Pliocene (TTS2) sediments are represented by the medium to coarse reddish sandstones of about 130 m thickness appearing *discordantly* over the Cheringoma Formation. The sediments are at first littoral and fossiliferous, grading upward to yellowish-grey unfossiliferous sandstone of continental deltaic origin.

The lower member (TTS1) of the Mazamba

Formation comprises red and purplish medium-grained sandstones with argillaceous cement and coarse bedding containing small gasteropods and lamellibranchs. The upper component (TTS2) is a coarse to medium arcosic sandstone with conglomerate horizons, cemented by calcic-argillaceous material, and locally by silica. This sandstone is red with grey or yellow bands, and the weathered conglomerates form a gibber surface in some areas, for example in the southeast of the study region near Semacueza. The conglomerate is composed of coarse and large river-worn pebbles derived from formations now west of the Rift Valley including granite, gneiss, quartz and basalt. Cherts of white, grey or red colour outcrop on the plateau, related to the rise of siliceous water through fractures during faulting silicifying the lime and sandstones of the Tertiary sediments.

Tertiary volcanics

Piercing the above sedimentary strata in the central western part of the plateau is a volcanic neck of nepheline basalt. This Pliocene intrusion is today a low rounded inselberg rising to 345 m, its summit at about the same level as the highest plateau remnant near Inhaminga which attains 379 m above sea level.

Quaternary to Recent (Age: ca. 3 Ma to Recent)

Weathering and eluviation of the Mazamba Formation during the Pleistocene resulted in the formation of two pedogenic units on the Cheringoma Plateau, upper siliceous sands (QP1) forming beige pinkish-yellow, orange or deep red (oxisoil) permeable sands. The pallid sands have an impermeable mottled clay horizon at about 100-150 cm depth and support forest, whilst the deeper chroma, without such a horizon, support miombo savanna. The impermeable horizon belongs to the second unit (QP2) underlying the first at various depths or typically near the surface in the dambos and drainage lines. The lower unit is much richer in iron oxides and kaolin clay forming high water table areas covered in grasslands.

The Rift Valley surface is a mosaic of recent argillaceous and arenaceous alluvium, with fine black hydromorphic silty clays in the lower parts. Alluvial fans occur at the foot of both sides of the Rift Valley, and on the eastern side have coalesced laterally to form an apron at the break in slope. The fans on the western side appear to be older than those on the Cheringoma side, related to possible differences in age of faulting and dislocation on either side. The alluvial fans are all clearly demarcated in the field or on air photographs by their cover of tall thicket or dry forest. Dry forest is typical on the sandier deposits which are, however, underlain by a compact impervious gravelly-clay.

On the Cheringoma Coast several kinds of dunes occur along a linear coastline interrupted at intervals by extensive estuaries of mangrove swamps. Low dunes of parabolic, blowout and parallel (swash bank) form occur. The parallel dunes with alternating vlei troughs are confined to the Zambezi delta areas where aggradation has been rapid. Between the dunes and estuarine swamps of the littoral and the sediment of the Cheringoma Plateau is a vast mosaic of freshwater and brack marshes and alluvia of the southern sector of the Zambezi Delta.

On the gentle seaward slope of the Cheringoma Plateau, between the Zambezi and Chiniziua rivers, is an extensive series of oval pans surrounded by forest. These pans have a similar genesis to those in central South Africa and will be treated with other fluvial processes in the following chapter.

5.6 HYDROGRAPHY

Marine and terrestrial waters meet and alternate intermittently, with the seasons, and the tides, over a broad ecotone formed by the shallow seas with Iow coast plains in Central Mozambique. The littoral here is classified as a swamp and barrier coast dominated by the arcate delta of the Zambezi in the north, and numerous estuarine deltas separated at intervals by long, linear, sandy beaches (Tinley 1971).

During the summer rains, vast areas of the coast plains are flooded behind low barrier dunes, leaching out much of the saline deposits of the previous dry season. In the winter dry season, these flats are invaded in large part by seawater at the surface, and in the subsoil, when high spring tides of 6.4 m amplitude have maximal reach. The high tidal regime is also responsible for damming up terrestrial waters, which together with the seawater, have strong scouring effects on outgoing tides.

To emphasize the breadth of this land-sea junction still further, the Urema Lake on the floor of the Rift Valley is more than 100 km in a straight line from the sea, and its bed is only about 12 m above mean sea level. On such flat ground a multitude of small and large habitat changes can be expected over extensive areas, wrought merely by changes in degree of waterlogging, and fresh or salt water influences.

LEFT: Figure 5.11

Hydrographic basins and water types of central Mozambique.

Water types of the Gorongosa ecosystem.

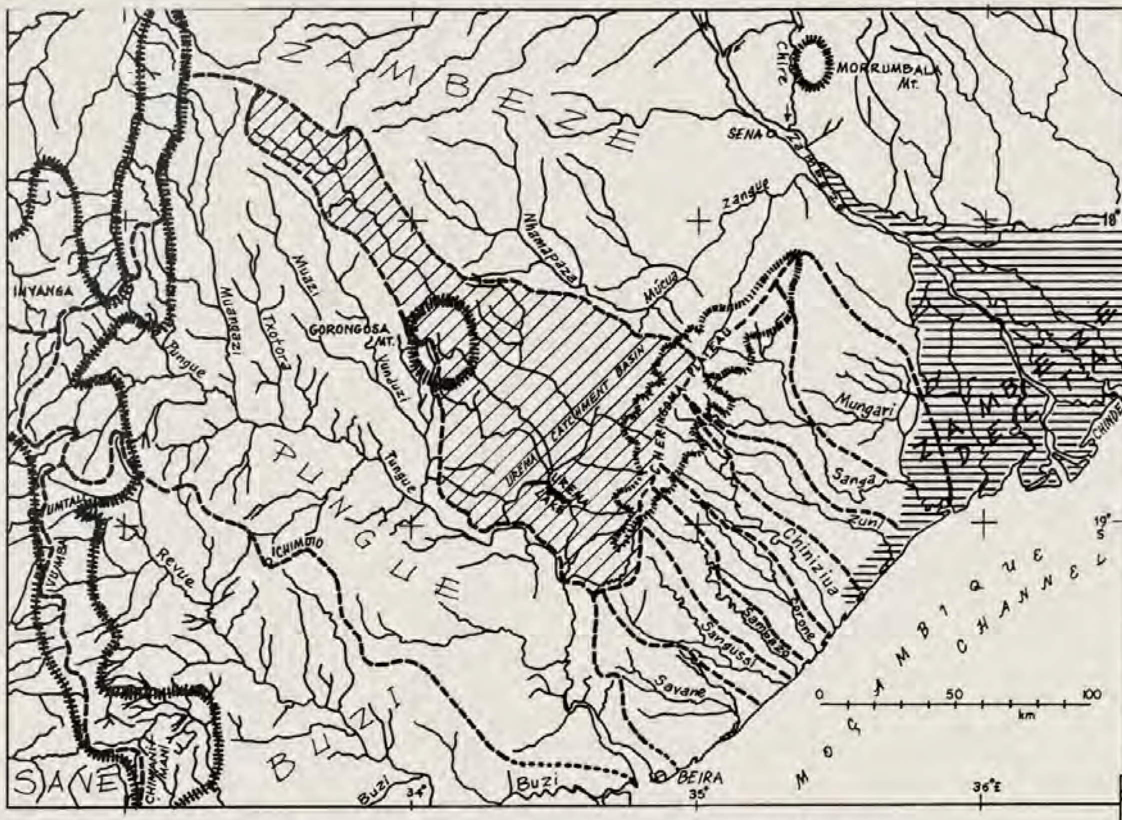
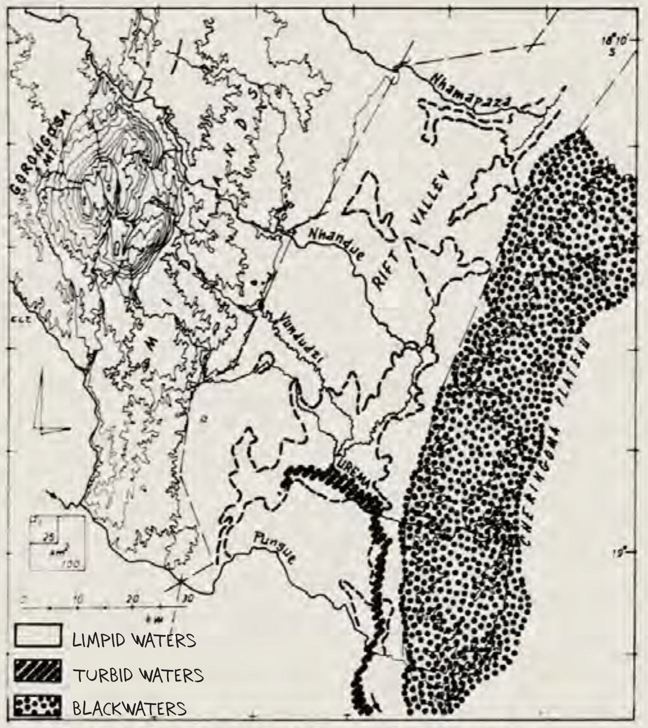
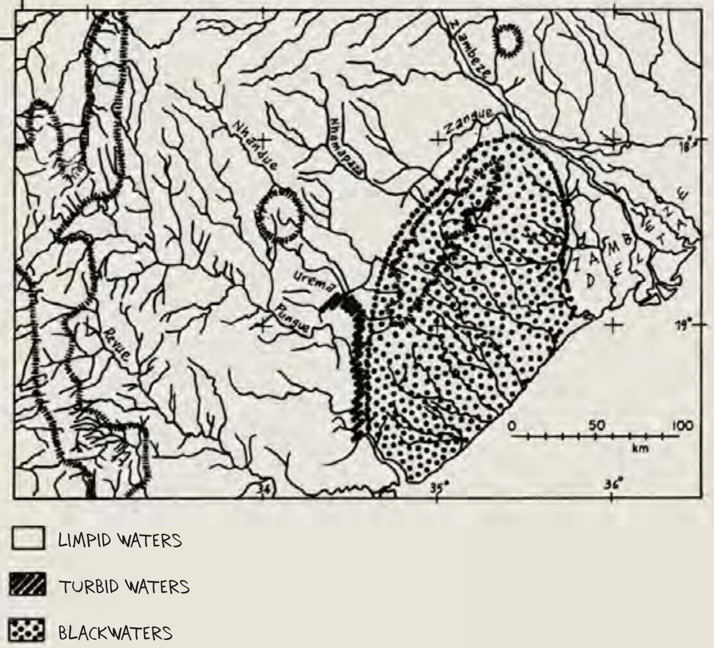


FIG 5.11 HYDROGRAPHIC BASINS & WATER TYPES OF CENTRAL MOÇAMBIQUE



WATER TYPES OF THE GORONGOSA ECOSYSTEM



Drainage

Contributing to this intimate junction of terrestrial and marine ecosystems are six drainage systems derived from: (1) the continental interior (the Zambezi, and to a lesser extent the Save); (2) the Great Escarpment (the Pungue and Buzi perennial rivers); (3) the Midlands (Manhica Platform) (seasonal 'sand rivers' as exemplified by the Nhandue and Nhamapaza which enter the Gorongosa region); (4) isolated massifs— (a) the radial perennial stream flow from Gorongosa Mountain, and (b) the perennial streams off the dipslope and scarpslope of the Cheringoma cuesta; (5) a lake system—the Urema Lake, which is the sole example from Central Mozambique; and (6) swamps, marshes and dambos of alluvial plains and drainage lines in plainsland (Fig. 5.10). Cutting across this seaward drainage at right angles is the Rift Valley which in the past (early to mid Pleistocene) linked Zambezi and Lake Niassa waters (Shire) with the Pungue, and Buzi Rivers, and possibly the Save.

This link was severed by the confluence of two alluvial fans which built out from opposing sides of the Rift formed by the Nhamapaza from the Midlands in the west, and the Mazamba from the Cheringoma Plateau. The divide occurs at the neck of the Tengane tando (Fig. 6.3), at an altitude of 59 m, and where the Rift Valley crosses the Zambezi River it is 25 m above sea level.

During the rains, however, the series of shallowly -flooded floodplain*s* at different (stepped) levels on the Rift floor, linked by small channels, would still allow barbel (*Clarias gariepinus)* and perhaps other fish to move across the divide between the two basins.

Thus high floods almost surround the Cheringoma Plateau entering the sea at the Zambezi Delta and between Beira and Sofala in the south. It will be remembered from the previous section that the Cheringoma seaward streams began as the fan distributaries of the rivers from the west on a broad land-sea junction before the Rift was down-faulted. This drainage was then truncated and a new riftward drainage initiated from both sides of the trough. Though greatly depleted by this beheading of large rivers, a seaward flow on the Cheringoma was maintained and riftward drainage fed by the high water table duplex sand aquifer along the crest and dip slope of the cuesta. This aquifer was formed by weathering and eluviation of the surface Plio-Pleistocene sediments resulting in a loose sand surface with an impermeable illuvial clay sub-soil. Runoff is consequently almost nil and the catch and release action of such a duplex sponge surface acts as an efficient aquifer, and is responsible for the high water table sands here and of most of the Mozambique coast. Many of these extremely leached acid sands that occur over an impermeable iron saturated pan horizon are tropical podsols.

Water types

Three main types of water can be distinguished in the Gorongosa region (Fig. 5.10), similar to that described by Sioli (1975, p. 200) for the Amazon Basin. These are:

Turbid waters

Loamy turbid water of yellowish-ochre colour with extremely low transparency, and a pH of 6 at the height of the dry season (9 October 1971). The Urema Lake on the Rift Floor, its outflow, the Urema River, and the Pungue River below its confluence with the Urema are the only examples in the region. Derived from fine defloculated clays and silts of the shallow lake bed. Where the Urema turbid waters meet the clear water of the Pungue they remain distinct for a considerable distance.

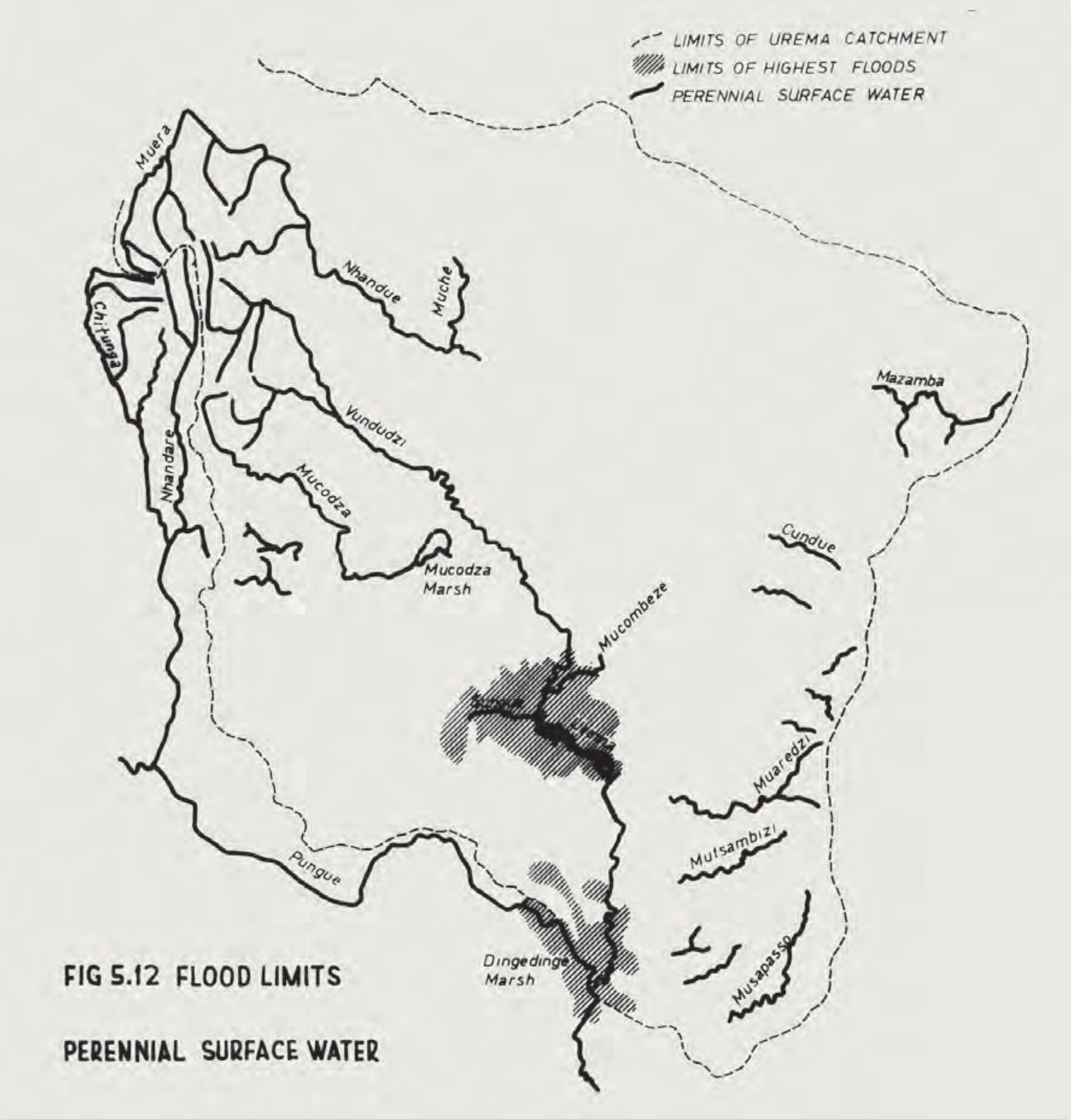
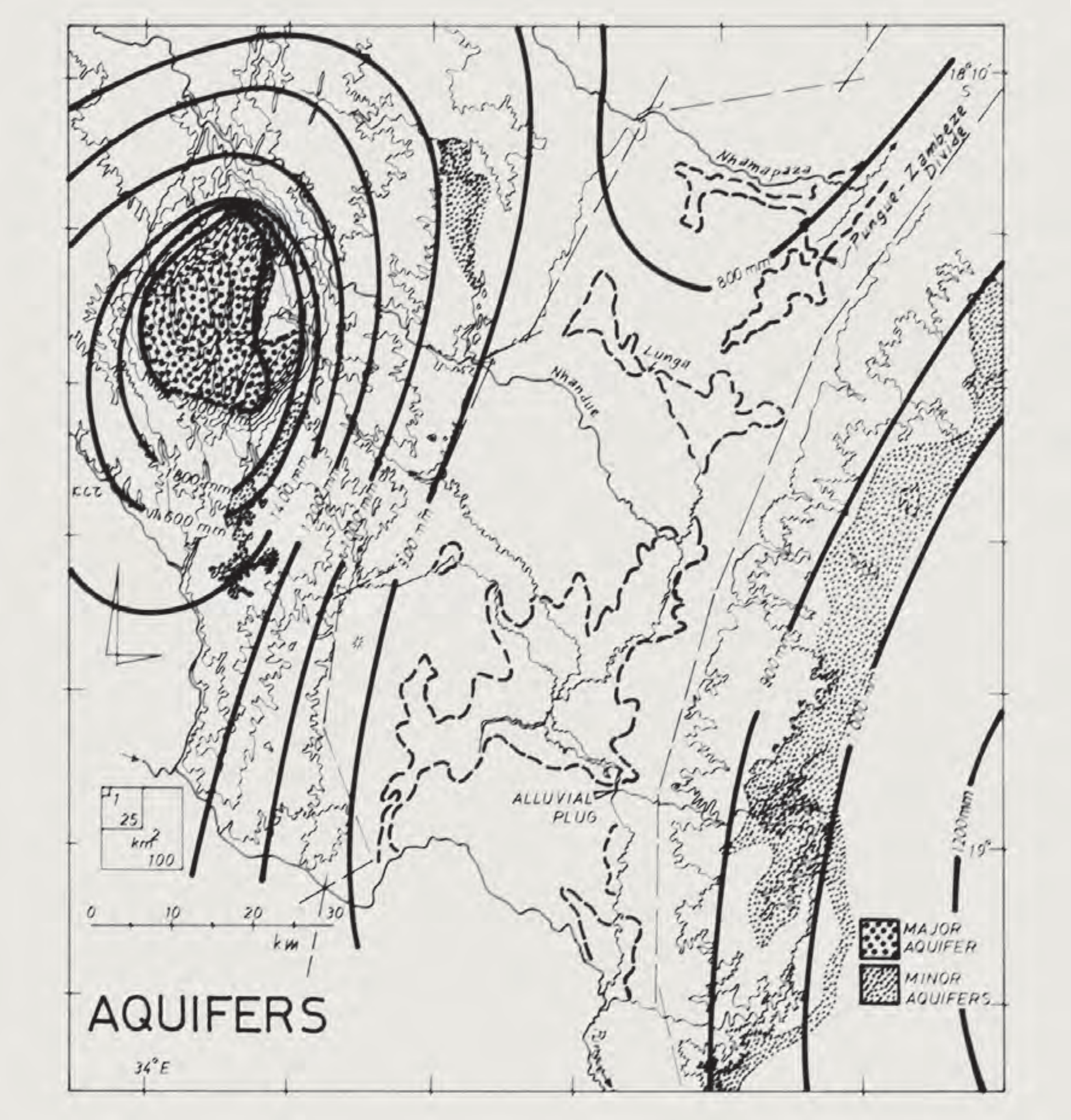


FIG 5.12 FLOOD LIMITS

PERENNIAL SURFACE WATER

Limpid waters

Limpid, pale-green colour, highly transparent in the dry season, with a pH of between 5.5 and 6. The rivers which rise on the continental interior (e.g. Zambezi), the Great Escarpment (e.g. Pungue), Midlands (e.g. Nyamapaza) and Gorongosa Mountain (e.g. Vundudzi) belong to this water type. The regional waters of this type derive mostly from mountain and deeply dissected landscapes of crystalline rocks. On Gorongosa Mountain the Vundudzi Stream has a pH of 5 and after traversing part of the Rift floor becomes a pH of 6. The Mucodza Stream from the mountain has a pH of 7 where it crosses the Rift floor.



OPPOSITE AND LEFT:
Figure 5.12

Flood limits, aquifers, perennial surface water.

Blackwaters

Water the colour of tea at different strengths, from light to dark; transparent, with a pH of 4.0 to 5.5. Waters derived from leached pallid sands over an impervious subsurface horizon (many are tropical podsols) on a subdued cuesta landscape e.g. the Cheringoma Plateau. Limpid waters and blackwaters are low in suspended matter, although the latter contains myriads of fine organic particles. The occurrence and significance of blackwaters elsewhere in the tropics is discussed in detail by Janzen (1974).

A fourth water type of minor importance in the region is represented by two perennial thermal springs—the one in a stream which flows into the Pungue River immediately west of the Park's southwest boundary below the Bue Maria ridge; the other, which maintains a permanent pan, little used by wildlife, is near the middle of the Rift floor east of the Bunga Inselbergs.

The lithologic, topographic and soil conditions in the headwaters of the limpid waters types determine their characteristics. The turbid water, however, is due to the confluence of acid streams from Gorongosa Mountain which flow through saline vertisols into the shallow montmorillonite clay bed of the Urema Lake causing chemical defloculation of the fine clay micelles. Wind waves assist in maintaining a high load of suspended matter by churning up the bottom, but it is not the primary cause of the whitewater condition. In the Amazon, turbid water results in a similar way where limpid water from the high Andes passes through the coalesced alluvial fan deposits at their base (Sioli 1975, p. 203).

The most striking change in water characteristics is displayed by some of the riftward draining streams which rise on the Cheringoma Plateau. The Musambidzi Stream originates from high water table sands where dambo waters have a pH of between 4 and 5. In its midcourse the drainage passes through limestone sediments which changes the waters to an alakalinity of pH 8, high enough for halophytes to occur and light deposits of calacareous tufa. This change occurs over a relatively short distance of several kilometres and is confined to the stream as the adjacent soils, even those on the limestones, are acid in reaction.

At the height of the dry season in the pre-rain spring torrid season (October 1971) the water temperatures of all samples in the Rift and adjacent uplands below the 200 m contour were between 27^0 C and 29^0 C, whilst on Gorongosa Mountain, above the 1,000 m contour, a forest stream measured 18^0C.

Aquifers

There are two major aquifers in the Gorongosa region, one on either side of the Rift Valley, which are responsible for through-the-year flow of water (Fig. 5.11). The most important of these quite different aquifer types is Gorongosa Mountain whose isolated high relief triggers its own orographic rain regime releasing perennial flows, one of which, the Vundudzi, traverses the heart of the park across the Rift Valley. The mountain catchment is approximately 600 km^2. The other important aquifer is the crest area of the Cheringoma Plateau where a sand mantle overlies impervious clays absorbing almost all rainfall and releasing it in streams seawards and riftwards. These streams, however, do not reach the Rift floor in the dry season, but disappear into their sandy beds and alluvial fans where the scarp slopes meet the Rift floor. They, therefore, do not contribute to the surface water resource of the Rift Valley, remaining available at the surface only on the slopes of the plateau itself. The effective catchment zone on the crest of the plateau, left by headward erosion from both sides, is a linear area of 120 x 25 km (i.e. c. 3,000 km^2).

High water table sands and blackwaters occur south of the study area on the Mozambique Coast Plain to where it ends at Mtunzini on the Natal (Kwazulu-Natal) Coast in South Africa. They reappear again in patches southwards along that coast where pallid duplex sands occur, and extensively again on the southern and southwestern Cape coasts and mountainland. Yet in-depth studies of high water table sands in southern Africa appear to be confined to that by Van Wyk (1963) in northern Natal and Zululand (Kwazulu-Natal), and by Henzen (1973) in his monumental study of the Cape Flats sandveld aquifer.

The largest perennial river in the system is the Pungue, but because of its position on the southern boundary limit of the park this river only sustains life contiguous to it in that part - wildlife on the left (north) bank and tribespeople on the right (south) bank. The drainage of the Gorongosa region forms part of the Pungue hydrographic basin which is about 29,500 km^2 in extent.

In the north of the park is a small but important perennial surface water in the lower course of the Muche River. This occurs despite the Muche having a catchment in the crystalline gneiss of the Midlands which are extremely poor aquifers. The reason for this surface water seems to be due to the extensive sandy infill of the broad lower Muche Valley (see Fig. 5.8) which acts as a sump in a similar manner to the duplex sands of the Cheringoma Plateau, trapping runoff from the sides as well as the direct rainfall.

The phreatic water table on the Rift Valley floor lies at about 8 m below the surface (at Chitengo Camp), implying that an impervious stratum occurs below that level. Replenishment of this water must be from the edges of the trough where the alluvia thin off against the old land rocks as most of the surface soils, including the sands, of the Rift floor are mostly impervious to percolation beyond 1 m depth. However, the deep cracking vertisol clays of the floodplains and slack-basins are underlain shallowly in many areas by sand and so are an important recharge of this sump. Recharge probably occurs at the time of first floods before the clays swell and seal off further downward movement of water.

Drainage regimens

The perennial surface water of the Gorongosa region is laid out in an N-shaped pattern linked together at the base by the Pungue River (Fig. 5.11). Lying at the centre of this pattern is the Urema Lake, which is the intermediate recipient of almost the whole region's drainage, which then passes on down the Urema River to the Pungue. The Pungue in the south and the seasonal Nyamapaza River in the north both flow away from the Urema catchment due to their intervening bar deposits, which now act as interfluves on the Rift floor isolating the Urema catchment. The central position of the Urema Lake in the floor of the Rift Valley thus makes it an effective local base level of primary importance to which all erosional and depositional processes are eventually related. This fundamental position of the Urema will only be replaced by the Pungue when either the convexity forming the critical height at its outlet is incised sufficiently to drain the lake, or when the lake is filled with sediment.

Urema catchment

The Rift Valley is a floodplain ecosystem reliant on both the amount and distribution of rain in the Urema catchment as well as that in the Rift Valley itself. The changes in this input are clearly displayed by the extension and contraction of the lake waters across the surrounding plains. During maximal flooding the Urema Lake expands from a dry season minimum of 10 km^2 to about 200 km^2 area. In the 10 summers between 1966 and 1976 four maximal floods have been experienced (1966/67, 1969/70, 1973/74, 1975/76) and six low to medium floods. The area of slack floodplains at the confluence of the Pungue and Urema Rivers, known as Dingedinge, expands from nil, at the heIght of the dry season, to 120 km^2 under flood waters (Fig. 5. 11). Whereas Gorongosa Mountain is the most important perennial resource, in flood periods the Nhandue River, which rises in the western crystalline Midlands, and the Pungue River also play important roles. During high flooding the Pungue waters effectively dam up the outflow from the Urema catchment thus favouring increased deposition of sediments and the preservation of the critical height at the outlet of the Urema. The Nhandue, like the Nhamapaza, is a broad ‘sand river’ whose flow rises and falls in empathy with every rainfall change. By contrast the Pungue, Gorongosa Mountain, and Cheringoma catchments provide a more sustained high water regime during the rains. At the same time the differential amounts and distribution of rain in the various parts of the catchments can result in large discrepancies in timing of floods from different directions, which has enormous consequences on changes and direction of fluvial processes. Maximal floods are typically recorded in January and February at the culmination of these differential inputs. For example, if the Cheringoma Plateau experiences a succession of heavy afternoon cumulonimbus thunderstorm rains, which develop into light stratus rain over the remainder of the region at night, the plateau streams come down in flood while other drainage stays at low flow. Under such conditions the Muaredzi Stream, which joins the Urema River at the lake’s outlet, floods into the lake and, only when the lake waters have reached sufficient height to cross the sill formed by the Muaredzi alluvial plug, do the waters reverse and flow back down the Urema River.

The flood waters from the mountain are relatively ‘clean’ but where they meet the runoff from the heavily cultivated, dissected Midlands they acquire a heavy load of red loam and sand from erosion.

The Nhandue, which has the largest catchment (c. 3,700 km^2) of all the streams entering the Urema basin, carries the largest quantities of sandy sediments during floods. Depending on the level of the Urema Lake, these flood waters are responsible for the cut and re-deposition of Rift Valley alluvia in the central sector of the Rift floor.

The Muera River which rises on the western rim of Gorongosa Mountain, directIy opposite the source of the Vundudzi and Nhandare Rivers, flows north into the Nhandue River. Together with streams from the northern slopes of the Mountain, the Nhandue River is kept wet at the surface all the way to where it meets the Rift Valley near the Muche River confluence. Above and below this sector, the Nhandue is a dry ‘sand river’ with water available to elephant and man below the sand, its depth dependent on the distribution of the rains and the severity of the dry season.

If Gorongosa Mountain waters flood before those of the surrounding areas, this causes the rise and partial flooding of the Urema Lake. Thus, when large scale floods enter from the Nhandue or push back from the Pungue, their erosional impact is buffered by the already flooded plains and deposition of sediments occurs as distributary fans back from the lake. The effectivity of fluvial processes during floods is thus dependent not only on the break in slope, but also on the prior degree of flooding or saturation. The consequences of the differential timing of flood events in the landscape development of the Rift Valley are dealt with later, where the processes at work in each topographic unit are detailed (Chapter 6).

Where the seasonal Nhandue River spreads out on the Rift floor a narrow deep channel, known as the Mucombezi, has been gouged out up to the converging delta at the head of the lake. This usually holds water throughout the dry season. Similar semi-perennial waters occur in cut-off riverbeds of the Pungue in the south of the park west of Chitengo Camp, and in the southeast between the Pungue and Urema Rivers.

As indicated in Fig. 5.11 the riftward draining Cheringoma streams are only perennial in their middle ravine courses, some reaching the Rift floor during the rains. Those of the seaward drainage are perennial closer to the coast, due to the general high watertabIe regime throughout their course, and are more seasonal at the surface in the mid and upper reaches of the larger rivers which are actively dissecting their catchments back and downwards.

At the driest period of the year the Urema Lake shrinks to an area of about 10 km^2, 20 times smaller than its maximal flood area. The total seasonally inundated area of the Rift floor sector which falls within the Gorongosa ecosystem is clearly demarcated by the distribution of the grasslands; the flood edge of present regimes is indicated by the relatively sharp tree-line junction of the savannas and other woody cover.

Dry season flow measurements

Although no figures are available on flood volumes or summer flows of the more important rivers and streams involved in the Gorongosa ecosystem, measurements were made at the height of the dry season, October, in 1971. These figures highlight how the entire ecosystem hangs on the slender thread of the Vundudzi Stream's perennial flow from Gorongosa Mountain which can easily be destroyed or altered to a seasonal flow by damage to the mountain's sponge cover of rainforest and grassland.

The Vundudzi Stream, which traverses the Rift floor and is the only perennial surface flow contributing to the Urema Lake and its overflow down the Urema River, was supplying only 0,6 m^3/sec (21 ft^3/sec) at the driest time. At the same time a volume of 0.2 m^3/sec of water left the lake's outlet, three times less than the input. The other mountain stream, the Mucodza, which contributes directly to the Rift floor provides a surface flow of 0.02 m^3/sec to its mid-course marshy delta and only half this amount is released below the marsh. Its waters, diminished by dense shifting cultivation between the mountain and the park, do not reach the Urema Lake during the height of the dry season.

At the same time, the Pungue River flow was about 16.5 m^3/sec as measured above rapids 2 km above its confluence with the Nhandare River. Near this confluence the Nhandare River, born on the southwestern sector of Gorongosa Mountain, had a volume of 1 m^3/sec. No measurement was made of the Muera Stream off the north-western part of Gorongosa Mountain which keeps the Nhandue River bed moist down to the edge of the Rift floor.

Rift and Cheringoma drainage towards the Zambezi

The section of the Rift Valley north of the Urema catchment is drained by the Macua, alias Zangue, which meets the Zambezi River opposite its confluence with the Shire River that drains Lake Malawi. Almost all the Zambezi-ward drainage entering this sector of the Rift Valley are seasonal, large 'sand rivers' rising mostly on the extensive area of friable Continental Cretaceous calcareous sandstones west of the Rift.

Of these the largest is the Nhamapaza River, whose fossil bar deposits form the northern boundary of the ecosystem on the Rift floor. It is a'sand river' for its entire length to where it joins the Zangue, but its subsurface water is much deeper and thus less easily available to elephant and man.

During exceptionally high floods, as in the summer of 1958, the Zambezi waters pushed back up the Rift Valley both ways, north up the Shire into Malawi and south, flooding Dimba Marsh in the Macua tributary. Such floods also inundated more than 18,000 km^2 of delta grasslands, and swept large numbers of buffalo and waterbuck out to sea (Tinley 1969). Thus, in the recent past, vast areas of alluvial grasslands of the northern Urema and southern Shire Troughs were all affected periodically by the additional flooding of Zambezi waters. The summer of 1958 was the last time the Zambezi was able to flood large areas of the central lowlands of Mozambique, as soon after this the Kariba Dam was completed. In addition to the effects of the dam, the flooding in the delta had been confined mostly to the main rivercourse by a series of dykes erected by the Sena Sugar Company to protect settlements and plantations. The reduced flooding has dried out the rich alluvial soils and they have become alkaline or saline. As alluvial grasslands are maintained solely by seasonal flooding, the removal of this periodic phenomenon has released the invasion of savanna and forest, which will in time eliminate the pure grass habitat.

The key to the survival of the Zambezi delta grasslands now lies almost entirely with the fresh water table runoff from the sandy dipslope of the Cheringoma cuesta abutting them. But these nutrient-deficient (Janzen 1974) peaty blackwaters carry no silt and the flooding is 'clean'. The southern sector of the delta includes the Marromeu Buffalo Reserve and the tapering end of the alluvial grasslands which enter the present study's montane to mangrove transect. The advent of a second gigantic water storage scheme on the Middle Zambezi, at Caborabassa, means that the southern delta alluvial grasslands are increasingly dependent on local flooding from the small rivers of the nearby Cheringoma Plateau. As saline waters spread far into these grasslands during high tides and encroach from the subsoil, the possibility of freshwater marshes being replaced by saline grasslands is very real. In addition, the entire Mozambique Coast is at present being eroded and sea invasion of mangrove swamps is common on the central coast. Only at the actual distributary mouths of the delta is there temporary accretion of sediments. On such a low friable coast, the balance between erosion and deposition is delicate and the effects of the large dams on reducing the supply of sand during floods for the maintenance of this delicately poised coastline is an unknown factor (Tinley 1971b).

Seasonal Pans

A feature of the Rift Valley is the myriads of small, seasonal, rain-filled pans. These are in addition to the numbers of much larger cut-off courses, slacks, and other past drainage depressions which also hold water for varying periods. Some of the pans are deep enough to hold water until July, but the reliability of these surface water islands is totally dependent on the distribution and amount of rainfall. Late rains result in longer lasting supplies, and midsummer droughts, or generally poor summer and autumn rains, result in their quicker loss to the system. From July onward they are mostly dust dry, and the remaining moist areas are the floodplain marshlands and actual riverine zones. The floodplains themselves become drier than the adjacent savannas at this season due to the salinity of their soils. Pans are less common on the riftward slopes of the Cheringoma Plateau but abundant on the flatter seaward slopes (Photo page 135) and rare in the hill miombo on the west.

There are, on the average, two pans per hectare (200/km^2) on the Rift Valley floor, giving a tremendously even spatial distribution of water in the rains and autumn. Each pan is about 20 m in diameter, or larger. As noted in the section on termitaria, many of the pans form an integral part of the geomorphic dynamics of termite hills, thus in many areas there are as many pans as termite hills, which average three to the hectare (300/km^2).

The key water cycle of the Gorongosa ecosystem.

LEFT:

Initial stage of orographic and forest generated rain-cloud development along the southeast trade-wind-facing scarp of Gorongosa Mountain.

Although these depressions can be linked temporarily during, and just after, heavy falls of rain they are in effect endoreic, islanded from one another. Together with the islands of termitaria thickets they are responsible for multiplying the diversity and abundance of resources in the savanna ecosystem. The archipelagos of seasonal pans allow the spread of wildlife and their utilization of the savannas before they are forced back to the permanent riverine zones in the dry season.

Summary of the Water Factor

In sum, despite the apparent abundance of water in the Gorongosa ecosystem, one particular water holds the key to life. This key is the perennial water from Gorongosa Mountain, the most important of which is the Vundudzi Stream—the heart of the ecosystem. Like the other mountain streams its flow is small, but it is a strong and constant one. Whether these mountain streams are reduced to a trickle that does not reach the Rift floor during a period of consecutive dry years is not known. The threat of a dam on the Pungue River in the gorge tract west of the Rift, and the canalization of water from below the dam, highlights further the importance of the mountain's supply. The mountain water is thus the

The key water cycle of the Gorongosa ecosystem. *Cont.*

RIGHT:

The catchment source area, on the summit of Gorongosa Mountain, of the perennial Vundudzi River which is the main feeder of the Urema Rift Valley lake.

TOP FAR RIGHT:

Bunga Inselberg (extreme right) where the Vundudzi River meets the Rift Valley after traversing the intervening Midlands (dry forest at left on fossil splay deposit).

LOWER FAR RIGHT:

The Urema Lake on the Rift floor, the main receptacle for drainage from both sides of the Rift Valley trough including three streams from the mountain. View to the east with converging delta on the left and Sungue arm on the right.

primary salient factor in the survival of the Gorongosa ecosystem and of more than 15,000 tribespeople living around the massif. Protection of this mountain catchment island is, therefore, of prime importance to ensure its copious, but at the same time tenuous, harvest of water.

The second key factor is a corollary of the first, and that is to damp down natural headward erosion of plainsland by protecting the critical heights of local base levels, which are fundamental for the maintenance of a flood and ebb regime. Together these two factors are the crux of the Gorongosa ecosystem.

5.7 SOILS

The 1:5 million soil map of Africa (D'Hoore 1964) and the 1:4 million soil map of Mozambique (Gouveia & Marques 1973) show that the Gorongosa–Cheringoma area contains seven main soil groups which are related to both the main physiographic features and the geology. These are: (1) Ferrallitic soils on Gorongosa Mountain; (2) Fersiallitic soils on the crystalline Midlands; (3) Brown and reddish-brown Aridosols on the Continental Cretaceous which forms part of the upland–Rift Valley junction In the north of the ecosystem; (4) Fluvio-lacustrine alluvium of the Rift Valley and southern sector of the Zambezi Delta which fronts the Cheringoma Coast; (5) Regosols (Regic Sands) of the Cheringoma Plateau, comprising psammo-fersiallitic and psammo-hydromorphic (Tropical Podsol) soils; and (6) Estuarine alluvium (marine muck soils) on the coast (Fig. 5.13). An excellent detailed soil study done by Laperre (1971) at the Luabo Sugar Estates provides a valuable guide to the complex mosaic of alluvial catena soils present in the Zambezi Delta.

Soil surveys of the Gorongosa Mountain area (Fernandes 1968a) and Gorongosa National Park (Fernandes 1968b) were mapped from air photos with field control, and the samples analysed in detail. Unfortunately, due to insufficient correlation between plant communities and soils, Fernandes grouped a number of quite different soils into single units, for example: dry forest on sand, knobthorn savanna on sandy clays and

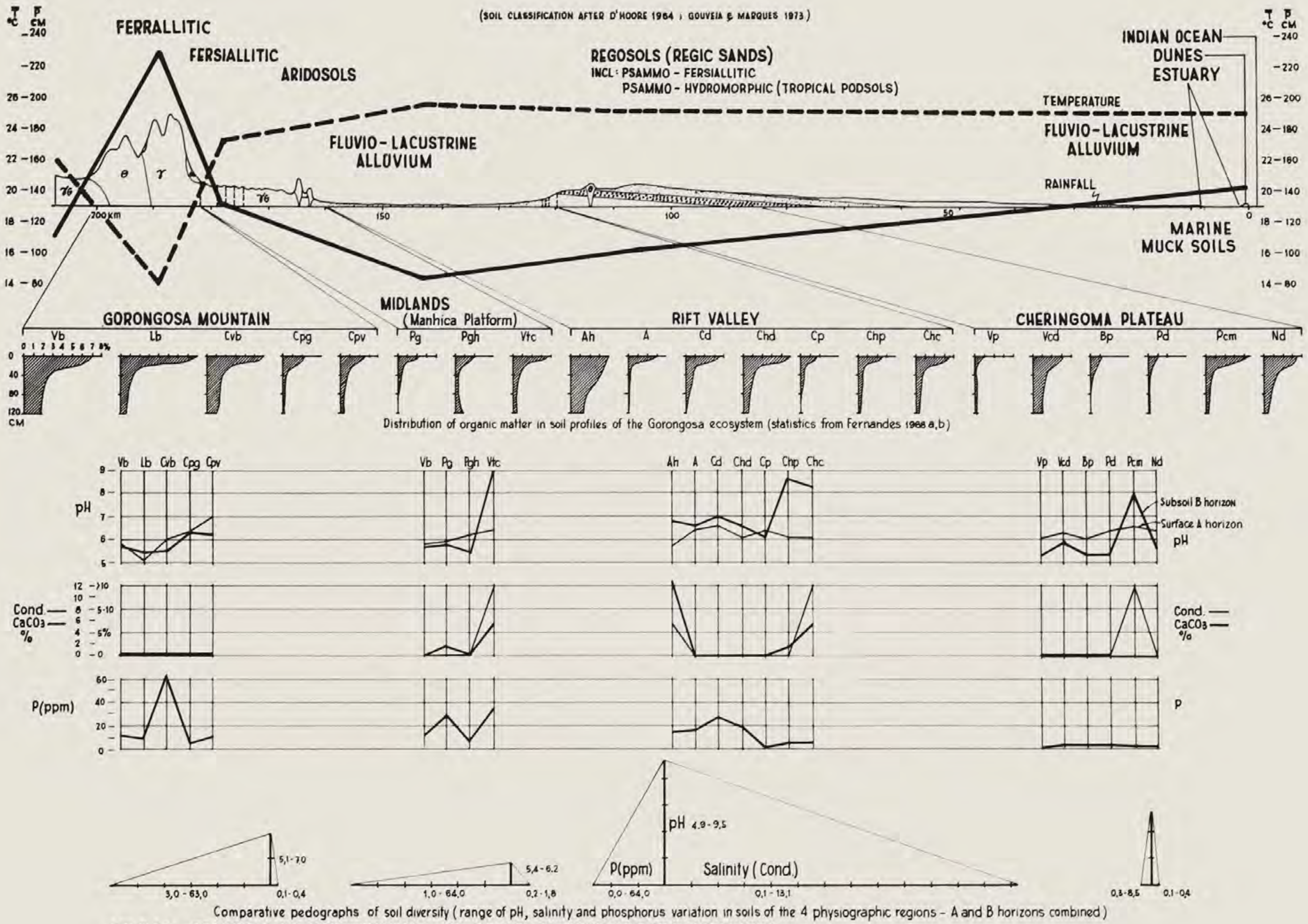


FIG 5.13 TRANSECT OF PHYSIOGRAPHIC SOIL GROUPS IN THE GORONGOSA ECOSYSTEM

LEFT: Figure 5.13

Transect of physiographic soil groups in the Gorongosa ecosystem.

fever tree woods on hydromorphic soils are all classed as one type. In addition, the boundaries to some of his pedo-units traced from air photos are unreliable as they were sometimes drawn along the outline left by veld fires, or along the tonal change on air photos depicting the contour separating wet and dry surfaces of the same bottomland soils. His two alluvial soils **A** and **Ah** are thus shown as a single unit on the maps (Fig. 5.14), the two types forming a mosaic. Finally, no soil survey exists of the seaward slope of the Cheringoma Plateau. For these reasons, I made a large number of soil pits and auger samples throughout all clearly defined communities and across their ecotones. Of these, 136 samples from 39 profiles were kept for basic analysis of pH, salinity and base status. These data will be correlated mostly with the profile bisect drawings of habitats in Chapter 8. Fernandes' 1968 data are used here to separate out the factors of ecological importance depicted on small scale maps adjacent to the main soil map (Fig. 5.14). Other relevant data are graphically represented for comparative purposes in Fig. 5.13 derived from statistics listed in the tables of Fernandes' work. Fernandes (1963a, 1963b) divided the soils of Gorongosa Mountain and the national park into seven groups of 21 pedo-units based primarily on their geological, and to a lesser extent their chemical or textural, relationships (Fig. 5.13 and 5.14; Table 5.1; Appendix l). Reference should be made to Fernandes' data for the descriptions of soil profiles and their detailed physical and chemical analyses.

Soil Development

The development of soils in the Gorongosa–Cheringoma area has been controlled primarily by physiographic and climatic influences on a diversity of geological parent material. The stepped physiographic sequence parallel to the coast has given rise to parallel sequences of climate, geology, geomorphology and ecology. Thus the soils of Gorongosa Mountain and the Midlands have developed chiefly under processes of denudation and colluviation, the Rift Valley and Cheringoma Coast by accretion and hydromorphism, the Cheringoma Plateau by eluviation and illuviation, and its riftward slopes have been subjected to vigorous erosive processes.

The ferrallitic soils on the mountain have formed primarily on fine-grained acid granite in a wet, cool environment promoting intensive weathering. Bases have been leached out in both residual and talus soils, but the highest phosphorus recorded in the ecosystem is contained in talus soils derived from gabbro and dolerite igneous rocks.

The Midlands are mostly sandy fersiallitic soils derived from metamorphic migmatitic gneisses and granite. Soils sampled in the metamorphic areas influenced by pegmatite dykes show a higher conductivity than the surrounding soils or the mountain. The compact red clay loams associated with dolerite dykes are also generally leached of their bases. One sample made by Fernandes (1968b, Profile 135, p. 39), however, showed relatively high calcium and sodium content indicating diminished leaching power of the lower and more seasonal rainfall of the Midlands. These features are well illustrated by the pedographs for Gorongosa Mountain and Midlands which are similar except for the smaller pH range and greater salinity range shown by the Midlands (Fig. 5.13). In construction of the latter pedograph, the values for the soils derived from the red clayey-calcareous Lapata sand and mudstones were excluded as they form an extremely small, though unique, occurrence in the ecosystem. These soils occur on the junction of the Midlands with the Rift Valley and have one of the highest contents of phosphorus and total bases in the ecosystem including calcium, potassium and sodium.

In the Midlands and the Cheringoma Plateau, catena sequences are formed by hill soils and their bottomland dambos (e.g. **Pg** and **Ph** in the Midlands, **Bp** and **Pd** on the Cheringoma). Thus a toposequence is superimposed on lithosequences as exhibited by Gorongosa Mountain and the Cheringoma Plateau.

The Rift Valley and alluvial front to the Cheringoma Coast have deposits of laterally changing sequences of soils related to differential sorting of coarse and fine detritus during the formation of alluvial fans or shifting of river courses on relatively flat ground (see Chapter 6). In the Rift Valley the prevalent fan depositional sequence comprises convex fingers of sandy stream beds with intervening fine clayey deposits in interdistributary slacks and interfan slacks or basins, comprising a mosaic of **A**, **Ah** and **Chc** with **Cp**, **Chp** and **Chd** formed on the sandier fingers or on splay deposits. A similar sequence is shown by the floodplain scrolls formed by abandoned levee and streambed courses in river meander belts on the plains. As catenas are repeated sequences of soils or vegetation (or ecosystems) related to topography, these alluvial versions can be called alluvia-catenas (comprising fan and scroll types) as opposed to a topo-catena. The depositional series are separated not only in space but also in time, as new sequences of sediments are deposited with each flood. Thus the alluvial depositional phases also exhibit chronosequences, which are made conspicuous by the different plant communities and stages of woody plant invasion of the floodplain grasslands.

As clearly demonstrated by Chapters 4, 5 and 6, soil development in the Rift Valley has been under the influence of strongly seasonal climatic and flood-ebb regimes with extreme variations in precipitation and extent of flooding. The Urema and other interfan basins have received sodium and calcium saturated sediments, not only from the Cretaceous and Tertiary limestones immediately adjacent to the Rift Valley, but also from the Precambrian crystalline Midlands rich in sodic plagioclases (albite, oligoclase and andesite) and, to a lesser degree, calcium from intercalated crystalline limestones (see Section 5.5 Geology). Thus the Nhandue and Pungue Rivers draining the crystalline Midlands contributed both quartz and mica-rich sediments as well as alkali felspars. The infusion of base rich constituents from all sides of the Rift Valley and their deposition in a seasonally water-logged siliceous-rich (particularly mica) environment, has favoured the formation of montmorillonite halomorphic clays over the greater part of the Rift Valley floor, probably under seasonally shallow lacustrine conditions. The sandier soils of the floor are all directly related to old fan distributary courses and splays; they are thus already leached in origin as well as by subsequent eluviation.

The final sediments deposited on the Cheringoma prior to downthrow of the Rift trough were alluvial fan materials of sands cemented by calcic-clay (the Mazamba Formation). Due probably as much to differential sorting in their depositional history as to subsequent eluvial processes, quartz sands, rich in sesquioxides (mainly iron), were formed at the surface. The calcareous material was leached downward and laterally to form a darker, impermeable, clayey illuvial subsoil with lime concretions at greater depth. Cemented ferricrete and ortstein formed at the interfaces of the phreatic high water table above the clay enriched zone, resulting in pallid highly leached **A2** and **B** horizons. These are referred to as 'Tropical Podsols', characteristic of large parts of the Mozambique Coast, classified as psammo-hydromorphic soils (Gouveia & Marques 1973) though some pedologists (Casimiro 1968) are reluctant to admit that tropical podsols are of more than local extent. Such soils produce 'blackwaters' and characteristically support highly acid bog communities, seasonally waterlogged or flooded grasslands, and heath (*Philippia*) scrub-thicket habitats. Exposure of the various limestone strata on the riftward slopes of the plateau has given rise to a lithosequence of red sandy-clays, brown calcareous marls, and colluvial melanic sandy-clays of blocky structure.

The Cheringoma Coast comprises a broad plain of coalesced alluvial fans formed by the headward eroding streams of the plateau's seaward slopes. The sands of convex surfaces and the deeper sands of distributary fingers are covered in forest and the interdistributary slack areas are acid dambo grasslands on high water table sands. These deposits are fronted abruptly by dark, heavy, clayey alluvium of fluvio-marine origin, partly from Zambezi Delta deposits and partly from estuarine (mangrove) and beach deposits. As can be expected from their complex geomorphic history, these deltaic soils are diverse occurring as mosaics and alluviocatenas (see Laperre 1971). The coastal environment is hot year-long, with high humidity and no real winter, high rainfall, and poor drainage due to impervious horizons and/or extremely flat relief. In addition, high tidal range results in a seasonal alternation of salt content of the phreatic water extending many kilometres inland. These soils support hydromorphic and halomorphic grasslands and large areas of papyrus and reed swamps. On the coast itself are low barrier and parabolic dunes covered in thicket with interdune slacks of freshwater habitats, where fine black peaty clays or silts are formed. The freshwater in these sites occurs as lenses overlying the deeper seawater in the sands.

Large areas of mangrove swamps occur at intervals along the coast. These organic-rich soils are inundated by seawater at high tides, exposed during low tides and flooded by freshwater during the summer rains. Within one kilometre of the coast, wind-born salt spray is continuously added by day, from the onshore trade winds, either being leached out by rains through lateral drainage or accumulating in the deep cracking impervious vertisols.

TABLE 5.1
The soils of Gorongosa Mountain and the National Park *(according to Fernandes 1968a, 1968b)*

	GEOLOGY & SOIL	LOCATION	VEGETATION (as listed Fernandes)
i	Acid Rocks		
	(1) **Pg** - brown granite-gneiss	Midlands	*Brachystegia* savanna
	(2) **Pgh** - hydromorphic (dambo)	Midlands	Dambo grassland
ii	Basic Rocks		
	(3) **Vb** - red basaltic	Gabbro of mountain, Midland dykes	Forest, thicket, savanna, grassland
	(4) **Lb** - basaltic lithosols	Mountain	Forest, grassland
iii	Colluvium (Talus)		
	(5) **Cvb** - red colluvium	Mountain, Midland dykes	Moist *Brachystegia* (miombo)
	(6) **Cpv** - reddish brown colluvium (mixed acid and basic)	Mountain and adjacent midlands	*Acacia nigrescens, Combretum, Pericopsis, Harungana*
	(7) **Cpg** - brown colluvium (granite-gneiss)	Midlands south of mountain.	Miombo savanna
iv	Calcareous		
	(8) **Vcd** - red indurated limestone	Cheringoma Plateau	*Senegalia nigrescens, Combretum, Diplorhynchus*
	(9) **Vtc** - red argillaceous limestone	Midland–Rift junction	*Brachystegia glaucescens* savanna woodland
	(10) **Pcm** - brown calcareous maris	Cheringoma	Thicket–savanna mosaic
	(11) **Chc** - grey hydromorphic	Rift margins and floor	*Acacia nigrescens,* mopane, *Dalbergia,* baobab savannas
v	Detrital fan material		
	(12) **Pd** - brown leached clays	Cheringoma	*Trachypogon* grassland, *Uapaca-Parinari* savanna
	(13) **Cd** - grey soils	Rift floor and margins	*Piliostigma, Acacia nigrescens, Combretum* savanna
	(14) **Chd** - grey hydromorphic	Rift floor and margins	Fever tree, *Hyphaene, Combretum imberbe* savannas
	(15) **Nd** - black soils	Cheringoma - Rift junction	Thicket–savanna mosaic (*Spirostachys* et al.)
vi	Sands (regosols)		
	(16) **Vp** - red sands	Cheringoma	Miombo savanna
	(17) **Cp** - grey sands	Rift sides and floor	Thicket–savanna mosaic
	(18) **Chp** - grey hydromorphic	Rift sides and floor	Savanna–dry forest mosaic
	(19) **Bp** - white or pallid sands	Cheringoma	Miombo–thicket mosaic
vii	Alluvium		
	(20) **Ah** - hydromorph clays	Rift floor	Floodplain grasslands
	(21) **A** - non-hydromorphlc alluvia	Rift floor	*Acacia nigrescens, Lonchocarpus, Piliostigma* savannas

SUMMARY OF SOIL FEATURES

	MOUNTAINS					MIDLANDS			RIFT VALLEY							CHERINGOMA PLATEAU					
	Vb	Lb	Cvb	Cpg	Cpv	Pg	Pgh	Vtc	Ah	A*	Cd*	Chd	Cp	Chp	Chc	Vp	Vcd	Bp	Pd	Pcm	Nd
Free draining	●		●	●	●	●		●		●	●		●			●	●			●	
Impervious		●					●		●	●	●	●		●	●			●	●		●
Hydromorphic (G)							●		●			●		●	●			●	●		
Calcareous								●	●						●					●	
Saline								●	●						●						
Sandy				●		●							●	●		●		●			
Latosols	●	●														●					

KEY
• certain soils are a mosaic of free-draining and impervious subsoils e.g. **A**, **Cd**

One of the major influences in soil formation across almost the entire region is the activity of termites, particularly the hill building *Macrotermes* termites. This biological influence involves mining of the subsoil which is transferred to the surface to build conical hills, 3.5 m in height and from 18 to 50 m in diameter, of particles of subsoil glued together with saliva. This process alone profoundly alters the physical and chemical properties, and thus the productivity, of a landscape. In poor sandy or crystalline regions they are islands of loamy fertility, and in bottomland clay areas they provide a better textured soil, retentive of moisture yet well drained. In high water table landscapes, whether sandy or of floodplain type, these small hills provide suitable sites for woody plant invasion above the seasonal flooding which maintains the intervening grasslands. The termite hills thus form nuclei for savanna or forest ecosystem components. Where base saturated subsoils are brought to the surface, the micropediments around the base of termite hills become highly alkaline or saline and thus support typical desertic or halophytic plant components. Under different local circumstances, either calcium or iron enrichment results from termite activities. Sites once occupied by termite hills, now truncated, can thus often be identified by either by patches of ferricrete (ouklip) or a concentration of calcium concretions.

The importance of termite hills in ameliorating, altering or accelerating geo-ecological succession can be appreciated when it is realised that on the Rift Valley and Delta alluvia there are an average of 3 hills per hectare (or 300/km^2). Densities of up to 6 per hectare occur on convex surfaces such as levees and are wider spaced on flat or faintly concave surfaces in these areas. The termite hills here average 3 m in height and 22 m in diameter. In the high water table, acid sands of the Cheringoma Coast the average is 1.5 per hectare (150/km^2), but these are nearly three times the diameter of those on heavy alluvia due to radial spread by erosion of their more friable consistence. The lower number per unit area may also be related to nutritional factors, particularly in 'blackwater' areas (see Janzen 1974). The low domes of nearly 50 m diameter take up more space per hectare than unmodified soils.

In the *Brachystegia* savannas (miombo) there is 0.5 to 1 termite hill per hectare on the average. No hill termitaria occur on Gorongosa Mountain, on the skeletal soils overlying limestone on the Cheringoma Plateau, in the mangroves or coast dunes, but termites are nevertheless active throughout most of these areas.

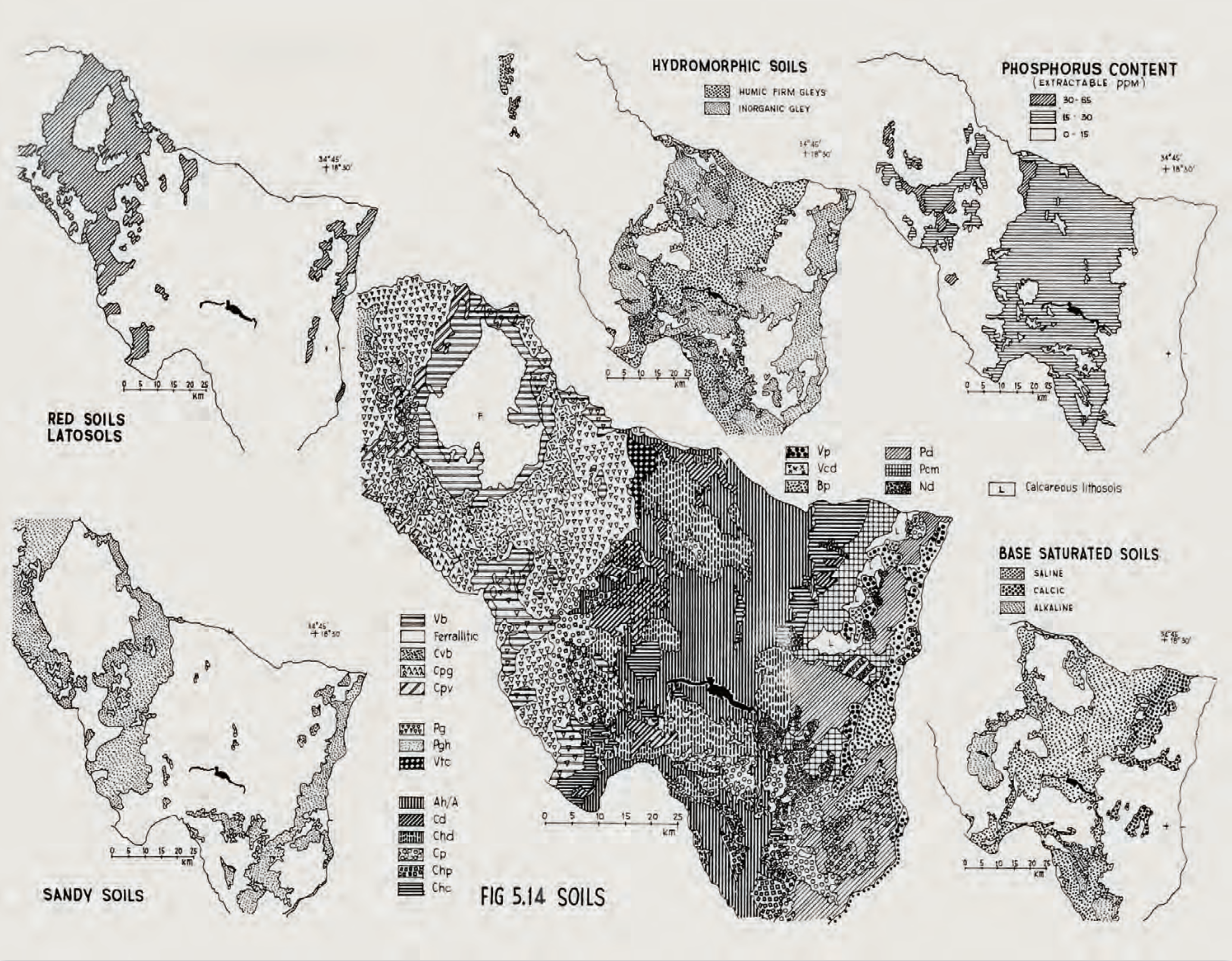
Physiographic Soil Groups

Rather than group soils at the primary level according to their physical or chemical characteristics, or geological origin, ecologically it is more important to group them as they are associated in the field, that is, related to physiographic or lesser units of the landscape. Thus Gorongosa Mountain contains five soils, the Midlands four, the Rift Valley seven and the Cheringoma Plateau and coast six (Fig. 5.12). These groups are then separated on the basis of their physical and/or chemical properties.

Although only two main soils were distinguished by the writer in the southern end of the Delta alluvia on the Cheringoma Coast (indicated by *Diheteropogon* and *Brachiaria* grasslands), Laperre (1971) recognised twenty

RIGHT: Figure 5.14

Soils (after Fernandes 1968).



two soil mapping units in the Delta close to the Zambezi River near Luabo, which indicates the kind of complexity which results from the multiplicity of influences at play in the deposition of sediments. However, the number of soil mapping units ultimately depends on whether coarse or fine levels of pedological criteria are used for their separation.

It is significant that of the twenty two soil units referred to above, almost all (except the tidal creeks) support floodplain grassland, that is, one kind of ecosystem dependant for its maintenance on adequate seasonal flooding. Thus soil moisture balance over-rides pedological criteria at the ecosystem level, but these criteria together with the degree of flooding or waterlogging, also related to microrelief, determine the species composition of the grassland.

The properties and features of the physiographic soil groups will be discussed briefly as they relate to edaphic, and thus their ecological, influences. Specific details can be found in Fig. 5.13 and 5.14,Table 5.1, Appendix 1.

Mountain soils

Of the five soils recorded Irom Gorongosa Mountain by Fernandes (1968a), three are colluvial talus soils and two are sedentary, derived from gabbro. Fernandes sampled the summit areas of the mountain with the aid of a helicopter, and designated the summit grasslands as skeletal rock outcrop soils, and basaltic lithosols. The higher parts of the entire mountain are micropegmatite granite, thus the soils will be ferrallitic. No profile description exists of soils covered in rainforest.

Summit grasslands

No profiles of summit soils were made and only the following data can be provided. The summit grassland soils are black turfy or peaty clayey sand underlain by reddish kaolinitic sandy clay and weathered rock (humic ferrallitic soils). The soils are hollow as they resound when stamped upon, due to pipe or underground drainage. Vlei areas and drainage line bogs become incised at intervals by formation of sinkholes (marked by clumps of tree ferns—*Cyathea*), which eventually link up to form narrow deep stream courses. Pipe drainage is characteristic of many mountain ferrallitic soils and the removal of the fine pallid kaolinitic material at depth, or its saturation, is also responsible for slumping on rounded slopes. Landslip scars are abundant on parts of the Gorongosa summits but are not large enough to initiate forest clumps as occurs on the Nyika Plateau in Malawi (Shroder 1976). The vlei or bog soils of the summit are acid organic hydromorphic peats of over 1 m depth in parts, underlain by brown to yellow compact sandy clay and weathered parent material.

Physical and chemical properties

The residual soils **Vb** and **Lb** have sandy clay loam, organic rich, surfaces with blocky or prismatic clayey subsoils, reddish brown in colour, with good to poor (**Lb**) permeability. These leached acid soils developed on basic rock have the highest organic matter content in the Gorongosa–Cheringoma transect.

By contrast the three colluvial talus soils have a more neutral pH, between 6 and 7, loamier surface and good permeability. The more clayey nature of the gabbro derived colluvium compared to the sandier loam texture of the other colluvia is well expressed by their organic content which is highest on the heavier compact **Cvb** and poor on the sandier **Cpg** and **Cpv**.

Fernandes (1968a) has mapped the greater part of the Gorongosa massif as **Lb** soils derived from basalt, despite his knowledge that the parent rock is micropegmatite granite. Some error in titling may be the reason for this. One soil profile seen by the writer, where hunters had dug an animal trap in the upper montane forest, showed a profile similar to the description given by D'Hoore (1964, p. 167, Profile 28) for a ferrallitic forest soil from the Ivory Coast.

On the northern slopes of Gorongosa Mountain are areas of amphibolite and pyroxene hornfels. These ferro-magnesian minerals weather at a rate sufficient to provide significant amounts of available cations and trace elements for plant nutrition (Bear 1965). No samples are available from this area nor are there many peasant cultivators established there who could verify the cultivable period or productivity of these soils. The northern xerocline slopes are covered in savanna and thicket.

The talus soils **Cvb** derived from gabbro basic rocks show the highest extractable phosphorus content in the transect (> 60 ppm).

Drainage and erodability

Excessive runoff occurs on the mountain slopes, but where deep latosol solums are moistened to great depth, landslips occur. A large area of slumped topography occurs on the bench of the southern slopes, formed by gabbro derived soils. The sandier talus soils are all highly vulnerable to donga erosion where protective rainforest has been removed for cultivation. By contrast the compact red clayey latosols are highly resistant to erosion even when bared for cultivation. The reason for this resistance to erosion is apparently due to their relatively high free iron oxide content which maintains a high aggregate stability (Van der Eyk et al. 1969, p. 95).

Environmental features

The greater part of Gorongosa Mountain is covered in rainforest, but the savanna and grassland slopes and summit grassland are subject to annual grass fires. Termite hills are absent from the main part of the mountain, thus termite influence will be mainly subterranean such as aeration of the soil and mineral input from the breakdown of organic material and from their excreta. The lower edges of the rainforest are being invaded by peasant shifting cultivators, which has resulted in considerable erosion of the slopes and riverine sites. The lower slopes and basal pediment of the mountain has a dense human settlement of shifting cultivators, those on the better textured clayey loam soils using the same cultivation sites for up to twenty years without requiring a fallow period (see Chapter 7).

Midland soils

Physical and chemical properties

The greater parts of the Midlands comprise poor sandy skeletal soils derived from Precambrian migmatitic gneiss. This general soil poverty is ameliorated by basic and pegmatitic dykes, which produce deeply weathered latosols with higher cation and trace element content. Their texture allows for good water absorbing and retaining capacities compared to the excessively permeable sandy **Pg** soils. The rapid filtration of rainwater through **Pg** soils, and apparent loss in joints and fissures, is probably responsible for the strongly seasonal nature of rivers which rise in the Midland crystalline region. The subsoils of the red latosols and the sandy fersiallitic soils, as well as their bottomland counterparts (**Pgh**), are all slightly more acid than their surfaces.

Vtc is a unique soil developed on Lupata sand and mudstones, a small occurrence of which is found between the Bunga Inselbergs and the Nhandue River in the west of the Rift. This soil is high in exchangeable cations, (particularly Ca and Mg), as well as high extractable phosphorus, and has the second highest organic content after the latosols. Both **Pg** and the dambo **Pgh** have low organic content, typical of sandy soils, but the dambo soil shows a subsequent increase at 120 cm, unique in the transect.

Most of the Midland soils are shallow (<40 cm), supporting *Brachystegia* savanna, but on interfluve crests and other sites are pockets of deep sandy soils to 120cm depth which support islands of evergreen thicket. Thicket development on termite hills in the crystalline soils is poor compared to those on alluvia or duplex sands, possibly due to poorer moisture retention as they are sandier in composition.

Drainage and erodability

Surface drainage of the Midland soils is excessive due to the steep topography. The sandy soils are droughty and are vulnerable to sheet and donga erosion where slopes are cleared for cultivation. The loam textured latosols are resistant to erosion and have better internal water relations than the more sandy or clay varieties. Most of the dambos in the Midlands are relics and are becoming extinct by active incision and headward erosion of stream sources. Erosion of dambos, as with other alluvia, takes place primarily by undercutting and slumping of the upper solum typical of duplex soils. The dambo gley soils are inundated or waterlogged for nearly half the year, and for the second half of the dry season are dry and extremely hard due to their high clay content. This seasonal swing from hydromorphic to xeric condition is similar to that of the alluvial vertisols where high salt content is an additional factor for their aridity in the dry season.

Environmental features

The skeletal hill soils all support closed canopy *Brachystegia* (miombo) savanna with a medium to tall grass layer, and are thus subject to annual, and sometimes twice yearly, fires. The dambo or drainage vlei soils support grasslands maintained by excessive hydromorphism, consequently they are burnt between midyear and the end of the dry season. The surface soils in the savannas are grey to black in the surface 10 to 20 cm due not only to finely divided litter, but largely to fine charcoal from aeons of fire.

Large areas of the Midlands south and east of Gorongosa Mountain have been modified by shifting hoe-cultivation. The longest permanent cultivation is on the latosols, and the shortest used are the sandy fersiallitic soils which require 15 to 20 years fallow to build up sufficient fertility for further cultivation. On the latosols, the primary *Brachystegia* savanna cleared for cultivation purposes is replaced during fallow by scrub-thicket. This secondary cover rehabilitates the nutritional status of the soil faster than under the primary cover allowing for much shorter periods of fallow (see Chapter 7). Apart from the moisture factor, soil productivity in sandy soils is tied almost exclusively to the nutrient level in the surface 10 cm.

Hill building termites occur throughout the Midlands and in addition mound building *Cubitermes* termites, which use faecal matter to cement soil particles, occur in the dambos. The litter in the miombo is largely consumed by termites and in this way bases and organic matter are transferred to, and concentrated in, the termitaria in otherwise extremely base deficient and nitrogen poor fersiallitic soils (Trapnell et al.1976).

Rift Valley soils

The soil groups of the Rift floor are clearly separated, yet related by the differential sorting of sediments during their deposition under fluvio-lacustrine processes. The fine sediments associated with the basins and slacks show a textural gradation from finest **Ah**, to **Chc** and **A**—the coarsest of the depression and levee soils. All the other soils **Cd**, **Chc**, **Cp**, and **Chp** are related to the coarser sandier materials of alluvial fans, splays and colluvium of the Rift sides.

Physical and chemical properties

The striking feature of the Urema Trough sector of the Rift Valley is the extensive area of open short-grass plains. This system of floodplain grasslands is based almost entirely on saline, black, hydromorphic clays of the humic firm gley type. Interspersed are patches of **A** (non-hydromorphic) and **Chc** soils forming a mosaic. The hydromorphic gley appears to be dominated by montmorillonite clay as evinced by the large areas of gilgai microrelief of alternating basins and rises, and by their deep cracking when drying, and swelling properties when wetted (Table 5.2). The underlying factor resulting in gilgai microrelief in some areas, and their absence in others on otherwise similar vertisols, appears to be the occurrence of sands below the clays. It is suspected that, where sands occur, they form a loose fluid subsoil (between 2 and 3 m depth) on which incipient sink-holes (the microbasins) can be formed by the expansion and contraction of the overlying clays.

These soils are saturated with calcium, magnesium, and sodium and contain a relatively high extractable phosphorus content. Free lime, as concretions, is found in patches within the profile, often in the friable greysandy clay beneath the gley horizon as shown by profiles exposed in donga erosion. In many areas the floodplain vertisols are underlain by sand at 3 and 4 m depth.

The **Chc**, or mopane and *Sporobolus* soils, are closely related to the hydromorphic gleys and appear to be their dry land counterpart, occurring at a slightly higher level or step in the micro-topographic sequence of slack deposits. Due to far less waterlogging and lack of actual inundation, the exchangeable cations in these soils, particularly calcium and sodium, show the highest values in the Rift.

The large termite hills built by *Macrotermes* termites on the convex surfaces of the hydromorphic gleys are ringed with basal pediments of white salt due to leaching of the salt-rich subsoil brought to the surface to form the growing apices of the hills. The evaporite deposits are usually bare of plants, or support one grass species, *Sporobolus virginicus*, and in the past were collected for domestic use by the tribes people.

Of the more leached sandy soils of fans and colluvial deposits one, **Chp**, has an impervious subsoil with high alkalinity. All the others, and the surface of **Chp**, are base deficient soils; **Chd** showing development of laterisation and redder chromas. Of this group **Cd** and **Chd**, with loamier topsoils, have relatively high extractable phosphorus content.

As clearly demonstrated by the profiles in Fig. 5.13 organic matter content is highest in the finer textured soils, particularly the hydromorphic humic gleys which crack deeply in the dry season, allowing for a high build up of organic material throughout the profile as it is washed into the cracks by the first rains. The poorest in organic material are the sandy **Cp** soils. In sum the pedograph for the Rift Valley shows the largest range of pH and salinity and a much lower phosphorus range but generalIy with higher overall content (Fig. 5.13).

The most saline soils in the transect occur in the Rift Valley, and these support ten different plant communities as a mosaic (Fig. 5.15). It is not clear whether certain soil factor combinations and/or drainage differences (Fig. 5.16) which influence soil moisture balance and the severity of sodic effects are at play, or whether plant

TABLE 5.2
Gilgai Soil Profiles

MICRO-BASIN		MICRO-RIDGE			
Site:	Urema floodplains of Rift Valley floor (near Sungue drainage)	**Landform:**	2^0 slope, alluvial plain	Substrate:	Vertisols of alluvial basin
Plant Cover:	*Echinochloa stagnina* and *Vossia cuspidata* grasses	**Plant Cover:**	*Cynodon dactylon* and *Digitaria swazilandensis* grasses		
0-5 cm	Black (10YR 2/1) clay, firm moderately developed blocky structure; no lime concretions; pH (H_20) 5,7; Resistance 660 ohms; abundant grass roots; relatively sharp lower boundary.	0-8 cm	Black (5Y 2/1) clay; very hard, strongly developed, blocky structure; wide and deep vertical cracks; no free lime; pH 6,5; Resistance 380 ohms; abundant grass roots; relatively sharp lower boundary.		
5-20 cm	Black (10YR 2/1) clay, friable granular structure; no lime concretions; pH 5,5; Resistance 620 ohms; frequent fine and medium roots; merging lower boundary.	0-15 cm	Black (5Y 2/1) clay; gley; very hard; strongly developed coarse blocky structure; slickensides; no free lime; pH 6,4; Resistance 210 ohms; frequent grass roots; merging lower boundary.		
20-50 cm	Black (1OYR 2/1) clay, gley, slickensided wedge-shaped aggregates; friable; break down to granular structure; no lime concretions; other profiles cantain some free lime deeper down; pH 5,4; Resistance 260 ohms.	15-45 cm	Black (5Y 2/1) clay; gley; extremely firm; coarse angular blocky structure; slickensides; no free lime; pH 6,1; Resistance 140 ohms; merging lower boundary.		
		45-60 cm	Olive black (5Y 3/1) clay; gley; strongly mottled red and orange soft Fe/Mn concretions; firm; moderately developed blocky to prismatic structure; slickensides; no free lime but other profiles contain lime concretions; pH 6,3; Resistance 90 ohms.		
Summary:	— Friable granular structure in easily broken aggregates with slickensides.	— Very hard to firm, strongly developed, coarse blocky structure with slickensides.			
	— Gley horizon deep.	— Gley horizon shallow.			
	— Brownish black colour.	— Olive black colour.			
	— More acid, less saline, moister soil.	— More neutral, more saline, drier soil.			
	— Seasonal Succession: In the midwinter dry season *Cynodon* and *Digitaria* invade the microbasins from the microridges where they have long turned brown, and form green patches amongst the remains of the hygrophilous *Echinochloa* and *Vossia*. The herbivores graze in the same pattern following the change in soil moisture.				

succession is responsible. The evidence displayed by Figure 5.15 shows one group of communities on topsoils that are leached and acid due to either their sandy nature or to excessive waterlogging, and a small group of halophytic communities on soils which are alkaline throughout the profile. It is significant that where the shallow sandy acid surface is truncated by sheet erosion the remaning profile is alkaline throughout. The removal of the sandy surface immediately alters the soil moisture balance to extremely xeric and sodic conditions. The succession of fine soils in the Rift Valley related to different periods of sedimentation, and microrelief control of length of flooding and waterlogging, shows that the hydromorphic base saturated vertisols evolve to aridosols, as typified by the mopane soils, solely as a function of reduction in moisture content.

Due to their much higher fines content, alluviosols and aridosols have a much higher available moisture content than most soils, but due to their salinity this moisture is lost to plants as it is bound up with the salts and the finest gleyed particles (Serrano 1973). For this reason the grasslands on the faintly inclined higher slopes of the floodplains dry out several weeks after cessation of the rains. The first grassland to go brown is the sodic *Sporobolus kentrophyllus* community. By contrast, the ferrallitic and fersiallitic clayey soils have a poor moisture retention capacity unless they are of a loamy texture (Serrano 1973). On the Serengeti Plains, where all soils have high levels of base saturation, Anderson and Talbot (1965) also suggest that physical factors such as effective depth above impermeable horizons, or absence of a gley horizon and texture, are more important than nutrient factors in determining the grassland pattern.

The relatively poor to restricted drainage in the sandy clay topsoils of the **Cd** and **Chd** soils provide temporarily waterlogged or puddled conditions for the shallower rooted grass stratum of the savannas, and floodplain grass species such as *Digitaria swazilandensis* abound as a lower layer amongst medium to tall *Panicum*, *Digitaria*, *Urochloa* and *Hyparrhenia*. *Hyparrhenia rufa* is typical of the heavier loamy clays and is used by tribal cultivators as an indicator of soil areas with high potential for cultivation on semi-permanent or recurrent basis (see Chapter 7 Man).

Gilgai, salt rings and pans.

FAR LEFT:

Gilgai microrelief on saline vertisol clays of the Urema floodplains. The microbasins are the dark oval patches of hygrophilous grasses separated by the light areas of lawn grasses on microrises and broader convexities. Isolated trees of *Hyphaene benguellensis*, and eroded (white) termite hills.

LEFT:

Mopane savanna woodland leafless in October, depicting mature community which originally invaded gilgai floodplain soil on the microconvexities resulting in a clumped physiognomic pattern. Seasonal rain-filled pans probably developed on eroded termite hill sites.

Gilgai, salt rings and pans.

TOP RIGHT:

Salt rings developed on micropediments of termite hills by downwash leaching of salts from saline subsoils brought to the surface by the termites. The evaporite deposits are either bare or sparsely covered by *Sporobolus virginicus*. Other hills have been eroded down to form pans (white centred). Large herds of buffalo concentrate on slack marsh pastures in background.

TOP FAR RIGHT:

Pans formed in the centre of salt rings by erosion of the termite hills, on convex area of the floodplains. Note initial stage of canalized game path link between main drainage line and the pans formed on termite hill sites (foreground).

BOTTOM:

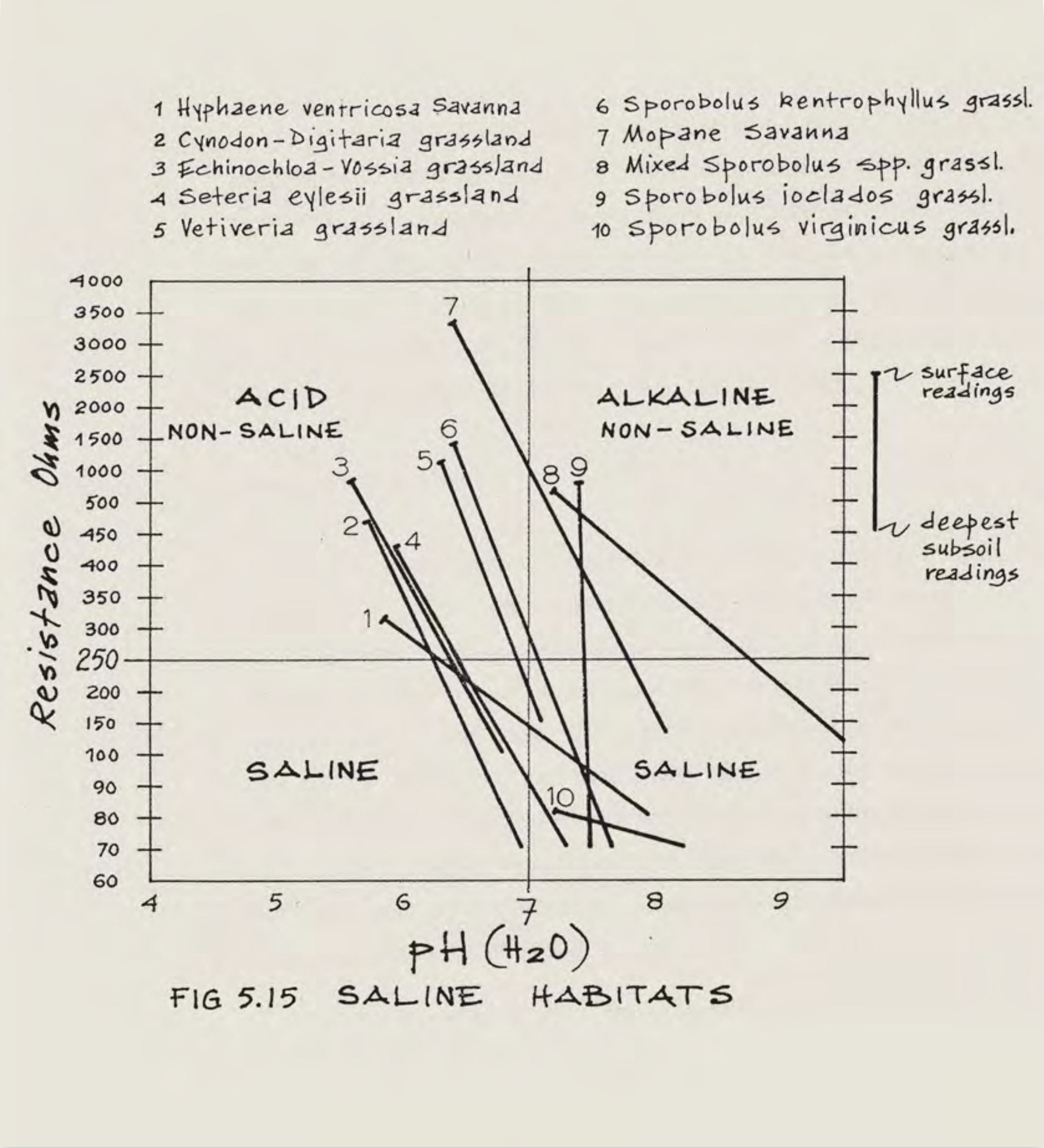
Large herd of buffalo in favoured saline soils.

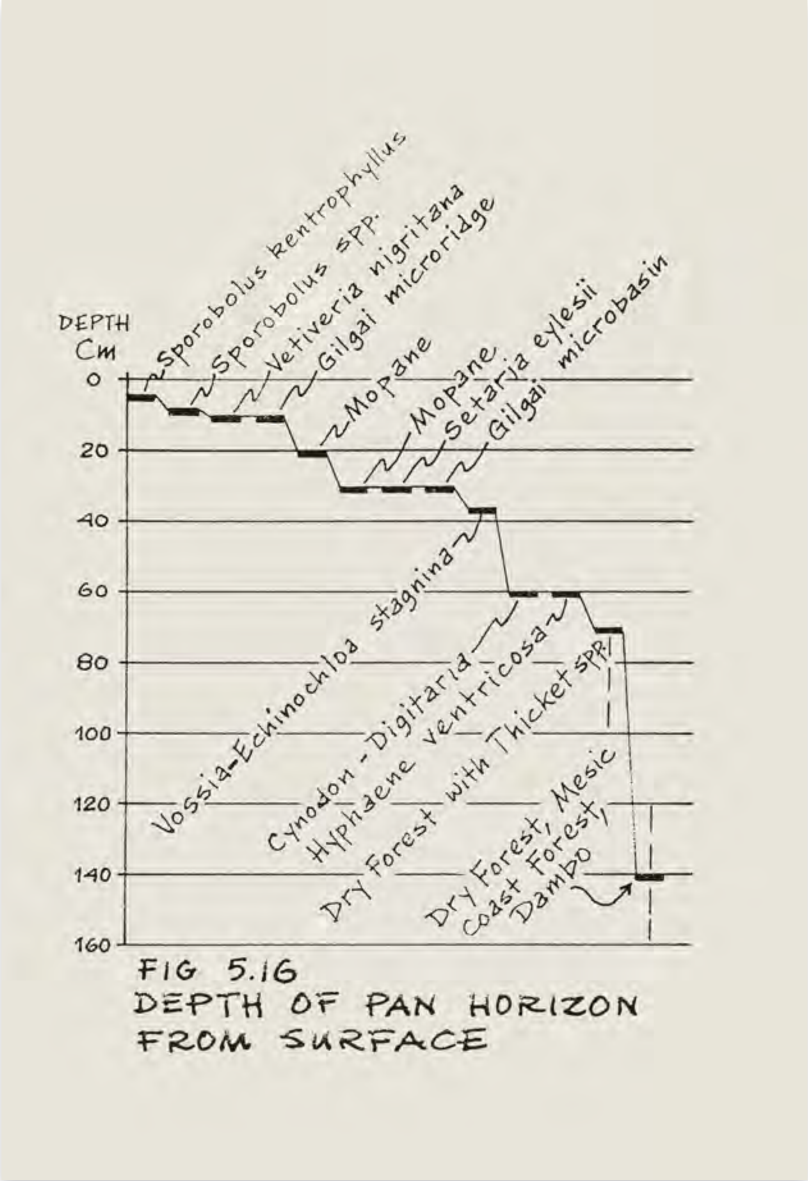
Drainage and erodability

Although all the Rift Valley soils are subject to seasonal waterlogging, anaerobic conditions are only long lasting in the gleyed soils, and temporary in the porous, sandier non-hydromorphic alluvium, fan and splay deposits. However, even the sand fan deposits which support dry forest are waterlogged in summer to within 50 cm of the surface.

At this depth free water is encountered as it is held up by the coarse gley at 120 to 150 cm below (Fig. 5.15).

The **Cd** and **Chd** soils tend to have a surface which is easily puddled, but is relatively free draining below 20 cm. Sheet erosion is evident on all these clayey surfaced soils, as can be seen by the pedestalled grass tufts. As shown in Chapter 6, the Rift Valley alluvial plain is now in an intermediate phase of erosion where most of the vlei basins are in the process of extinction through headward erosion of nickpoints and donga formation. Despite their deep cracking nature, the humic gley vertisols are strongly cohesive and erosion is primarily by donga formation from undercutting and slumping. For this reason most of the basin and slack areas on the Rift floor are perched above the incised drainage, and will remain vlei areas until lateral incision breaches the low gradient responsible for the time lag between incision and loss of vleis.





FAR LEFT: Figure 5.15

Saline habitats.

LEFT: Figure 5.16

Depth of pan horizon from surface.

TABLE 5.3

Examples of the differential penetration of unseasonal and first summer rains on the Rift Valley Floor *(recorded 24 hrs after cessation of rain)*

RAIN INFILTRATION cm depth	RAINFALL
Example 1. Unseasonal Rain of 4 mm on 27 Aug 1971 *(drizzle from stratus)*	
10	Base of bare termitarium (sandy clay)
6-7	Sandy clay loam *Piliostigma, Acacia* [sic], *Sclerocarya* Savanna—**Cd**
6	Beneath mulch of flattened grass (*Urochloa, Panicum, Digitaria)* **Chd**
5-6	Microperennial *Cynodon-Digitaria* floodplain grassland on vertisol—**Ah**
5	Beneath base of grass tufts (*Panicum, Digitaria*)—**Cd/Chd**
4-5	Saline soils with a 5 cm sand veneer (*Sporobolus* grass cover—**Chc**
4	Deciduous thicket on sand (bare of leaves)
1	Sheet eroded (sand veneer removed) sodic clays—**Chc**
0	Dense mulch of flattened grass.
Example 2. First summer rain of 11 mm on 14 Oct 1971 *(torrential rain from coalesced Cumulonimbus thunderstorms from the SE)*	
12	*Echinochloa-Vossia* vertisols (Dingedinge area)—**Ah**
10	*Borassus* clay loam —**A** soils
8	Thicket on sand
8	*Urochloa-Digitaria-Panicum* sandy clay—**Chd**
7	Saline soils with a 5 cm sand cover—**Chc**
5	Sandy clay loam *Piliostigma, Acacia* [sic], *Sclerocarya*—**Cd**
2	Sheet eroded sodic clays—**Chc**
Example 3. First summer rain of 32 mm on 24 & 25 Oct 1972 *(steady rain from SW frontal stratus)*	
30	Dry forest on sand
25	Beneath pile of elephant dung on **Cd** soils
22	Beneath base of large tufted grasses on **Chd** soils
21	Beneath mulch of flattened grass and leaf litter on **Cd** soils
20	*Acacia nigrescens* savanna—**Chd** soils
14	Summit of termite hill covered in thicket
14	Saline soils with a 5 cm sand veneer (*Sporobolus* grass cover)—**Chc**
14	Microbasins of gilgai on floodplains—**Ah** soils
10	Bare ground with algal patena—**Chd** soils
10	50° rainward slope of termite hill
6	Microconvexity of gilgai on floodplains—**Ah** soils
2	Sheet eroded sodic clays—**Chc**.

Effective flooding and/or waterlogging is thus cumulatively less effective resulting in aridification of the hydromorphic base saturated vertisols and their conversion to aridosols. Hydromorphic grasslands are consequently being replaced on every front by savanna and thicket, and forest elements are invading the donga drainage lines due to increased aeration and alteration of the water balance to a riverine free-water situation. Concentration of sheetwash and lateral subsoil drainage towards the incised drainage lines thus magnifies the seasonal alternation of flood and xeric extremes on the alluvial plains, and maintains all year mesic to wet conditions on the incised drainages. In addition to the larger donga incisions are many small nickpoints initiated on the gentle slopes of the alluvial basins.

If floodwaters from Gorongosa Mountain spreadout on the Urema Plains before heavy falls of rain have occurred locally, a considerable amount of this water flows down the deep cracks in the vertisols to the underlying phreatic water table, before the profile is sufficiently wetted to expand and become impervious.

In addition to the wash of material from erosion toward depressions, the Urema Lake waters derive a direct daily input from 3,000 resident hippo, which graze the surrounding grasslands at night. Due to their habit of establishing footpaths outward from lakes or rivers and between basins, hippo are a major influence in initiating and accelerating incision of floodplain and vlei basins, and thus their dessication and reduction in size.

Environmental feature

Except for the short floodplain grasslands of *Cynodon dactylon* and *Digitaria swazilandensis* which usually escape fire, all the Rift valley savannas are burnt annually. The most destructive fires are on the sandy clay **Cd** and **Chd** soils where tall *Hyparrhenia* grasses occur, and also a giant form of *Panicum maximum*, which attains 4 m in height reaching into the lower branches of the savanna trees. On the treeless floodplains large conflagrations occur on the vertisols supporting tall *Vetiveria nigritana* and *Setaria eylesii* grass areas. Fires begin chiefly in May (earlier in dry years) and occur through until the first rains in November or when the grass fuel is exhausted. Most forest and thicket patches escape being burnt due to the change to shorter grass cover on their edges or suppression of grass by trampling by wild ungulates.

In the past, shifting cultivation and cotton cultivation took place in the south of the park between the floodplains and the Pungue River. Over 20 years have elapsed in which no further disturbance of the surface soils has occurred, though extreme compaction or surface capping is still evident in some areas of secondary scrub.

The soils of the Rift Valley are muddy and soft in the wet season where the surface is composed of clay and/or loam, and these and the sandy clays and vertisols, in particular, set in the dry season and become extremely dry and hard requiring a pick to construct soil pits.

Cheringoma Plateau soil

Physical and chemical properties

Due to the final phases of geologic deposition, the summit of the plateau is of inherently infertile silica sands. According to the explanatory notes on the geological sheets, these subsequently underwent a genesis of eluviation and illuviation which resulted in the development of a mosaic of sandy red latosols with peaty, highly acid bogs in the dambos and depressions. Active, deep ravine erosion of the riftward faulted slopes of the cuesta exposed the limestones and marls underlying the sand mantle of the summit. Of these only the marls (**Pcm**) have resulted in soils with high base saturation and alkaline subsoils. The remainder of the Cheringoma soils are thoroughly leached, as demonstrated by their subsoils having a higher acidity than the surface. This contrasts with the Rift Valley soils where all but the sandy **Cp** soil are neutral or have more neutral or alkaline subsoils. The cuesta soils are also all markedly deficient in extractable phosphorus. The soil diversity pedograph for the Cheringoma Plateau shows the lowest ranges for phosphorous and salinity, but a much larger pH range than the mountain or the midlands due to the influence of the limestone geology (Fig. 5.12).

Organic matter is again lowest in the sands **Vp** and **Pd** and highest in the heavier textured **Vcd**, **Pcm**, and **Nd** soils, and of these the highest content throughout the profile occurs in the red **Vcd** latosols derived from crystalline limestones.

In sum, the plateau soils can be classified as sandy latosols (**Vp** and **Vcd**) with good internal drainage, podsolic pallid sands (**Bp**) overlying groundwater laterite or clay (**Pd**), the base saturated marls (**Pcm**) which are aridosols, and the heavy textured melanic **B** soils derived from colluvium. Of these only the marl is base-rich, all the others soils are hiqhly leached, though the subsoil of the melanic **Nd** contains up to 28 mEq/100g of calcium. No effervescent reaction is shown with dilute hydrochloric acid however, indicating the absence of free carbonates.

Drainage and erodability

The dambo system of the Cheringoma Plateau is formed by a duplex soil with a free draining, eluviated sand surface (**Bp**) overlying a leached, impermeable clay subsoil (**Pd**). Where the overlying sands are eroded off to expose the **Pd** clays the sponge effect of the sands (which traps all the seasonal rainfall) is destroyed, and dambos become extinct. The most highly erodable soils are the **Pd** clays which appear to be very deeply weathered, exposing white kaolinitic clay at 20 m. These soils and the underlying weathered geology erode by means of slumping on a large scale once headward donga erosion is established. The most dramatic area eroded in this manner is the southwest section of the plateau where small flat-topped remnants of the older duplex surface remain as interfluves or peninsulas.

The red sandy latosols, like their gabbro and dolerite derived counterparts from the Midlands, are relatively resistant to erosion and these form scarps where backwearing of the riftward slopes is occurring. In the central and northern section of the plateau, active erosion of the plateau summit materials is held up or damped by the exposure of limestone or sandstone strata which are resistant to headward incision. In other parts soil truncation has occurred over extensive areas leaving a veneer of skeletal soil over strongly cross-jointed, horizontally bedded, limestones. Solution cavity slumping seems a prerequisite for growth of the ravines which have cut back into the plateau. As in the southwest of the plateau, active headward erosion of the seaward slopes of the central area has also occurred with narrow deep valleys formed in the clayey sediments.

Toward the end of the rains, springlines are evident on the slopes of the rounded landform of the plateau crest where the impervious clay horizon comes to the surface. Some of these impermeable horizons, cemented as ferricrete (ouklip), are now exposed at high levels and form the present surface capping of tributary interfluves in valleys of the seaward drainage.

In sum, there is active reduction of the old surfaces, which are efficient high water table aquifers as they trap the total rainfall, and extension of waterlogged and/or xeric clay surfaces each supporting different ecosystems. Into the latter, fingers of forest are invading the banks of the incising donga drainage. In areas where active sheet erosion of the pallid **Bp** sands is taking place, the large hill termitaria are the last surfaces to be eroded, relics of the first pioneers of the dambos of the past. The termite hills have thus acted as the first sites for woody plant invasion in a high water table system and now act as the last sites of thicket and forest clumps, when the intervening terrain is being converted from closed savanna and forest to open scrub savanna or grassland.

Environmental features

The Cheringoma Plateau crest has a seasonal mean summer rainfall of between 1,000 and 1,200 mm, with a winter dry season interrupted frequently by light showers from tailing-off coastal rains. The autumn and midwinter is characterised by high humidity at night due to nocturnal orographic fog, and the heavy guttation of plants on high water table substrates. Unlike the Rift Valley and hinterland, no mild period occurs on the plateau and the coast (Fig. 4.13). As in the remainder of the system, annual veld fires occur sporadically over the dry season period from the autumn until spring.

At the heads of the riftward drainage are dambo relics which are waterlogged until the mid dry season, and newly formed scarp-edge dambos which are waterlogged by lateral ooze from the sand-clay contact exposed by scarp retreat.

Cultivation on the plateau is associated mainly with settlements found along the old road to Inhaminga some 10 km from the present road and rail route along the divide, on the riftward slopes. Both the red latosols and some stream margins in various soil types have been cultivated in patches. More recently, ravine forest has been cleared for cultivating on talus soils on the alluvial floors at the outlets to the ravines. See Fig. 6 and in Chapter 7.

Termite hills built by *Macrotermes* are abundant on the plateau crest and attain their largest dimensions (6-7 m high) on the pallid duplex sands and dambos, and their highest density of 3 per hectare. In the skeletal soil areas on limestone, termite hills are rare or absent.

Cheringoma Coast soils

The Coast soils have resulted primarily from re-dispersal and deposition of the plateau summit sands and sandy clays over the duplex **Bp-Pd** on the one hand, and from riverine and estuarine (marine alluvium on the coast front) on the other, deposited in a seasonally flooded or waterlogged environment of extremely low gradient.

Physical and chemical properties

All the fan and slack soils are extremely leached, acid, high water table sands which are cemented in parts as ferricrete or ortstein under the heath communities. The coast deltaic alluvium of the Zambezi heavy textured dark soils is a mosaic of many types related to their depositional history and microrelief. Some are leached with porous subsoils (e.g. that supporting *Diheteropogon* grassland), and others are highly saline with firm gley subsoils (e.g. *Brachiaria* grasslands).

The estuarine or mangrove soils were not sampled. Estuarine soils develop under reduced conditions and have a high sulfide content derived from seawater during tidal inundation and from the high input of raw organic material from the mangroves and their associated animal life (D'Hoore 1964, p. 72; Odum & Heald 1975). Within estuaries there are mosaics of soils with different properties, one kind supporting *Rhizophora* and another *Avicennia* (D'Hoore 1964). Analysis of *Avicennia marina* soil from the central west coast of Madagascar facing Mozambique showed an alkaline (pH 7.2) yellowish brown clayey surface horizon overlying an acid (pH 5.4) greyish blue, rusty-orange mottled, sandy clay subsoil. Extractable cations were highest in the surface (especially Na and Mg) and extremely low in the subsoil (D'Hoore 1964, p.135, Profile No.5). Evidence for the importance of the mangrove ecosystem as a highly productive substrate in littoral marine waters is advanced by Odum and Heald (1975, pp. 129-136). The estuarine mangrove swamps of the Cheringoma Coast are protected within bays formed by low barrier dunes covered in thicket, and long sand spits form the estuary mouths.

Drainage and erodability

Features of the seaward dipslope of the Cheringoma cuesta are the acid, sandy dambos, bogs and vleis (some with ortstein hardpan), swamp forests, heaths and white, powdery, kaolinitic clays rimming the eroding edges of forest patches, and myriads of termitaria. All the seaward drainage is thus characteristically of the blackwater type which develop on podzolised profiles.

Surface permeability of all the cuesta sands is high, if excessive, but high water table conditions pertain at varying depths between 80 and 200 cm below the surface. Due to this high porosity and low relief, the sands trap almost the whole annual rainfall except that intercepted by the plant cover and lost by evaporation. The major water movement through the soils is lateral, giving rise to oozes, springlines and bogs.

Extensive areas of the sandy high water table coast plains thus become shallowly flooded to about 20 cm during the summer months. The flooding clearly shows how the grasslands and wooded cover are separated by microrelief, the latter confined to the convexities of the plains, which escape flooding. The heavier textured delta soils which lie between the seashore and the inland sands of the cuesta are also flooded during the summer months by runoff from the cuesta. In the winter dry season high tides and invasion of saline phreatic water has major reach inland, with lesser influence during the rains. As an extreme example; during construction of the Caborabassa Dam, subsoil invasion by saltwater penetrated the Zambezi Delta to 70 km inland in the dry season killing fields of sugar cane.

As the coast is a plainsland of low altitude above sea level, striking erosion is evident only on the beaches and mouths of estuaries. To a lesser extent, lateral undercutting of banks by the major streams of the seaward drainage results in slumping of banks and their cover. Scattered over the plains are many scoop-outs, some of which form small lagoons or pools, which appear to have been formed by floodwaters breaching the sides of streams and removing an oblong depression of sand.

Except at the actual estuary mouths, where accretion is occurring to form temporary spits, the whole Cheringoma Coast, in keeping with the remainder of the Mozambique Coast, is in a phase of erosion (Tinley 1971 b). Beach erosion by waves has already exhumed extensive areas of semi-consolidated mangrove and reed swamp muck soils. Extensive sections of dead and dying mangroves now stand exposed to direct wave action at high tide. Wave action is undercutting the low barrier dunes causing extensive slumping and death of the dune thicket cover carried with the sand. Slumped areas then become initial sites for parabolic dune formation by wind erosion. Evidence of old scars shows that dune formation has occurred in a saltatory manner related to phases of sea erosion or to accretion.

Environmental features

Soils of relatively high organic content on the coast are the floodplains, swamp forest, peat bogs and mangroves. The savannas and dambos are poor in organic matter, particularly as they are burnt annually, and the forested sands are rich in organic matter only within 5 or 10 cm of the surface. As soils are derived chiefly from a silica dominated geology they are both inherently poor and extremely leached with electrical resistance (R) readings as high as 17,300 ohms in the podzolic (**Bp**) sands; compared to the most leached dry forest soils in the Rift Valley floor which attain 7,200 ohms. The red sands covered in *Brachystegia* savanna are much less leached, with readings of 7,100 ohms, comparable with the sandy ferrallitic miombo soils of the Midlands with readings of 9,700 ohms. By bringing to the surface the deeper kaolin clay horizons, termite hills in the highly leached podzolic sands, provide islands of heavier textured and more fertile soils with a dramatic change in resistance to 700 ohms.

The alluvial grasslands are burnt twice annually by hunters to attract game, in the normal dry season period and during dry spells in the midsummer rain season. This produces a quiltwork of grasslands at different stages of growth, attractive to the large wildlife population of the adjacent Marromeu Buffalo Reserve. Here over 23,000 wild ungulates are concentrated in an area of 1,600 km^2. Buffalo make up 16,000 of this total and some of the herds number over 2,000 animals. These herds seldom move far from their preferred pastures, and high nutrient return must be responsible in part for the virility of these floodplain delta grasslands (Tinley 1969; 1975). The ungulate population on the strip of the delta alluvium south of Marromeu is very much lighter, and in small highly dispersed groups in the coast hinterland on the Cheringoma.

Shifting cultivation occurs in patches, related mostly to the distribution of lumber activities. Forests are cleared for cultivation and utilised for up to 5 years before new clearing is required. As an indication of the high water table properties of these soils, rice crops are grown in succession related to the degree of waterlogging. The dambos are not generally used for cultivation unless they have been incised by stream action.

In sum, the coast soils are predominantly highly leached, high water table quartz sands with groundwater laterite and ortstein developed in the subsoils. They are the poorest soils in the whole transect and support some of the richest forests. Other sands are podzolic with a pallid subsoil overlying an impervious **C** horizon. The only base saturated soils in the entire area of the coastward slopes of the Cheringoma cuesta are the heavy clay alluvia of the southern end of the Zambezi Delta near the sea. Forest and grassland are on physically and chemically similar high water table sands, microrelief, and thus degree of waterlogging and flooding being the sole control of their spatial distribution—forest on convex surfaces and grassland on flat or shallowly concave surfaces. *Brachystegia* savanna on the duplex pallid sands is seral to forest and that on the deep sandy red latosols has a well developed grass stratum, and thus appears to be in a state of homeostasis as a savanna system.

Kinetic evolution of soils

In the Gorongosa–Cheringoma transect, two examples of quite different textured soils will be used as examples of soil evolution influenced by external geomorphic changes and internal pedogenic changes. This succession can be under an unchanging climate or due to changes in climate. One is the firm humic gley of bottomlands (alluvial vertisol), and the other the sandy groundwater laterite, both of which are developed under hydromorphism and weather to form similar tableland morphology on almost any scale. The changes occurring within these soils due to external and internal influences are made strikingly conspicuous by the changes in their vegetative cover, related principally to changes in their soil moisture balance.

Alluvial vertisol

The fine textured clays, probably dominated by montmorillonite, with deep cracking and swelling properties and a strongly gleyed subsoil, are typical of the slacks and basins of the Rift floor. These base-saturated clays were probably laid down in shallowly flooded depressions, followed by drying out and evaporation in the dry season. A succession of fine vertisols were deposited on the faint slopes formed by the slacks or basins so that the upper members were less influenced by flooding, and the lower lying members influenced more by hydromorphism. As changes in degree of waterlogging and length of flooding occur, related to changes in run-off, the vertisol soils, which support floodplain grasslands, are invaded from the margins by clay savanna tree species including mopane *Colophospermum mopane, Acacia borleae* and *Acacia polyacantha*.

If the same climatic regime is maintained, the major factor responsible for reducing soil moisture content is the incision by headward migration of nickpoints, which breach the local base levels responsible for the original hydromorphic conditions.

By providing better drainage conditions, which decreases the internal waterlogging of the vertisol, increased alkalization of the **B** horizon takes place modifying the acid surface soil increasingly toward neutral or alkaline conditions. In this manner, in simplistic terms, a hydromorphic soil evolves into an aridosol.

The subsoil claypan becomes increasingly compacted or cemented to a hardpan or calcrete (in arid regions). Incision and headward erosion of nickpoints exposes the pan horizon and a stepped topography results from the microscarps formed and the redeposited material from the nick points. On each surface released from excessive waterlogging a new invasive phase of savanna trees occurs, giving different even-aged stands on successive surfaces.

In this way hydromorphic grasslands are invaded and replaced by mopane, for example, as the soil becomes an aridosol. This is well exemplified elsewhere in southern Africa such as in northern Botswana on the ‘fossil’ slack soils of a mega-Okavango Delta. Further soil evolution then depends on the durability of the hardpan to erosion and thus contraction of the aridosol area and its replacement by broken down, transported and redeposited soil and/or pan rubble material, which either provides further heavy clay areas or a mosaic of sand and clay as shown in the Limpopo Valley in Mozambique.

Sandy groundwater laterite

The example used here is from the high water table sands of the Cheringoma Plateau, which were laid down in a littoral freshwater fan environment. Extreme leaching, due to maximal rain penetration on a quartz sand surface, resulted in illuviation and deposition of nutrient-poor clay to form a pan layer. At this stage only grasslands of the dambo type could have been supported over the greater part of the cuesta due to low relief and maldrainage conditions (see Fig. 6.3).

Changes in primary base level resulted in incision of fan interdistributary slacks and the dambos, increasing aeration through more efficient runoff. The iron-rich claypan which developed under waterlogging became more cemented over large areas forming ferricrete (ouklip) and ortstein. In its indurated state ferricrete is well drained due to jointing and irregular cracks, and allows invasion of woody plants. However, invasion of woody plants is not dependent on the final cemented state of ferricrete but commences in the claypan state where better drained convex surfaces or incised sites occur.

Under the same geomorphological processes described above for the vertisol, tablelands are formed where the ferricrete is exposed and the grey, more clayey, kaolinitic material below the pan horizon is extended at the expense of the surface sands and hardpan. Under such conditions clay systems (e.g. *Acacia*, mopane) replace the sand system (e.g. forest, miombo or *Terminalia*). The eroded, transported and redeposited sands either form coalescing fans of duplex sands at the break in slope, as shown along the Rift–Cheringoma junction, or the material results in aggradation and braiding of existing rivers.

The above examples of continuous or kinetic change in soils, rather than development towards a stable end point (climax), are paralleled by the vegetative cover, the ecosystems and their faunal components. These aspects as related to geomorphic and edaphic changes are dealt with in Chapter 6.

Most soils, even in residual sites are, therefore, polygenetic as they bear the imprint of more than one soil-forming episode due to changes in soil endoclimate (moisture balance) and/or to climatic change. It is important to emphasise that different soil forming conditions do not require a change in climate per se, but can evolve solely through the influences of geomorphic and edaphic change.

5.8 SOIL MOISTURE BALANCE

Introduction

The soils of the Gorongosa–Cheringoma area are summarised in graphic form by Figure 5.13. Although the plant species composition in various communities may be influenced by soil properties such as nutrient status, pH, salinity and texture, the overwhelmingly important factor determining the spatial distribution of forest, savanna and grasslands is soil moisture balance. This balance is a function of a single feature, or several in combination, such as texture and consistence, presence or absence of a pan horizon, distance of this horizon from the surface, macro and microrelief, and salinity.

Although most of the data in this section refer to the Gorongosa–Cheringoma transect, the writer obtained evidence on edaphic features from a diversity of systems across southern Africa. Soil pits, dug to a maximum of 7 m depth, and auger samples were made at different seasons, and before and after rains. Whilst no quantitative soil moisture determinations were made, the moisture status of profiles were empirically assessed by sight and feel. The most accurate method for determining the subtleties of microrelief control of drainage and soil moisture balance on plainsland is by traversing and observing surface flow during and just after rain, and at flood and ebb periods. This procedure is not only precise but is conclusive and rapid, and a prerequisite for meaningful interpretation of measured and plotted levels.

Ideally, the kind of in-depth study required of this subject is that exemplified by Branson et al. (1970; 1976). They use two measurements, osmotic stress, and physical soil moisture retention force or tension (stress). Together these are called ‘total soil-moisture stress’ and the use of this measurement is more meaningful than the standard soil moisture-content analysis. For example, clayey and sandy soils with the samemoisture content have different stress values or moisture availabilities (Branson et al. op. cit.).

General Features and Examples

In montane situations, with high orographic rainfall, grasslands occur on soils with an impervious or poor subsoil drainage (indicated by mottling in the subsoil horizons). Forest occurs on free-draining or relatively porous soils of a reddish orange chroma (indicating better aeration), and swamp forest occurs in boggy drainage lines or vleis. The soil under grassland is waterlogged when rains occur and dries out excessively during dry periods. The forest soils are moister, and at the same time better aerated, even in swamp conditions where there is either running surface water and/or the trees are clumped on mounds above the general anaerobic bog conditions. It is significant that as soon as grass soils in montane areas are incised by donga erosion and slump scars, resulting in better moisture conditions and aeration, forest initials are the primary invaders on the new surfaces (e.g. see photographs in Schroder 1976). Many of the mature forest patches in these sites are primary, and not fire relics, as interpreted by the majority of workers (e.g. Chapman and White 1970) including geomorphologists influenced by the fire-only approach (Schroder 1976).

In sandy lithosols, as exemplified by the crystalline Midlands, miombo savanna occurs on excessively drained soils of less than 50 cm depth immediately overlying quartz-rich parent material. Where deeper soils of about 100 cm or more depth occur, the miombo is invaded in the field layer by thickets of forest components. In the shallow soils, the pervious parent rock is close to the surface and excessive through-drainage occurs. In the deeper soils a larger amount of rainwater is trapped. The soils from the two sites have the same physical and chemical properties, the only difference being the depth and thus their moisture balance. In sands or sandy lithosols, savannas or pure grasslands can occur either on those with a pan horizon or on very deep sands with no impervious pan within reach of the annual rain penetration. In the latter case adequate water occurs only during the rains. In arid areas such as the Kalahari, some savanna trees die back to ground level during years of less than mean rainfall and coppice with the advent of the next rains. Where pan horizons occur throughout, forest, thicket and closed savanna are separated from grassland by microrelief. The grassland on slightly lower ground, where there is excessive waterlogging, produces a dambo or vlei grassland. Such an edaphic complex is well illustrated by the 'dambo miombo' on the Cheringoma Plateau.

Dune forest/thicket occurs on some of the youngest and most infertile geomorphic surfaces. Its luxuriance would appear to be a function of soil moisture balance, as certain talus soils (**Cvb**) on Gorongosa Mountain have a very high phosphorus and nitrogen content, and these may support forest, grassland, or savanna under different soil moisture regimes.

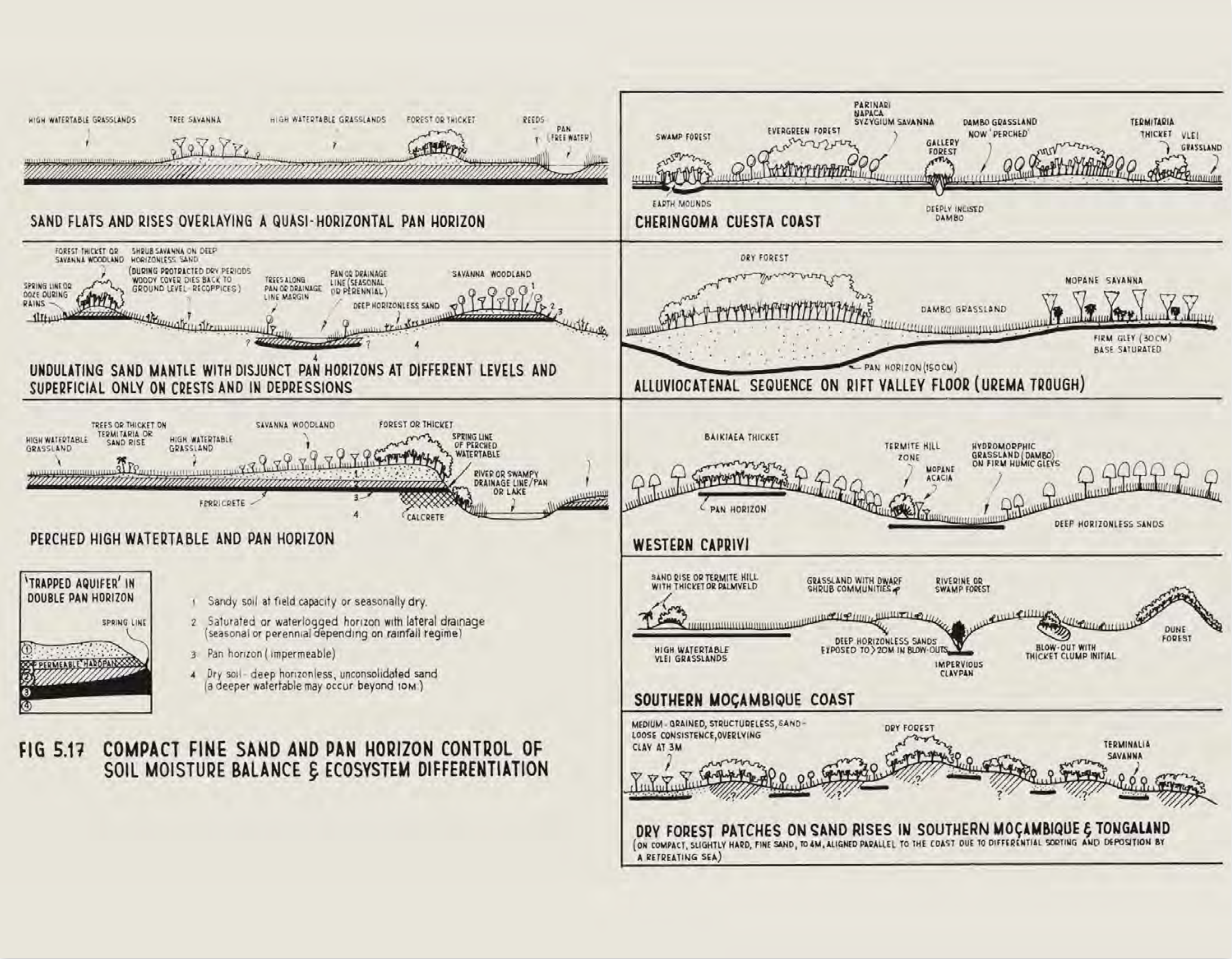
The influence of fire on plant communities is conspicuous where a delicate balance exists in the soil moisture content of virtually the same soils under different conditions of relief, and forest is thus confined to high moisture sites such as gullies. Only a change in the rainfall regime to pluvial conditions would allow forest to spread and coalesce under such conditions. On the Cheringoma Plateau, however, savanna and grasslands are, with the exception of the deep Karoo sands, all under active invasion by forest (forest extension) as dambos are incised on the one hand, and savannas on high water table sands are encroached from forest initial clumps on termite hills and those around tree bases (Figs. 8.19, 8.20).

On the Rift Valley floor, in the driest climatic regime of the transect, forest occurs in two sites only: on duplex sands of fan deposits; and in riverine (levees) sites on free-draining, loamy soils. The savannas are either on clays with seasonally extreme soil moisture conditions (e.g. mopane) or on deep sandy soils (e.g. *Burkea*).

Thickets on the Rift floor are associated with similar sites, as is forest, and these include especially termite hills, which provide a similar moisture balance to the duplex sands or riverine levees. Better water penetration, availability and aeration are shown by termite hills which rise above the vertisols and support large thicket clumps (including forest components) or are reduced to saline patches, if accumulations of salts from the saturated subsoils are brought to the surface by the termites.

In Gazaland, between the Save and Limpopo rivers in southern Mozambique, vast areas of sands and clay soils provide a mosaic of substrates which determine the occurrence of miombo, mopane, forest, thicket and grassland. In the higher rainfall coast sector, deep red sands support miombo savanna and scattered through this are islands of white, or pallid, duplex sands which support dry forest. The sandy clay soils with an impervious gley are either dambos or support mopane; red sands with subsurface calcrete support mixed baobab, acacia and broadleaf savannas as well as thickets. The distance of the calcrete from the surface, and thus the effective entrapment of rainfall, appears to determine the kind of cover. In the lower rainfall interior miombo replaces dry forest on white duplex sands and mopane is predominant on the clays.

In sum, edaphic control of ecosystems is through soil moisture balance with forest occurring on high water-retaining, but relatively well-drained sites, and grassland and savanna on both gley soils or deep horizonless sands, which exercise the same seasonal extremes of moisture availability. For this reason, forest is typically found on the youngest geomorphic surfaces such as talus, foredunes, duplex sands of alluvial fans, riverine strips, donga and slump scars, rock outcrops and termite hills; but within a topo or alluviocatena, the sites may be the oldest as they were the first to be exposed above excessive flooding or waterlogging. Savannas are typical of planation surfaces of low relief or of excessive drained hill country, such as Northern Mozambique or the Midlands west of the Urema Trough, and grasslands occur both on planation surfaces and poorly drained hill country.



LEFT: Figure 5.17

Compact fine sands and pan horizon control of soil moisture balance and ecosystem differentiation.

It is important to point out that the plant cover as individual species, and not as habitats, does not necessarily maintain or follow the same sites throughout an isohyetal gradation, but follows the moisture balance most suitable for life requirements in a particular zone. For example, in a transect from the Rift floor eastwards to the coast, the forest occurs on those sites with the best year-round moisture availability.

Availability of moisture is also impaired in soils of high salinity as the moisture becomes tied up with the salts once the rains cease (Brady 1974). The evidence of soil chemical properties in the Gorongosa–Cheringoma transect show that the most fertile soils are those of talus slopes, basic rocks, and floodplain alluvia and all these support different ecosystems. The most leached, infertile soils also support a variety of ecosystems from pure grasslands to evergreen moist forest. The determining factor is soil moisture balance, which is also the fundamental control of productivity. This is especially so in the base saturated floodplain soils where insufficient flooding or too little rain (e.g. midsummer drought) results in rapid browning of the grass from aridification and increased salinization within the soil.

Thus the nutrient differences noted, for example, between soils supporting forest and savanna, may only hold for those examples cited, and be a function of the differences of organic and element input in the two habitats under the original causal differences of soil moisture balance.

Pan Horizons, Duplex Soils and Compacted Fine Sands

Definition

Pan is used here as a collective term for all subsurface impermeable horizons in the soil whether they are compacted or indurated. Pan horizons have more than one genesis and vary in morphology (Mohr & Van Baren 1959; U.S.A. Soil Survey Staff 1960; Termier & Termier 1963). The indurated or cemented types include ferricrete (ouklip), calcrete, silcrete, et al. The compact or claypan horizons are either perched or firm gley illuviated horizons. They are formed below the surface but, like the cemented types, may be exposed at the surface by truncation. Argillic horizons can also be a developmental stage toward the true pan or cemented horizon, so that it is possible to have all stages in the same area. Some of these horizons are fossil and bear no relation to present surface configurations.

Duplex soils are those with abrupt textural and consistence or structural transition (Van der Eyk et al. 1969, p. 253) between the surface horizon and the subsoil.

Compact fine sands (e.g. supporting sand forest) are very fine grained and sufficiently coherent for steps to be cut and used in the profile pit contrasting with loose sands of coarser grade which collapse.

Distribution

Impermeable horizons occur in many of the world's soils and are particularly associated with sandy soils and alluvia. In southern Africa they are well developed In the Kalahari sands (especially in the northern region) and Mozambique sands, in the Highveld grasslands, in valley soils and in aridosols (e.g. Van der Merwe 1962; Azevedo 1945; Sys 1960; Ganssen 1963; D'Hoore 1964; Gouveia & Marques 1973).

Occurrence and disposition

Pan horizons may be horizontal, undulating or inclined and of varying thickness according to the 'genesis'. They occur in a variety of topographic and drainage situations and are absent in others. In sandy, undulating country these horizons can be near the surface on the crests of convexities, absent or very deep on the slopes and near the surface again in depressions (Fig. 5.16). This is sometimes due to truncation of a fossil horizon which is left as a remnant on the crests, eroded away from slopes and deposited in the depressions or re-incorporated in the depression with a deeper fossil horizon. The disposition of impermeable horizons does not necessarily follow the present day surface undulations, which may have been formed subsequently by cut and fill processes.

An important type of pan is the groundwater calcrete, which deposits out and grows upward towards the surface as massive hardpan sheet of coalesced concretions (Netterberg 1969; 1971). For example, an area of deep red sands underlain by lime rich waters or lithology may support only pure grasslands as the annual rainfall is not trapped by a pan horizon or change in texture. In the dry season these deep sands become completely dried out, killing back any woody plant initials. Only in consecutive years of high rainfall, or when the calcrete has grown sufficiently close to the surface to allow tap roots of woody plants to become established, does woody invasion occur. In sandy areas which have been bared by overstocking or other influences, rain penetration is much deeper than where there is a grass cover as no evapo-transpiration pumps the sand dry again; woody invasion is thus encouraged in these sites by better water relations allowing the establishment of tap roots to reach the deeper permanent moisture sources.

Pan horizon control of hydrology and their function as aquifers.

The pan layer acts as a moisture barrier until a relatively high moisture level is built up. This gives a much higher field capacity than that encountered in freely-drained soils (Brady 1974 and personal data). Sandy soils have a high infiltration capacity, high total conductivity and high permeability, with extremely low moisture holding capacity (Brady 1974). Yet endoreic freshwater lakes, occurring along the Mozambique coast and the upper Zambezi and Lulua–Sankuru branches of the Congo River, rise on Kalahari Sand plains due solely to the presence of pan horizons.

When the pan horizon becomes waterlogged (saturated), drainage is lateral in this horizon and in the porous soil immediately overlying the impermeable layer. If the pan is overlain by loamy or sandy clay material, water is more easily lost by evaporation from the soil surface than if it is covered by loose sand. Loose sand is full of airspaces and this inhibits water loss by evaporation, hence a pan horizon covered by loose sand is highly efficient as an aquifer. In addition, surface runoff is minimal and almost the whole annual rainfall is trapped by such duplex sands. The distance of the pan horizon from the surface, as determined by depth and microrelief of the covering soil, plays a fundamental role in moisture balance. The distance affects the amount of saturation possible and, with texture, the degree or rapidity of water loss by runoff and evaporation together determine the extent of moisture retention. Where perched gleys occur in sandy or friable soils as in the South African Highveld, only grasslands are supported as the soils are too wet during the rains (growing season) for woody seedlings and are extremely dry and hard subsequently in the winter dry season, when fire and frost are additional deleterious factors to soil aridity.

Firm humic gley soils are only hydromorphic due to poor drainage and once they are drained become aridosols. Their fine content and high salinity reduces moisture availability drastically and their surface becomes puddled or capped so that a great part of the annual rainfall is lost by sheetwash, thus increasing soil aridity further. Hence the efficiency of pan horizons as aquifers depends on their being covered by a sand mantle.

Because of the high water holding capacity of many pan horizons, lateral flow can be maintained even during droughts, as there is sufficient soil moisture for rapid saturation to occur in times of less than mean annual rainfall. The preceding degree of saturation is a fundamental factor governing rain and flood effectivity in plainsland hydrology. As the hydrology of plainsland lacks the dynamic of slope gravity as a force in the transmission of water, the lateral movement of water in the impermeable layers is sensitive to the presence of extraneous factors, which alter the water tension away from the direction of flow. Boreholes, drainage canals, or headward erosion of nickpoints, and tree roots are examples of factors which alter lateral water tension. Deep sands with uniform texture are areic, the total season's rainfall penetrates to a certain depth and then is dried out by evapotranspiration of the grass cover with the advent of the dry season.

In some areas several water tables are separated by dry soil or dry cemented layers, the upper water-bearing zone is then called a 'perched' water table or aquifer (Lobeck 1939, pp. 116-117). Because plains catchments are shallow, variable in distance from the surface and sensitive to extraneous factors, they need to be of large area to be efficient as aquifers. The best example of the efficiency of duplex sands as aquifers in the study area is afforded by the perennial streams which rise on the Cheringoma Plateau. Where the sand mantle is removed by erosion exposing the subsurface claypan, streams dry up and dambo drainage lines are invaded by savanna.

Pan horizon control of the spatial separation of ecosystems or communities, and of succession and phenology.

The presence or absence of a pan horizon, its distance from the surface, and soil permeability to rain (which is a function of texture and relief), are the most important combination of factors governing soil moisture content and thus the spatial distribution of woody cover and grasslands (Fig. 5.16). The surface texture of soils thus determines the level of moisture recharge and the amount of water remaining in the soil after rain and subsequent evaporation and, as Walter (1971) points out, this is far more important than the amount of rain.

It has been pointed out above that excess of soil moisture on a perennial or seasonal basis is a major factor determining the presence of open grasslands. The only other worker who has stressed this fact, from his study of the significance of the spatial separation of wooded cover and grasslands in Central and Southern Africa, is Michelmore (1939). It is surprising how rarely this work is referred to and how it has been overlooked, with the result that the conventionally held dogmas on grassland genesis persist: for example that the Highveld grasslands are due to frost and fire, or only to the former. A glance at road cuttings throughout the Highveld shows the real factor responsible for the predominance of grasslands—impeded drainage due to perched gleys and ouklip. They are in fact classified as gley-like podzolic soils (Van der Merwe 1962).

The important feature not mentioned by Michelmore (1939) is that it is not only excessive water-logging during the growing period in the rains, but also the excessive drying out of the soils in the dry season, that kills back any woody plant root development. In the Highveld woody plant invasion occurs where the best water balance and aeration pertains, such as on rock outcrops and in gullies. Protection from fire is the reason generally put forward for the presence of woody plants in these sites. The Highveld pan horizons are prone to excessive drying out as they are within 40 cm the surface. Where these grasslands are sheet eroded, or incised by headward erosion of nickpoints, they are invaded by arid savanna from the west, by moist savanna and forest elements from the north and east, and by sub-desert in the southwest. These invasions are due to changes in soil moisture balance.

Pan horizons at greater depth (down to 200 cm) covered in sandy surface soils are able to absorb the total annual rainfall and these are the sites, depending on micro-relief and rainfall regime, where either the densest type of woody vegetation occurs and/or where dambos occur. Such relationships occur in south central Africa through a rainfall regime of about 200 mm to 1,500 mm. The importance of a sandy surface which minimises runoff and ensures maximum entrapment of rainfall is also the fundamental factor determining the spatial separation of grassland and dwarf shrubland in desert regions.

In Bushmanland, which is Karroid subdesert, grassland occurs on rounded and plains (tableland) relief where soils are covered with a sand veneer. Where this sand is truncated by sheet erosion, dwarf shrubs invade the base saturated subsoil, now at the surface, to the exclusion of the grasses. In a similar manner Karroid dwarf shrubs are invading Highveld grasslands where the duplex base-rich subsoil is exposed at the surface by erosion of the friable mantle which permitted seasonal waterlogging and, thus, the predominance of grasses. Therefore the explosive invasion by desertic systems (Karoo) are not necessarily due to a change in climate at all, but rather to soil moisture and pedological changes influenced by normal geomorphological processes, which are in turn accelerated or initiated by misuse of land.

A similar relationship exists across south central Africa north of the Tropic of Capricorn where sands overlie base saturated clayey subsoils. Where erosion is removing the sand, moist savanna systems (e.g. miombo, *Burkea, Terminalia*) are being replaced by arid savanna systems such as mopane and *Acacia*. This invasion is not confined to the tension zone where active replacement is occurring, but also around the islands of clay formed by termite hills where nuclei of arid systems are spreading and coalescing as the sands are truncated or thinned by erosion.

Where pan layers or fine compact sands occur in sand country their presence is made conspicuous by denser and/or taller woody cover than the surrounding deep horizonless sands. Striking examples include *Acacia erioloba* (ex *giraffae*) woodland patches in the Central Kalahari on the crests of convexities surrounded by scrub savanna on deep sand; *Terminalia prunioides* thicket in the eastern part of the Etosha Basin; and *Baikiaea* thicket in the Caprivi surrounded by savanna woodlands of *Dialium, Pterocarpus, Burkea, Ricinodendron* and *Erythrophleum* on deep horizonless sands. Dry forest on the Mozambique Plain occurs on duplex pallid sands or on bands of fine compact sands surrounded by miombo savanna on adjacent deep, medium-grained red sands. On the Mozambique coast, deep horizonless sands (20 m - 30 m) behind the fore-dunes are covered in pure grasslands, which merge with vlei grasslands on high water table sands. Here, as with the Central Kalahari scrub, adequate moisture is only available at the time of the rains, and with the onset of the dry season the sands dry out as the grass cover uses up all the available moisture, and woody plants die back to ground level and coppice again the following year. To add to this determinant of scrub physiognomy are factors such as fire and frost (in the Kalahari and Namibia). Thus both deep (≥30 m) horizonless sands and sands with a pan horizon in the same area are responsible for a pure grassland cover due to extreme moisture regimes. Mobile dune areas which are bare allow for the same maximal penetration of rain as sands bared by other causes such as overstocking, and here dense woody plant invasion of thicket or forest occurs. As verified by personally collected field evidence across southern Africa, 'Fire acts mainly in widening the boundaries of open grasslands formed by other causes . . .' (Michelmore1939). Where there is surface flow of water in dambos, or the presence of mounds above stagnant conditions, swamp forest occurs, and this ends abruptly where it meets the stagnant bog conditions responsible for the vlei grassland (see also Michelmore 1939).

The prevailing opinion regarding the forest patches in upland and montane is that they are relics, which they evidently are in many cases as evinced by the presence of isolated straight-boled canopy trees surrounded by grassland—relics of a former more extensive forest cover. As important is that the majority of forest patches are related to soil sites with optimal moisture retention and aeration under the present climate and geomorphic dynamics, whilst the grasslands are on seasonally extreme sites. The forests on the Nyika Plateau in Malawi are generally looked upon as relics from fire, whereas the geomorphological work of Schroder (1976) shows that all the forest patches in his study area on the Nyika were related to slump scars which ameliorate the water balance markedly. The forests in his study area are, therefore, not relics at all but initials in various stages of development. A similar relationship pertains in the Drakensberg where grasslands occur on impervious montmorillonitic clays of flat and steeply rounded terrain, and the forest patches are confined to deeper or moister soils of talus slopes, rock outcrops, slump and donga scars, ravines and stream banks.

From desert to about a 1,000 mm of rainfall which is strongly seasonal, clay soils are the most xeric substrates, sands have a greater availability of moisture depending on the presence or absence of a pan horizon, and deeply fissured stony or rock outcrop areas which allow for maximal absorption of rain, have the best water relations hence the dense thickets associated with outcrops (see also Waller 1971). Thus duplex sands and rock outcrops, like riverine strips which are exotic to arid regions, enable high rainfall systems, or their elements, to extend far into arid areas compensating for lower rainfall. This is illustrated by the rainforest initial *Trema orientalis* which I discovered at Ameib in Namibia amongst granite inselbergs in a rainfall area of 230 mm p.a. At the same time, saturated clays and deep sands carry arid biome components into and through moist regions, exemplified by *Salvadora persica* which extends from the Sahara to the Namib on sodic clays (Tinley 1975).

One fundamental principle emerges from the apparent diversity of situations under which forest, savanna and grassland are to be found—and that is that they are separated out by the soil moisture regimes of the various substrates in any particular area or region and these determine their basic spatial occurrence. This differential selection is determined by the moisture demands and tolerance of the various systems, or their components, under the particular circumstances of climate, relief, soil properties and competition. It is important to emphasise that competition exists not only between habitats but within habitats as well, exemplified by the savannas which are duplex systems comprising grass and woody strata. The subject of scrub encroachment being a function of soil moisture change when the grasses are removed from competition by overgrazing or erosion is well described by Walter and Volk (1954) and Walter (1964, 1971) for sandy clay soils in Namibia.

Walter (1971) gives another example of soil moisture subtleties. *Tamarix* trees can be grown in desert if the soil is kept moist through the profile until the taproot has reached the groundwater, after which they require no further aid. As this cannot happen under natural conditions, the area remains bare desert. This example questions whether the even-aged stands of old *Acacia erioloba* in the Kalahari are not related to exceptional years of consecutive high rains which wet the profile deep enough to allow the taproots to reach deep groundwater.

By occurring on sites with different soil moisture balance in different climatic zones these systems or their components are in fact occurring in the moisture balance sites sufficient for their requirements as described, for example, by Smith (1949). One or other system expanding or contracting, depending on whether geomorphic processes or significant climatic change occurs, allows for such opportunism—accelerated or retarded by the action of fire, frost, man or animal.

Generally the effect of consecutive years of high rainfall in the arid zone (<600 mm) is opposite to the moist zone (> 600 mm). In the arid zone there is an increase of woody plants as their roots can grow deeply enough to secure sufficient ground moisture to become established, and drought years promote the extension of grassland. In moist regions high rainfall promotes grasslands and forest, and drought years promote extension of savanna.

Contrary to the repeated statements that the savannas of Africa are mostly (if not all) secondary anthropogenic systems (e.g. Walter 1964), these are totally refuted not only by the biotic richness and uniqueness of this major biome type, but also from the evidence of the controlling influence of soil moisture balance across the continent.

As can be appreciated from the above data, the presence and disposition, or absence, of a pan horizon not only influences the type of plant cover possible, and thus the phytomass physiognomy and structure composition, but will also profoundly influence phenology. Onset of deciduousness in savanna trees for example is triggered by loss of available soil moisture and/or low temperatures. Midsummer droughts over a two-month period (typically January and February) in areas of poor moisture balance allows for evapotranspiration to deplete the soil moisture sufficiently to cause unseasonal leaf fall, followed by a repeated leaf and flower flush in many trees with the onset of rains again in March (see Chapter 8). In consecutive years of less than mean rainfall, the pre-rains woody flush in the arid savannas is repressed until the advent of the first rains three to four months later, when they flush simultaneously with the grass strata. Here again there is a differential effect caused by the recharge capacity and moisture balance of the particular soil.

The effect of plant cover type on the water balance of pan horizons

Large quantities of water are necessary for the metabolic requirements of growing plants. A given quantity of water in the soil is moved from the hydrosphere to the atmosphere far faster through the metabolic energy of plants than would be the case from direct evaporation. The tremendous amounts of water transpired by plants are proven by numerous quantitative studies, some of which are reported in university textbooks. A typical example from 'Temperate Lands' reads 'A single corn plant (in Kansas) between May 5th and September 8th transpired 54 gallons of water. An acre of such plants (6,000 plants) would transpire during the season 324,000 gallons of water, which is equivalent to a sheet of water 11 inches deep over the entire acre. It has been estimated that an acre of red maple trees growing in soil with ample moisture may lose in a growing season an amount of water sufficient to cover the acre with 28 inches of water. Of the total quantity of water absorbed by the roots of plants as much as 98% of it escapes from the plant by transpiration' (Robbins et al. 1959:185-198).

In clays the prominence of fine capillary pores is conducive to unsaturated flow whilst in sands the large pores encourage saturated flow (Brady 1974). Hence duplex sands have available a large water storage capacity but are sensitive to use by dense woody plant cover which creates a multiplicity of local tensions and leaves little for lateral movement of water.

For example, an area of dry forest on duplex sands at St. Lucia (South Africa) was cleared for pineapple plantations. In two summers the pan horizon became fully saturated in the absence of the dense woody cover and lateral flow began, reactivating springs and oozes on slopes which had not flowed for more than 20 years. This moisture was sufficient to kill the margins of forest patches which abutted on the 'fossil' drainage of the slopes. A similar response occurs where miombo on duplex sands is cleared for cultivation and the pan horizon becomes saturated and fills towards the surface, drowning the crops.

The woody cover on duplex sands is thus self-preserving in the natural state where the pan horizon is kept from being waterlogged for too long by evapotranspiration. A report in the Farmers Weekly (June 2, 1971, Vol. 120, p. 13) records the die-back of eucalyptus in the plantation areas of Natal and Eastern Transvaal due to insufficient moisture. The measure recommended to resolve the problem of die-back is to thin out the plantations to relieve water stress. Natural die-backs to restore the balance between available soil moisture and cover density also occurs in the arid savanna where scrub-thickets of *Acacia mellifera* are killed (thinned out) by drought years. The restoration of springs which had not flowed for several decades in the Tsavo National Park occurred when overpopulation of elephant transformed thicket into open grassy savanna.

Overstocking, cultivation and autumn fires can together or singly extend the area covered in thicket, resulting in the extinction or diminution of freshwater springs and streams. This non-climatic phenomenon is documented over many parts of the continent. The vegetation which uses only the surface of soils is grassland, and it is only under grassland that a very high field capacity can be attained and maintained (Tinley 1971a).

Influence on primary productivity

The base saturated hydromorphic floodplain soils support a high year-round production of grass only because they are well watered. Once drainage becomes more effective their productivity is confined to the rain and flood-ebb periods only. In the savannas, grasslands and deserts, primary production is controlled almost entirely by the incidence of rain. Walter and Vlok (1954), and Walter (1964, 1971) have shown that primary production increases proportionally to rainfall in a linear relationship for Namibia.

The presence of pan horizons in certain situations such as dambos or vleis allows for a much longer primary production deep into the dry season. In deep sand areas and soils with a pan horizon close to the surface (e.g. perched gleys of the Highveld), or on saline aridosols, primary production of shallow rooted grasslands is totally reliant on amount, distribution and the interval between rains.

Structural control of landscape development

Where pan horizons, especially the cemented forms, are exhumed by erosion of overlying soil, these more durable substrates slow down the rate of landscape change and impose a tableland morphology, with all that implies, in geomorphic succession and moisture balance of its various facets. The most important factor of structural control is its influence on the soil moisture balance of each land unit. These land units comprise plateau, waxing slope, scarp, talus and waning slope. Once cemented, hardpans are not impervious as are their clayey developmental stages, but allow deep rainwater penetration along fissures (refer to final section in soils above).

Compact fine sands

The surface of the broad Mozambique Coast Plain is composed predominantly of duplex sands of various kinds (pers. data). These sediments and the profiles they form are polygenetic. On the one hand, they are derived from erosion of the hinterland and deposited in giant, laterally coalescing alluvial fans (e.g. fossil Limpopo–Save Delta) on the continental margin from the Zambezi, south to Mtunzini on the Zululand Coast (Umlalazi River mouth). In the area affected by the Limpopo, extensive areas of fine, red Kalahari sands occur, these are possibly derived from stripped off Kalahari sands in the hinterland and redeposited over the boulder beds overlying older ferricretes and calcretes that now outcrop as scarps.

On the other hand, these fluvial fan deposits were re-sorted and redistributed by a transgressive marine phase when the Pliocene Sea covered the greater part of the Plain and again during its regressive phase in the Pleistocene (King 1972b) when new sediments from inland would have been spread in fan sequences. The combined influences of fluvial and marine littoral processes (including wind) resulted in parallel systems of dunes and slacks. The most conspicuous of these today are probably related to periods of stillstand in retreat of the Quaternary Sea to its Recent position.

On the Mozambique Coastal Plain, south of the Save River to about Lake St. Lucia, a characteristic feature, seen from the air, are these depressions (fossil estuaries) and low rounded (eroded) dune lines parallel to the present coast. This feature is made conspicuous by similar lines of disjunct, dark forest patches surrounded by large areas of tree savanna, or treeless grassland.

Investigation on the ground shows that in the more arid (600 mm) inland sectors of the plain, the dry forests occur on duplex sands with an impervious claypan horizon at about 70 cm to 120 cm depth. Seaward, where the rainfall increases to 1,000 mm, the dry forest patches are confined to fine, strongly compacted sands (without clay) which alternate with extremely loose, median grained sands supporting savanna (*Terminalia* or miombo) with an impervious claypan at 3 m depth. The fine compacted dry forest sands in the late autumn are dust dry to 3 m depth, whilst free water collects at 3 m depth under *Terminalia sericea* savanna. It is possible that a greater sump is formed at depth (beyond 3 m) by the linear fine sand deposits which may then be recharged by direct rainfall as well as by lateral movement of water from the adjacent savanna duplex sand. Deeper pits are required in the dry forest fine sand patches to unravel their soil moisture story in full.

Comparison of the 1940's air photo coverage of the Mozambique Plain with recent photos shows clearly, that in the interval of 30 years with annual veld fires, the dry forests have neither decreased nor increased in size. They are aligned and associated with duplex sands and/or compacted fine sands deposited in parallel irregular patches, probably by the retreating Pleistocene Sea and the closely following fluvial fan sequences.

In other areas, such as on the seaward slope of the Cheringoma Plateau, evergreen moist forests occur on duplex sands with an impervious horizon at 150 cm to 250 cm depth, and here their slightly higher microrelief separates them from the abrupt change to dambo grassland of the adjacent flat drainage lines, which also have an underlying much shallower impervious pan horizon. Microrelief, and thus degree of waterlogging alone, appears to separate these contrasting ecosystems here (Fig. 8.19B and 18.9C).

Summary point

These field observations indicate that soil moisture balance is the most significant edaphic feature as it over-rides all other properties, or influences their effects.

RIGHT:

Field observation into soil moisture.

REFERENCES / CORRELATION STRUCTURE AND SURFACE

Anderson, G.D. & Talbot, L.M. 1965. *Soil factors affecting the distribution of the grassland types and the utilization by wild animals on the Serengeti Plains.* Tanganyika Journal of Ecology, vol. 53, pp. 33-56.

Azevedo, A.L. 1945. *Os solos de Angola e a agricultura.* Impr. Nac. de Angola, Luanda.

Bear, F.E. 1965. *Chemistry of the soil.* 2nd edn, Reinhold Pub. Co. NY.

Besairie, H. 1960. *Monographie geologique du Madagascar.* Tananarive.

Boocock, C. & Van Straten, O.J. 1962. *Notes on the geology and hydrogeology of the Central Kalahari Region, Bechuanaland Protectorate.* Trans. Geol. Soc. S. Afr., vol. 65 (1), pp. 125-171.

Brady, N.C. 1974. *The nature and properties of soils*. 8th edn, MacMillan, NY, London.

Branson, F.A., Miller, R.F. & McQueen, I.S. 1970. *Plant communities and associated soil and water factors on shale-derived soils in northeastern Montana.* Ecology, vol. 51, pp. 391-407.
—1976. *Moisture relationships in twelve northern desert shrub communities near Grand Junction, Colorado.* Ecology, vol. 57, pp. 1104-1124.

Casimiro, J.F. 1968. *Um caso de podzolização em Moçambique.* Agron. Mocamb, vol. 2 (2), pp. 91-95.

Chapman, J.D. & White, F. 1970. *The evergreen forests of Malawi*. Commonwealth Forestry Inst., University of Oxford.

Coelho, A.V.P. 1959. *Primeiro reconhecimento petrográfico da serra da Gorongosa (Moçambique).* Bol. Serv. Geol. Min., vol. 25, pp. 13-71.

Cole, Monica M. 1960. *Cerrado, Caatinga and Pantanal: the distribution and origin of the savanna vegetation of Brazil.* Geog. J., vol. 126 (2), pp. 168-179.
—1963. *Vegetation and geomorphology in Northern Rhodesia: An aspect of the distribution of the savanna of Central Africa.* Geog. J. vol. 129 (3), pp. 290-310.

Cooke, H.B.S. 1964. 'Pleistocene mammal faunas of Africa, with particular reference to Southern Africa' in *African ecology and human evolution.* C. Howell & F. Bourliere (eds), Methuen, London, pp. 65-116.

Darracott, B.W. 1974. *On the crustal structure and evolution of southeastern Africa and the adjacent Indian Ocean.* Earth Planetary Sci. Lett., vol. 24, pp. 282-290.

De Bruiyn, H. 1971. *'n Geologiese studie van die panne van die westelike Oranje Vrystaat.* M.Sc. Thesis, University of the Orange Free State, Bloemfontein.

D'Hoore, J.L. 1964. *Soil map of Africa scale 1 to 5000 000: explanatory monograph.* CTCA PubI. No. 93, Lagos.

Dixey, F. 1927. *The Mlanje Mountains of Nyasaland.* Geog. Rev., vol. 17, pp. 611-626.
—1938. *The Nyasa–Shire Rift.* Geog. J., vol. 91 (1), pp. 51-56.
—1955. *Some aspects of the geomorphology of central and southern Africa.* Trans. Geol. Soc. S. Afr, Annexure to vol. 58.
—1956. *The East African Rift system.* Cal. Geol. Min. Resources, Supplement No. 1.

Du Toit, A.L. 1937. *Our wandering continents.* Oliver & Boyd, Edinburgh & London.
—1954. *The geology of South Africa.* 3rd edn., Oliver & Boyd, London.

Farmers Weekly 1971, June 2, vol. 120, p.13.

Fernandes, J.F. 1968a. *Os solos da Serra da Gorongosa e sua capacidade de utilização.* I.I.A.M. Comunicações, No. 7.
—1968b. *Os solos do Parque Nacional da Gorongosa.* I.I.A.M. Comunicações, No. 1975.

Fisher, R.L., Johnson, G.L. & Heezen, B.C. 1967. *Mascarene Plateau, western Indian Ocean.* Geol. Soc. Amer. Bull., No. 78, pp. 1247-1266.

Flores, G. 1964. *Geology of the Cheringoma Uplift.* Relatórios inéditos da Mozambique. Gulf Oil.
—1970. *Suggested origin of the Mozambique Channel.* Trans. Geol. Soc. S. Afr, vol. 73, pp. 1-16.

Flower, M.F.J. & Strong, D.F. 1969. *The significance of sandstone inclusions in lava of the Comoros Archipelago.* Earth Planet. Sci. Lett., vol. 7, pp. 47-50.

Fourmarier, P. 1967. *Esquisse géologique de Madagascar, ses relations avec le continent africain.* Bull. des Seances, Acad. Royale des Sci. d'Outre Mer, No. 2, pp. 290-322.

Furon, R. 1963. *Geology of Africa.* Oliver & Boyd, Edinburgh & London.

Gabão, G. Dos Santos 1969. *Carta Sismo-tectónica de Moçambique actualizade até 31 Dezembro de 1967.* SMM 48, mem. 46, Lourenço Marques.

Ganssen, R. 1963. *Südwest-Africa: boden en bodenkultur.* Reimer, Berlin.

Gouveia, D. Godinho and Marques, A. Sá E. Melo 1973. *Carta dos solos de Moçambique (Esc. 14 000 000).* Agran. Moçamb., vol. 7 (1), pp. 1-64.

Green, A.G. 1972. *Seafloor spreading in the Mozambique Channel.* Nature Phys. Sci., vol. 236, pp. 19-32.

Grove, A.T. 1969. *Landforms and climatic change in the Kalahari and Ngamiland.* Geog. J., vol. 135 (2), pp. 191-212.

Hallam, A. 1973. *A revolution in the earth sciences.* Clarendon Press, Oxford.

Henzen, M.R. 1973. *Die herwinnjng, opberging en onttrekking van gesuiwerde rioolwater in die Kaapse Skiereiland*. Nasionale lnstituut vir Waternavorsing, Suid–Afrikaanse Wetenskaplike en Nywerheidsnavorsingsraad. (3 Vols.).

Holmes, A. 1965. *Principles of physical geology.* 2nd edn. (Revised), Nelson, London.

Janzen, D.H. 1974. *Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae.* Biotropica, vol. 6 (2), pp. 69-103.

King, L.C. 1962. *Morphology of the Earth.* Oliver & Boyd, London.
—1963. *South African scenery.* 3rd edn. (Revised), Oliver & Boyd, London.
—1972a. *The Natal Monocline.* University of Natal, Durban.
—1972b. *The coastal plain of southeast Africa: its form, deposits and development.* Z. Geomorph. N.F., vol. 16 (3), pp. 239-251.

Kutina, J. 1975. *Tectonic development and metallogeny of Madagascar with reference to the fracture pattern of the Indian Ocean.* Geol. Soc. Amer. Bull., vol. 86, pp. 582-592.

Laperre, P.E. 1971. *Zambezi Delta soils for the production of sugarcane: their classification, morphology, chemical and physical properties.* Agron. Moçamb., vol. 5 (4), pp.237-260.

Liebenberg, E.C., Rootman, P.V. & Van Huyssteen, M.K.R. 1976. *The South African landscape: exercise manual for map and airphoto interpretation.* Butterworth, Durban.

Lobeck, A.K. 1939. *Geomorphology.* McGraw-Hill, NY & London.

Loxton, R.F. 1962. *A simplified soil-survey procedure for farm planning.* Soil Res. Inst. Dept. Agric. Techn. Serv., Govt. Printer, Pretoria.

McCarthy, M.J. 1967. *Stratigraphical and sedimentological evidence from the Durban region of major sea-level movements since the late Tertiary.* Trans. Geol. Soc. S. Afr., vol. 70, pp. 135-165.

McKenzie, D.P. & Sclater, J.G. 1973. *The evolution of the Indian Ocean.* Sci. Amer., vol. 228 (5), pp. 62-72.

Michelmore, A.P.G. 1939. Observations on tropical African grasslands. Journal of Ecology 27, pp. 282-312.

Mohr, E.C.J. & Van Baren, F.A. 1954. *Tropical soils.* Van Hoeve, The Hague, Interscience Pub. London & NY, (1959 impression).

Mouta, F. 1956. 'L'effondrement de I'Urema extreme sud des "rift valleys" au Mozambique (Afrique Orientale Portugaise)' in *First Meeting of East-Central Regional Committee for Geology* (Dar es Salaam), CCTA, pp. 121-123.

Netterberg, F. 1969. *The interpretation of some basic calcrete types.* S. Afr. Archaeol. Bull., No. 24, pp.117-122.
—1971, *Calcrete in road construction.* CSIR Res. Report 286, NIRR Bull., No. 10.

Oberholzer, W.F. 1968. *Carta geológica de Moçambique. (1:2 million).* Serviços de Geologia e Minas de Moçambique, Litho Emol, Lourenco Marques.

Odum, W.E. & Heald, E.J. 1975. 'Mangrove forests and aquatic productivity' in *Coupling of land and water systems.* A.D. Hasler (ed.), Ecological Studies No. 10, Springer-Verlag, pp. 129-130.

Pócs, T. 1975. *Affinities between the bryoflora of East Africa and Madagascar.* Boissiera, vol. 24, pp. 125-128.

Real, F. 1966. *Geologia da bacia do Rio Zambezi (Moçambique).* Junta de Invest. do Ultramar, Lisboa.

Robbins, W.W., Weir, T.E. & Stocking, C.R. 1959. *Botany: an introduction to plant science.* Wiley NY, Chapman &Hall, London.

Saint-Ours, J. 1956. *Étude morphologique et géologique de l'archipel des Comoros.* Bull. Acad. Malgache, vol. 34, pp. 7-39

Scholz, C.H. 1976. *Rifting in the Okavango Delta.* Natural History, vol. 85 (2), pp. 34-42.

Serrano, J.F. 1973. *A capocidade utilizável para a áqua em grandes grupos de solos de Moçambique.* Agron. Moçamb., vol. 6 (4), pp. 259-266.

Shroder, J.F. 1976. *Mass movement on Nyika Plateau, Malawi.* Z. Geomorph, N.F. vol. 20(1) pp. 56-77.

Sioll, H. 1975. 'Amazon tributaries and drainage basins' in *Coupling of land and water systems.* A.D. Hasler (ed.), Springer-Verlag.

Smith, H.G. & Hallam, A. l970. *The fit of the southern continents.* Nature, vol. 225, pp. 139-144.

Smith, J. 1949. *Distribution of tree species in the Sudan in relation to rainfall and soil texture.* Sudan Ministry Agric. Bull., No. 4.

Sys, C. 1960. *Notice explicative de la carte des sols du Congo Belge et du Ruanda-Urundi.* INEAC, Bruxelles.

Takehara, M.O.H. 1967. *Revised standard soil colour charts.* Japan.

Tarling, D.H. 1971. *Gondwanaland palaeomagnetism and continental drift.* Nature, vol. 229, pp. 17-21.

Teale, E.O. 1924. *The geology of Portuguese East Africa between the Zambezi River and the Sabi River. A consideration of the relation of its tectonic and physiographic features.* Trans. Geol. Soc. S. Afr., No. 26, pp. 103-159.

Teale (Thiele), E.O. & Wilson, R.C. 1915. *The geology of Portuguese East Africa between the Zambezi River and the Sabi River. A consideration of the relation of its tectonic and physiographic features.* Geog. J., vol. 65, pp. 16-39.

Termier, H. & Termier, G. 1963. *Erosion and sedimentation.* Van Nostrand, London.

Tinley, K.L. 1969. *The ecological limits of Gorongosa National Park, Moçambique, and the maintenance of wilderness.* Report to the Mozambique Government, Fauna Branch of Vet. Serv.
—1971a. *Lake St. Lucia and its peripheral catchment.* Wildlife Soc. S. Africa, Pinetown.
—1971b. 'Determinants of coastal conservation. Dynamics and diversity of the environment as exemplified by the Moçambique coast' in *Nature conservation as a form of land use.* Proceedings SARCCUS Symposium, Govt. Printer, Pretoria, pp. 125-153.
—1975. *Habitat physiognomy, structure and relationships.* Soogdiernavorsingsinstituut 1966-1975, Symposium proceedings, Publ. of University of Pretoria, New Series No. 97, pp. 69-77.

Trapnell, C.G., Friend, M.T., Chamberlain, G.T. & Birch, H.F. 1976. *The effects of fire and termites on a Zambian woodland soil.* J. Ecology, vol. 64 (2), pp. 577-588.

USA Soil Survey Staff 1960. *Soil classification: a comprehensive system—7th approximation.* Soil Conservation Service, US Dept. of Agric., Govt. Printer, Washington DC.

Van Der Eyk, J.J., Macvicar, C.N. & De Villiers, J.M. 1969. *Soils of the Tugela Basin.* Town and Regional Planning Commission, Natal, vol. 15.

Van Der Merwe, C.R. 1962. *Soil groups and subgroups of South Africa.* 2nd edn. (revised). Govt. Printer, Pretoria.

Van Wyk, W.L. 1963. *Ground-water studies in northern Natal, Zululand and surrounding areas.* Geological Survey Mem., No. 52.

Walter, H. 1964. 'Productivity of vegetation in arid countries, the savanna problem and bush encroachment after overgrazing' in *The ecology of Man in the tropical environment.* IUCN Publ. New Series No. 4, Morges, Switzerland, pp. 221-229.
—1971, *Ecology of tropical and subtropical vegetation.* Oliver & Boyd, London.

Walter, H. & Vlok, O.H. 1954. *Grundlagen der weidewirtschaft in Südwestafrika.* Verlag Eugen Ulmer, Stuttgart.

Wellington, J.H. 1955. *Southern Africa: a geographical study.* vol. I, Cambridge University Press.

Wild, H. 1975. *Phytogeography and the Gondwanaland position of Madagascar.* Boissiera, vol. 24, pp. 107-117.

Wright, J.B. & McCurry, P. 1970, *Comment on paper by M.F.J. Flower & O.F. Strong (1969)*. Earth Planet. Sci. Lett., vol. 8, pp. 267-268.

PART 2

CORRELATION

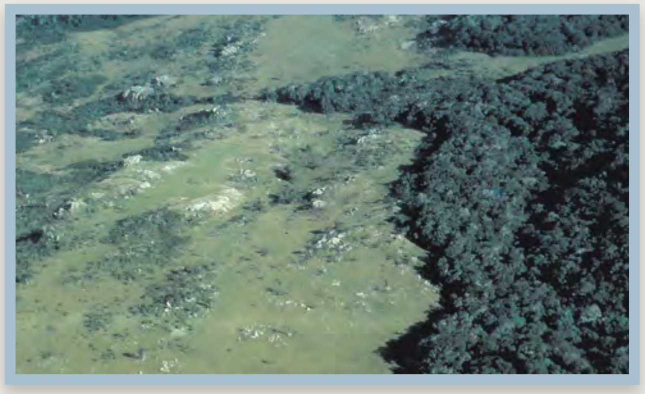
Chapter 6

Process and Response

OPPOSITE:

Sampling *Mimosa pigra* seedlings on the floodplains with Pedro and Signet.

Process and Response



6.1 NATURAL SYSTEMS

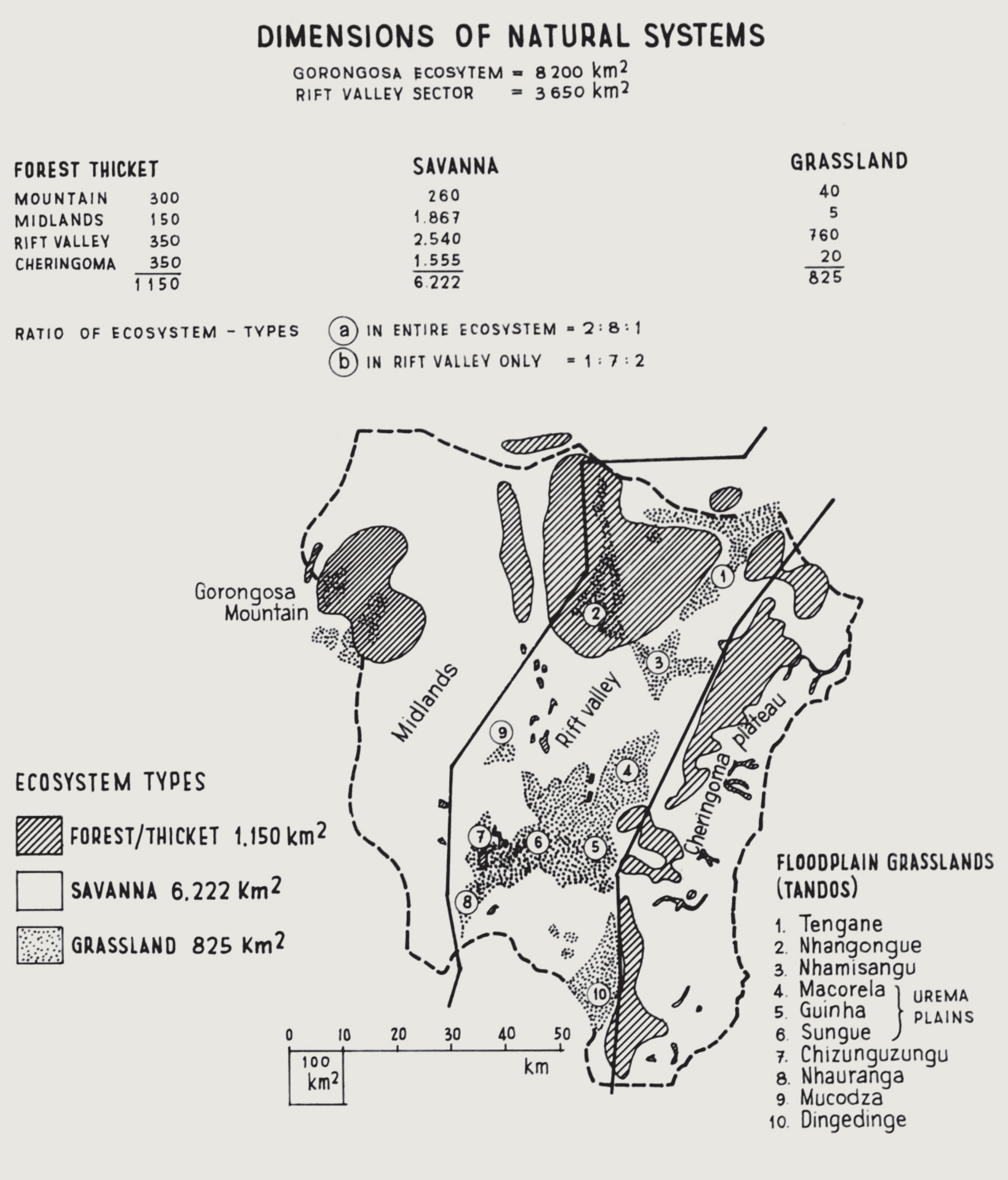
Three ecosystem-types make up the natural systems of the study area; these are forest/thicket, savanna, and grassland. The various ecosystems and communities constituting each type are dealt with in Chapter 8.

Forest and thicket are grouped together as both have similar structure and physiognomy and are only clearly separable on floristic criteria (Tinley 1975). Low scrub-thicket is confined to second growth on old cultivation sites, the coast dunes, and montane and coast fynbos communities. Savanna is a duplex ecosystem-type composed of a woody plant stratum of one or more layers, associated with a herbaceous grass stratum forming the ground layer. The tree canopy is closed to open, scattered or clumped in spacing. Apart from dwarf shrubs, grasslands are devoid of woody plants except where they are being invaded by elements of the other two ecosystem types. In these circumstances, the definition of a grassland remains inviolate until the woody invasion emerges above the grass stratum altering the physiognomy and structure to a savannoid form. The various criteria defining physiognomy, structure and community relations are dealt with elsewhere (Tinley 1975).

In the Gorongosa system of 8,200 km^2, savannas occupy 6,225 km^2 (76%), forest/thicket 1,150 km^2 (14%) and grasslands 825 km^2 (10 %)—a ratio of 8:2:1. Of these, the largest single block of forest (300 km^2) is on Gorongosa Mountain, and the Urema Plains is the largest grassland area (400 km^2). Referring solely to the main wildlife concentration area of the Rift Valley, which is 3,650 km^2 in extent within the study area, savannas comprise 2,540 km^2 (70%), floodplain grassland 760 km^2 (21%) and forest/thicket 350 km^2 (10%)—a ratio of 7:2:1. The very small areas occupied by these ecosystem-types such as the strips of riverine forest, termitaria thickets and dambo grasslands are not included in the above calculations despite their

RIGHT: Figure 6.1

Major ecosystem patterns.



DIMENSIONS OF NATURAL SYSTEMS

GORONGOSA ECOSYTEM = 8 200 km²
RIFT VALLEY SECTOR = 3 650 km²

	FOREST THICKET	SAVANNA	GRASSLAND
MOUNTAIN	300	260	40
MIDLANDS	150	1.867	5
RIFT VALLEY	350	2.540	760
CHERINGOMA	350	1.555	20
	1150	6.222	825

RATIO OF ECOSYSTEM – TYPES ⓐ IN ENTIRE ECOSYSTEM = 2 : 8 : 1
ⓑ IN RIFT VALLEY ONLY = 1 : 7 : 2

ECOSYSTEM TYPES

▨ FOREST/THICKET 1.150 km²

☐ SAVANNA 6.222 Km²

░ GRASSLAND 825 Km²

FLOODPLAIN GRASSLANDS (TANDOS)

1. Tengane
2. Nhangongue
3. Nhamisangu
4. Macorela } UREMA PLAINS
5. Guinha } UREMA PLAINS
6. Sungue } UREMA PLAINS
7. Chizunguzungu
8. Nhauranga
9. Mucodza
10. Dingedinge

FIG. 6.1 MAJOR ECOSYSTEM PATTERNS

disproportionate importance. Hence the above figures are approximate and merely serve to illustrate the kind of proportional relationships of ecosystems and their components under present circumstances, which can be contrasted with the past and future situation interpreted in the following section.

The major pattern of the ecosystem types is depicted in Fig. 6.1, showing a central disconnected series of floodplain grasslands on the Rift floor, and forest/thicket concentrated mostly in the north and along the east with an isolated block on Gorongosa Mountain in the west. The largest savanna area comprises the Midlands and adjoining central western part of the Rift Valley floor, but this is not a solid block as it is traversed by a network of narrow, often discontinuous strips of riverine forest and thicket, which are the lines of contact between the larger forest/thicket blocks. On the Rift Valley floor the large island thickets on termite hills play the same role, acting as stepping stones between major forest/thicket areas.

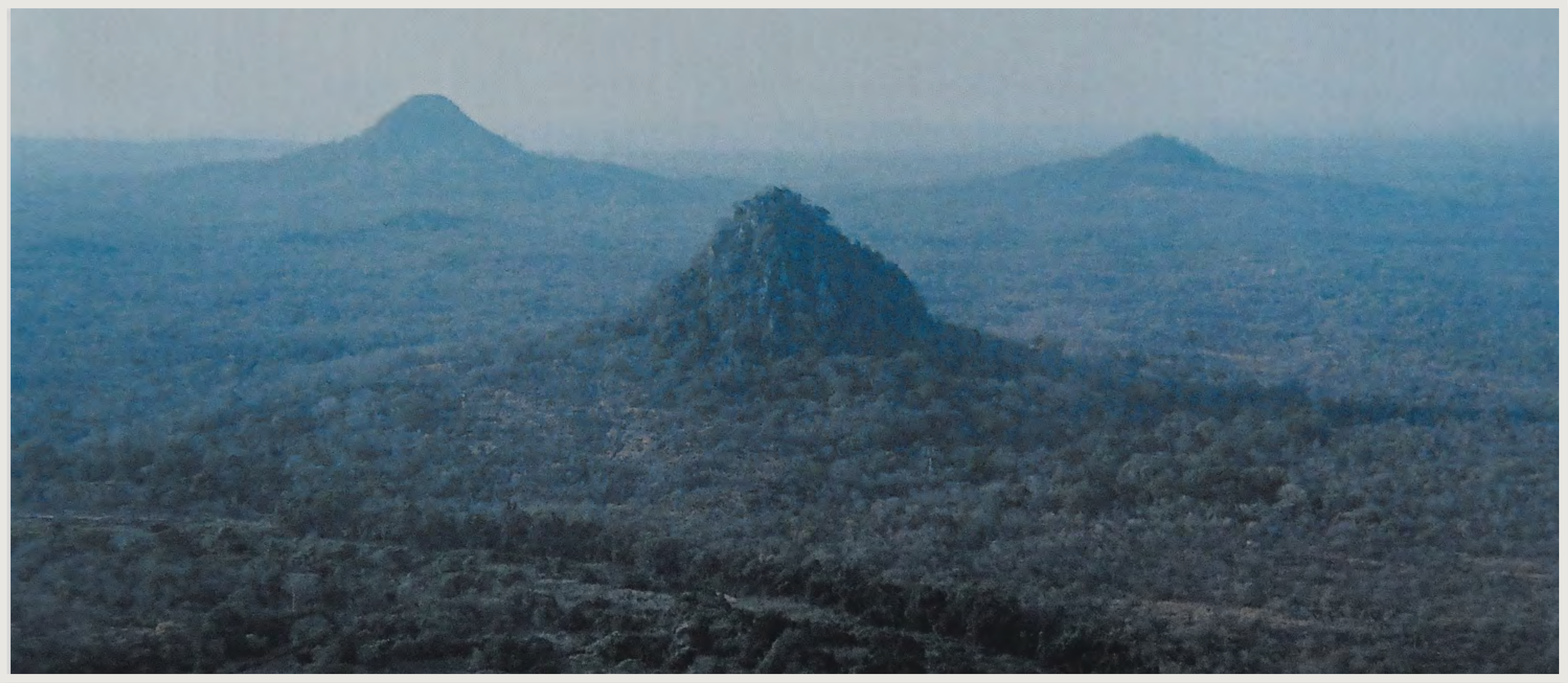
All three ecosystem-types are associated with both denudational and aggradational land surfaces in the study area. Forest and thicket occur on erosional landforms such as scarps, incised river courses, ravines and dongas, and on depositional landforms of talus, levees, and duplex sands of splay bars and fan distributaries, and around the base of inselbergs. All these sites are characterised by having high water-retaining, yet well-aerated, substrates. The savannas occur on sharply dissected hill country with skeletal soils, typified by the Midlands, as well as on low convex surfaces of depositional landforms such as the Rift Valley and coast, where they are separated by microrelief from excessively flooded or waterlogged substrates occupied by grasslands. Generally the savannas are on better to excessively drained sites with seasonal contrasts in soil moisture content. By contrast, most of the grasslands in the Gorongosa–Cheringoma area owe their existence to seasonally excessive flooding or waterlogging, whether on residual impermeable soils in mountain or hill sites, on gleyed alluvia (floodplain grasslands), or on the lower parts of catenas and duplex sands (dambo grasslands) of depositional landforms. In some areas, as on the Cheringoma Plateau, new grasslands are formed on erosional landforms along the seepage slopes formed on the convex crest of retreating scarps. Both woody ecosystem types actively invade the grasslands where excessive waterlogging or flooding is reduced.

Although ecosystems are most easily distinguished by their plant cover, on the basis that vegetation is an integrated expression of the ecosystem, certain faunal components closely tied to particular habitats are useful ecosystem and biome indicators. In this region it is far easier to use birds as faunal indicators, as the grazing components of the wild ungulate spectrum are common to both the savannas and the grasslands. However, it is possible to characterise the ecosystem-types into: a disjunct reedbuck system (the lechwe is the ideal indicator for floodplain grassland but they do not occur off the continental interior); a northern and eastern nyala/suni system; and an isolated blue duiker montane system, interspersing the larger sable, hartebeest, impala system.

6.2 GEOMORPHIC AND ECOLOGIC DYNAMICS

Introduction

The Gorongosa–Cheringoma transect provides a unique spectrum of geo-ecological processes. In this diversity there exist extremely friable substrates subject to relatively rapid differential rates and kinds of change under the climatic regime of Recent and contemporary time. These substrates and the ecosystems they support are extremely vulnerable to natural erosional processes, and clearly demonstrate the multidirectional nature of successional changes within one area. These changes are made conspicuous by the contrasting vegetation physiognomies, quite apart from their compositional differences.



LEFT:

Inselberg miombo landscape

Two main processes are dealt with in this section: substrate replacement (geomorphic succession), and the in-situ changes of soil moisture balance (edaphic succession) of residual sites by changes in drainage. The response of ecosystems and habitats will be related as units to these substrate changes and specific intrasystem plant and animal succession will be dealt with in Chapters 8 and 9.

In this work, the terms succession and dynamics are used in reference to both geomorphic and ecologic processes in the kinetic sense (Drury and Nisbet 1971), and not in the traditional, generally accepted, rigid developmental-climax connotation defined by Clements (1916, 1928) and augmented and refined by Odum (1969), Whittaker (1970) and others, for plants alone. Field evidence in southern Africa, such as of forest—the 'oldest, most complex system'—occurring on the youngest geomorphic surfaces of dongas and dunes, makes nonsense of many assumptions used to formulate plant succession in the traditional context. A timely and valuable reassessment of this subject in a geo-ecological context has been made by Drury and Nisbet (1971, 1973), but unfortunately they jeopardise their argument by dismissing some valid findings of the traditional plant ecological school, and proven evidence of uplifted planation surfaces in geomorphology.

The use of the term 'kinetic' signifies continuous change without an endpoint (Drury and Nisbet 1971). The Oxford Dictionary defines kinetics as the 'science of the relations between the motions of bodies and the forces acting on them'. This is a clear description of geo-ecological relations, and those between the biotic associations and their components within an ecosystem. Succession in an ecosystem context can be defined simply as the sequential process of changing from one state to another through internal and/or external influences. Such changes involve the ecosystem in its entirety (as will be demonstrated in this section), one or more of its constituent trophic or strata levels, or only a segment of one level.

The terms 'progressive' and 'retrogressive' are used in plant ecology to specifically signify whether lower life forms are being replaced by higher life forms in succession, or vice versa. However, in mammalian ecology the exact opposite significance pertains as the highest diversity and zoomass of wildlife occur in the lower plant life form habitats (e.g. floodplain grasslands), thus succession to a higher closed plant community (e.g. forest) would be retrogressive from a mammalian ecological viewpoint. In geomorphology, the surface replacing another is qualified merely by young, mature, or old depending on its stage of development within the cycle. The term retrogression is defined as a return to a less advanced state, a degeneration in the attainment towards the traditional ideal of the climax community. As many discrete ecosystems within the same region show no sign of being replaced by others, they are all climax at that moment in time, but in the overall pattern of geomorphological cycles they are at the same time climax and successional. All changes are, in fact, progressive in the sense that upward, downward, lateral or cyclic (multidirectional) successional changes are occurring within a greater geomorphic cycle of landscape evolution which in turn involves all life processes on regional and continental dimensions through geologic time.

The geomorphic cycle of erosion begins with the incision of a planation surface and passes through three stages of development—youth (initial dissection), maturity (when relief is greatest), and finally the relief is worn down to the planation surface of old age. The last stage completes one cycle of erosion, and simultaneously, provides the surface on which a new cycle is initiated (vide King 1963, 54, pp. 202-204; Holmes 1965, p. 472). The controversies surrounding cycles of erosion are as legion as those which surrounded continental drift, and discussion of these aspects can be found in Pitty (1971, pp. 48-78), Small (1972, pp. 157-286) and Thomas (1974). The African experience across the subcontinent shows an epi-cyclic series, as shown by Dixey's and King's works now being substantiated by recent plate tectonic and continental margin studies such as those referred to under Section 5.3 and Thomas (1974). The use of nickpoint cycles in southern Africa is used by Partridge (1973) for correlating and dating landscape changes.

As geo-ecological processes are responsible for altering the soil moisture balance of substrates, a more lucid picture of interrelations is obtained by using the relevant sections (e.g. Section 5.8) with the present one.

It should be emphasized that the examples of soil moisture balance from across the subcontinent, coupled with the evidence from Gorongosa, are presented not only to put the subject in greater perspective but also to counter any notion that these features are peculiar to Gorongosa. This notion would minimize the far reaching implications that these interactions have outside the study area in the field of conservation management, and in interpretations within other disciplines.

The studies from the Gorongosa–Cheringoma area substantiate and augment the outstanding works of

Michelmore (1939), Smith (1949), and Cole (1963) in elucidation of the fundamental relationships of vegetation systems and substrates in Africa. It is surprising how seldom these works are referred to in ecology, particularly as they are based on verifiable field evidence across the continent.

The lack of appreciation that geomorphic surfaces and the systems they support are in a perpetual state of flux is summed up by Monica Cole (1963, p. 290). ‘The views of the various writers on the African vegetation, taken either separately or in combination, fail to explain satisfactorily either the present distribution of forest and savanna or that of the many vegetation associations included within them. They have failed to appreciate that geomorphological processes, themselves governed partly by the prevailing climate, are continuously modifying the relief and drainage, the soils and the micro-climate, thereby creating conditions more favourable for some plants and less favourable for others, and bringing about the extension of some vegetation and the recession of others of which only relicts may remain’.

Monica Cole (1960, 1963) has elucidated the relationships between vegetation and geomorphic erosion cycles. Generally grasslands or savannas occupy the planation surfaces, and forest or thicket occurs on younger incised surfaces of scarp slopes or along drainage. In the Gorongosa–Cheringoma Coast area these relationships are clearly depicted by the spatial distribution of the major natural systems. Montane grassland, Rift Valley grassland, dambo grassland/and savannas are generally related to flat or gently undulating planation surfaces. Forest and/or thicket occurs on deeply weathered slopes, stream incisions or sand deposits such as splay bars, distributary fans, scarp fans and coast dunes. The control of vegetation on these sites is a function of moisture balance as exerted by the presence or absence of impervious horizons and the control of soil drainage by eroson or depositional processes in geomorphic succession.

In sum, periods of dissection and deposition (cut and fill) will favour forest/thicket extension due to better moisture retention and aeration, and more stable periods of planation (levelling) will promote grassland and/or savannas on soils with a poor moisture balance, often with perched impervious horizons, which are waterlogged in the growing season and extremely dry in the winter. As these factors are the fundamental control of the disposition of natural systems, they influence all life patterns and successional relationships, and thus the evolution of landscapes and their living components. This theme will be expanded in subsequent sections and summarised in the final chapter.

As some Gorongosa examples show the full cycle of geo-ecological succession in one area, they have enabled a more complete record to be obtained, which on the one hand contradicts in part some of Cole’s (1963) thesis regarding system relationships with the age of surfaces and, on the other, hopes to synthesize holistically the significance of these changes in an evolutionary context. Such a context comprises geomorphic, edaphic and plant interactions, and the part played by animal prime movers in the evolution of ecosystems (Ch. 8.5, 9.7 and Part III).

Gorongosa Mountain

The striking feature of geo-ecological relations on the mountain is the predominance of rain forest on the steeper dissected surfaces, and of grasslands on flat to strongly convex surfaces. The grasslands on the upper catchments of the Nhandare and Vundudzi Rivers appear to be extending, and the forest retreating, mainly in response to annual fires. But airphoto evidence shows that these areas are becoming lower in relief due to the action of local base-levels of resistant rock where the 1,400 m and 1,500 m contours cross the valleys. This implies that change in soil moisture balance is possibly at the root of the efficiency of fire in extending the grassland cover. This cannot be verified until soil profiles have been made on the mountain summit area.

The most important event in the evolution of the Gorongosa ecosystem was the river capture of part of the upper catchment of the Nhandare by the Vundudzi. As shown by the Mucodza stream which rises on the lower part of the mountain, this zone has a lower and more seasonal rainfall, resulting in a weak perennial flow which only reaches the Mucodza marsh on the western margin of the Rift Valley at the height of the dry season. Until the Vundudzi cut back and captured the upper high rainfall catchment, it too would have only reached the edge of the Rift. At this earlier time the Pungue River would have been responsible for flooding a larger shallower Urema Lake area than at present, aided by the seasonal floods of the Nhandue River.

As the Pungue River built up alluvial fans at its junction with the Rift, these blocked off and initated new courses to the southeast, cutting off the perennial supply to the Urema basin. The enlargement of the effective catchment of the Vundudzi by headward erosion and river capture enables it now to traverse the Rift floor and maintain a shallow lake at the height of the dry season. This has been a fundamental factor in enabling large concentrations of wildlife to develop in this sector of the Rift Valley, as elsewhere they are forced to migrate long distances due to the complete drying out of surface waters.

In the geological time scale this sole supply of perennial water to the Urema Basin and the Nhandare flow, is doomed to ever decreasing volume due to gradual beheading of their sources by encroachment from headward erosion of the radial drainage on the western slopes of the mountain. Thus as a natural event, these two major rivers, which rise on the mountain, are having their effective catchment area reduced in size. Such a normally slow process can in this case be rapid as the uppermost source areas are flat, thus any micro-rise can form a critical height for a new divide. In this way, capture of source areas by faster eroding inface, or scarp streams, diverts waters away from the major rivers that traverse the summit. Thus the concentrated flows of the Nhandare and Vundudzi are gradually being taken off into myriads of radial streams, which in separated form are ineffective as perennial water sources for the country surrounding the mountain. Shifting cultivation on the slopes of the mountain greatly accelerates these normal erosional processes, and in many places has already been responsible for altering perennial streams to seasonal flow with heavy sediment loads. The contrasting muddy and clear waters in different sections of the same stream, or in adjacent streams, testifies to the state of their catchments.

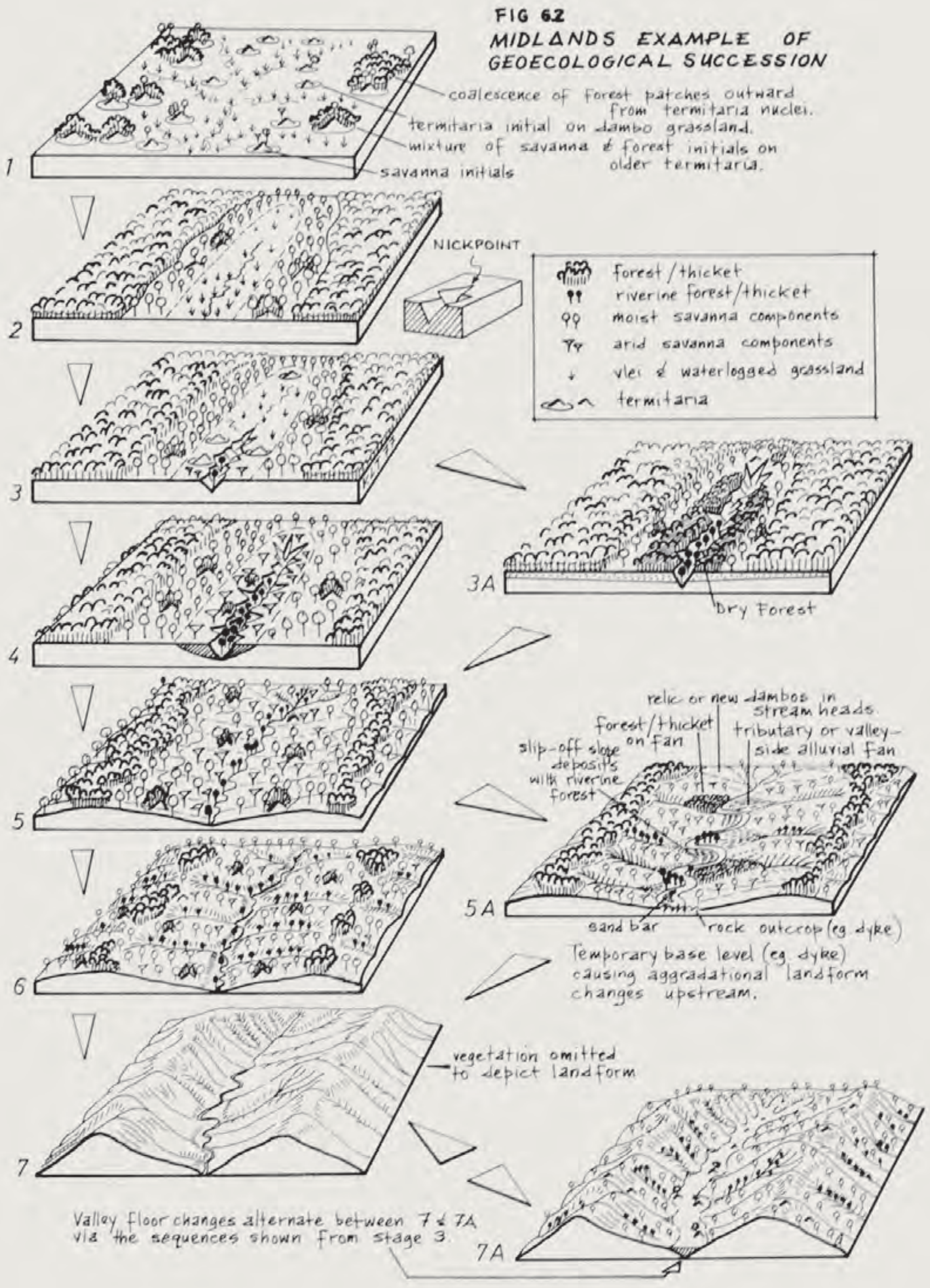
Riverine forest/thicket occurs as a radial and annular pattern outwards from the mountain along stream banks. New riverine forest invades the incised fingers of amphitheatre drainage on precipitous mountain slopes and those developing around its base. Erosion of the larger ravines on the eastern scarp has formed cone fans and laterally confluent debris slopes covered in forest. These fans are all now incised, the trenched courses lined with narrow strips of taller riverine trees.

Midlands

The sharply dissected Midlands support a sea of closed *Brachystegia* savanna. The hill and valley-side substrates provide skeletal sandy and stony lithosols with narrow moisture lines along the network of streams which cut their slopes. Here strips of riverine trees connect with larger patches of forest on slip-off slope deposits, and infill above resistant rocks in the stream courses. The original Midland landscape and its subsequent alteration by diastrophic and geomorphic processes can be deciphered from the few small relics of forest savanna dambo mosaic on the remains of flat interfluve crests.

Immediately west of Gorongosa Mountain, on the broad interfluve between the Nhandue and Vundudzi (Midland) rivers, are areas of low undulating terrain with dambo grassland on the concave or flat surfaces, and forest patches surrounded by savanna on the faint convex surfaces. This mosaic system represents the remains of the Midland planation surface and is replicated today, in form if not in kind, by the extensive dambo-forest mosaic of the Cheringoma Plateau at present undergoing rapid surface replacement. These substrates (not necessarily the eco-system they support today) are relic end-Tertiary planation surfaces. Change in base level, and downwarping with renewed faulting in the Plio-Pleistocene, set in train another cycle of headward incision whose nickpoints have now reached the relic dambos on the broader interfluve crests. Some of these dambos have been protected by outcrops of resistant rock. Elsewhere this dambo-forest mosaic has been stripped off by erosion to expose skeletal sandy and stony lithosols formed on the underlying Precambrian metamorphic rocks as the rivers entrenched their courses. Some of the deepest remaining soils are on the crests of the sharply dissected interfluves.

The salient features of this geo-ecological sequence shows forest/thicket and/or savanna (depending on the soils) initially on the oldest surface (the interfluve crest) and grassland on the dambo, the youngest surface. Savanna occupies the deeper sands on the crest and the margin between the dambo and the forest (Stage 1 in Fig. 6.2). Nickpoint incision changes the entire water balance of the dambo and the hygrophilous grassland is invaded by thorn savanna, if they are base saturated clays, or by dry forest if the dambo soils are duplex sands. At the same time riverine forest/thicket invades the donga incision. The donga represents the first phase of surface replacement, by which the dambo soils will be stripped off and lateral valley widening will consume the sands on the interfluve crest, thus reducing the area of forest/thicket (Stages 2 to 4). Up to stage 4, therefore, the forest ecosystem-type occurred on the oldest local geomorphic surface, and was reduced by valley side erosion to remnants and finally extinguished by erosion processes. At the same time this type now invaded the youngest local surfaces (donga and drained dambo



EXPLANATORY NOTES FOR Fig. 6.2

(1) Probable original situation (possible Plio-Pleistocene Surface, now relic), as shown in interfluve in 5A, with extensive dambo grasslands and small thicket islands of forest and savanna components on termite hills. Invasion of convex intervening ground (initial interfluve surfaces) between termite hills is beginning.

(2) Expansion, coalescence and maturation of forest/thicket and savanna on faintly convex surfaces, with dambos confined to faintly concave surfaces (initial valley surfaces). Convex surfaces are sands and concave surfaces are either duplex sands or clays.

(3) Donga incision of dambo floor by ascending nickpoint, resulting in increased runoff and decrease of waterlogging. Termite hill initials forming on dambo drainage and first invasion taking place by forest and/or savanna components. Riverine trees invade along the fresh donga cut. If dambo soils are base-rich they are invaded by arid savanna components (e.g. acacia and mopane).

(3A) If dambo soils are duplex sands they are invaded by dry forest.

(4) Headward migration of nickpoint and lateral dendritic incision of dambo. Remaining dambo soils now only seasonally waterlogged. Maturation of forest and/or savanna on dambo. Increased velocity of sheetwash off the dambo margins and erosion of interfluve sands.

(5) Complete removal of dambo soils and the systems they supported, replaced by sandy lithosols derived from the underlying crystalline geology and the formation of shallow V-shaped valleys. Valley widening by wearing back of streamheads eating into the interfluves, removing the sands and thus reducing the area under forest to narrow irregular strips on the interfluve crests. Extension of miombo or mixed savanna onto most surfaces, and riverine trees up all stream cuts.

(5A) In its development to stages 6 and 7 valley cutting may exhume a resistant rock barrier which acts as a temporary base level and causes aggradational sequences to occur upstream of the barrier. These features include braided river beds, slip-off slope deposits, confluence deposits, and valley side fan and splay deposits all of which are typically invaded by the forest/thicket ecosystem type. Incision of the structural barrier leads to stage 7. Dambos surviving on the remaining broad interfluves and the stage described above are best shown in the area immediately west of Gorongosa Mountain.

(6) On the interfluves the remaining sands and their forest cover are reduced to isolated remnants, and savanna extends. Renewed valley cutting leads to stage 7.

(7) The present stage of landscape evolution over most of the Midlands: valley and spur topography. Deep V-shaped valleys with narrow interfluves and fine dendritic tributary patterns. Sandy lithosols predominate and are covered in an unbroken closed miombo savanna. Narrow strips of riverine forest along stream banks, dambos mostly extinct.

(7A) In valley heads, deep valley cutting can alternate with phases of aggradation forming new dambo systems, often with steeply inclined floors. The dambo infill may be eroded via the developmental processes from stage 3.

SUMMARY: The least number of ecosystems and communities occur in the primary stage (1) and in the present mature stage (7). The greatest diversity occurs in intermediate stages 3, 3A, 4 and especially in 5A when a new series of landforms are developed by aggradation.

LEFT: Figure 6.2

Midlands example of geo-ecological succession.

soils), leaving the savanna ecosystem type on the oldest local surface. In the subsequent stages, and perturbations within the cycle (Stages 5 to 8), savanna is the oldest system on the oldest local geomorphic surfaces, although these hill substrates are undergoing sheetwash, and forest is the newest, invading on the youngest eroding surfaces of stream banks and valley deposits which have the best water relations. Where dense dendritic drainage develops on hill and valley sides, riverine forest/thicket can occupy as much area as the intervening savanna cover.

Except for the old planation remnants, the stage of old age is not attained anywhere in the Midlands, although locally in some tributary basins exposure of resistant rock, a structural barrier, has held up valley incision and aggradation has occurred upstream from these temporary base-levels. In such areas, as exemplified by the Burumazi and Mudicapinda tributaries of the Nhandue River, northwest of Gorongosa Mountain, a low polyconvex topography has developed as valley-widening erosion has outpaced valley-deepening. Here the duplex sands, and other planation substrates, have been stripped off and redeposited on slip-off slopes of meander lobes, and as lateral valley side fans. Extensive confluence deposits occur where lesser order streams are dammed up by floods of larger streams; all these sediments are invaded by dry forest/thicket cover. When the temporary base-level is incised, rejuvenation of the aggraded sector will occur resulting in the steep valley and spur topography typical of the Midlands, and the forest/thicket system on the valley sediments will be eliminated with their substrates. However, the riverine type will replace it, albeit as a narrow strip on each bank.

Dambo development does not seem to be determined solely by attainment of grade or the occurrence of a temporary base level. Many dambos on the Midland slopes above the Rift Valley in the southwest of the Park occur in valley heads with flat floors sloping downward to 10 or 15 degrees. These appear to have developed by one or a combination of factors. Either concentrated flow has been disrupted or reduced by beheading from more active tributaries and headward erosion, or phases of excessive mass wasting and sheet flow aggrade the upper drainage sources. In both cases un-concentrated or lessened flow has resulted in build up of sediments due to incomplete transportation and its fixation by hygrophilous grasses. The relatively steep down-valley gradient of these dambos appear to be as a result of sheetwash as shown by the high pedestaled grass tufts on the dambo floor. Where these dambos are incised by ascending nickpoints, the original 'V 'or 'U' valley shape is exhumed. Thus phases of degradation and aggredation in valley heads could also be related to pluvial and interpluvial influences quite apart from the presence or absence of temporary base levels. Such dambos may be able to lower, and thus narrow, their floors by sheetwash alone if they are sufficiently protected by their grasscover from nickpoint development. Leopold et al. (1964) point out that since an increase of precipitation, or canalizing of flow, will trench valley alluvium if sediment load is reduced, either climatic or geomorphic factors can change the relation of sediment load to discharge which is responsible for changes in depositional and scouring phases. Thus planation, which is a function of sediment-loaded waterflow and base-level restriction, is changed to trenching under the same discharge when sediment is reduced and the base-level lowered (Leopold et al. 1964). Removal of plant cover on hill slopes by cultivators can alter this trend in a relatively short time as shown by examples from the Midlands, where many incised rivers and low order streams have choked or braided courses filled by sheet and rill erosion of the valley heads. This example of a man-activated cause of deposition on hillslopes shows that steep dambo floors can be formed at the heads of streams by an excess of available detritus moved during one or two rainstorms of high intensity. The new sediments are fixed by hygrophilous grasses and further sheetwash sediment is trapped by the cover. Under natural conditions of dambo formation at the heads of streams, a similar situation would seem to be required where ground-cover was relatively sparse on an excess of mass-wasted material moved by an intense rainstorm occurrence of short duration. In other sites, clearing of cover for cultivation initiates nickpoints and causes deep donga erosion and heavy sedimentation down-river, smothering crops and habitation. Careless land use activities, including overstocking, accelerate natural processes and can initiate new cycles of erosion.

The process of headward erosion and back-wearing of slopes giving rise to isolated mesa, butte and koppie remnants on the one hand, and exhumation of hard massive rock cores, such as Bornhardt or domed inselbergs, by truncation of a deeply weathered regolith (Thomas 1974), on the other, produces outcrop relics and new outcrop surfaces respectively. The difference in origin and evolution of these two inselberg types has far reaching implications in the dynamics of biogeographic relations. The remnants from back-wearing processes present disjunct relics of systems which were once far more extensive and continuous expanses associated with one of the landscape facets, such as escarpment or riverine forest, and grasslands or savanna of the oldest planation surface on the summits. In other situations, forest is on the oldest, highest surface and is replaced by savannoid systems on the back-wearing slopes and pediments as shown in Fig. 6.2 This represents a sequence of fragmentation, and eventually extinction with elimination of the topographic remnants. The second outcrop type becomes larger in surface area with each erosion cycle exhuming further resistant rock which could lead to fragmentation of other systems, and coalescence and predominance of the outcrop surfaces. However the Bornhardt inselberg type also undergoes weathering and erosion as traced by Thomas (1974).

The effectiveness of prominences in trapping rainfall to their precincts is evinced by the occurrence of forest/thicket on easterly and southerly aspects, facing moisture-bearing winds, and the contrasting insolation and weathering regimes of these moister aspects with the drier northerly and westerly aspects. Small outcrops support forest/thicket, due primarily to deep percolation and better retention of rainwater along joints and fissures compared to the surrounding plains. Any advantage afforded this cover from fire or the concentration of weathered minerals in the vicinity of outcrops is of secondary importance.

The deep northwest–southeast valleys of the main rivers crossing the Midlands, and their tributaries transverse to this, provide a dense criss-cross pattern of moister poleward and eastward facing slopes and drier equator-ward and west facing slopes. This kind of slope differentiation contrasts with that of the adjacent Rift plains and the broad, flatter interfluve areas on the Midlands where there is no aspect differentiation except of the microscale

From the above account it may be thought that the replacement of a ‘simple’ plainsland landscape by a deeply incised ‘complex’ mature hill and valley landscape, as exemplified by the Midlands, implies equal or parallel diversification of ecosystems because of the exposure of new land facets and aspect differentiation. The Midlands example, however, shows that ecosystem diversity is not necessarily synonymous with, or a function of, topographic diversification when all substrates are derived from a single lithology. The Midlands are covered predominantly by one ecosystem, a closed canopied miombo savanna, whose monotony is relieved only by forest/thicket strips along stream banks and around the bases of occasional rock outcrops. In the Gorongosa–Cheringoma transect, the Midlands support the poorest diversity of ecosystems and the richest occur on the Rift Valley floor and the coast—both plainsland alluvial fan surfaces.

Rift Valley

The Rift Valley plains have been formed predominantly by sequences of alluvial fan deposits from rivers debouching from the high ground on both sides of the trough. The sorting and differential emplacement of coarse and fine sediments, in and between fans respectively, has given rise to the two major features of the Rift floor: (a) sandy distributary channel fillings now supporting forest/thicket, and (b) slack basins or flats of fine clays which form the extensive open floodplain grasslands (Fig. 6.4). The slacks are composed of the finer flood sediments, deposited in slack water or shallow lacustrine conditions formed by ponded flood waters. The deposits between fan distributaries, formed by braided drainage with bars and splays, are either of mixed sediments, sandy clays, silt loams and fine sands supporting savannas, or of fine clay in interdistributary slacks.

The terminology used here is basically that given in the introductory textbooks on geomorphology by Lobeck (1939, Ch. 7) and Thornbury (1954, Ch. 7). More comprehensive treatments of fluvial processes are given by Leopold et al. (1964) and Chorley (1969). In dealing with fluvial deposition, confusion can result from the variety of synonyms used for floodplain features. The Urema Basin sector of the Rift Trough does not conform to the classic or typical floodplain, which is formed by the lateral swinging of a river passing through an area of low relief, exemplified by the adjacent lower Pungue River and the Zambezi Delta. As noted in Section 5.6 and above, these floodplains have instead been formed by a process of centripetal drainage from the sides of the trough, the present floodplain surfaces comprising the irregularly shaped, shallow basins formed between the outer edges of alluvial fans. Terms such as backswamp, swale, slough, slade or slack could be used for these ‘fan front’ deposits. The term slack is preferred as it most accurately describes a situation of ponded floodwaters. Apart from this basic difference in origin, all features typical of floodplains occur on the Rift floor.

It is likely that with the original formation of the Rift Valley, the Zambezi River, or at least its floodwaters, contributed in large measure to the build up of the alluvium

RIGHT: Figure 6.3

Evolution of Rift Valley systems by fluvio-lacustrine processes.

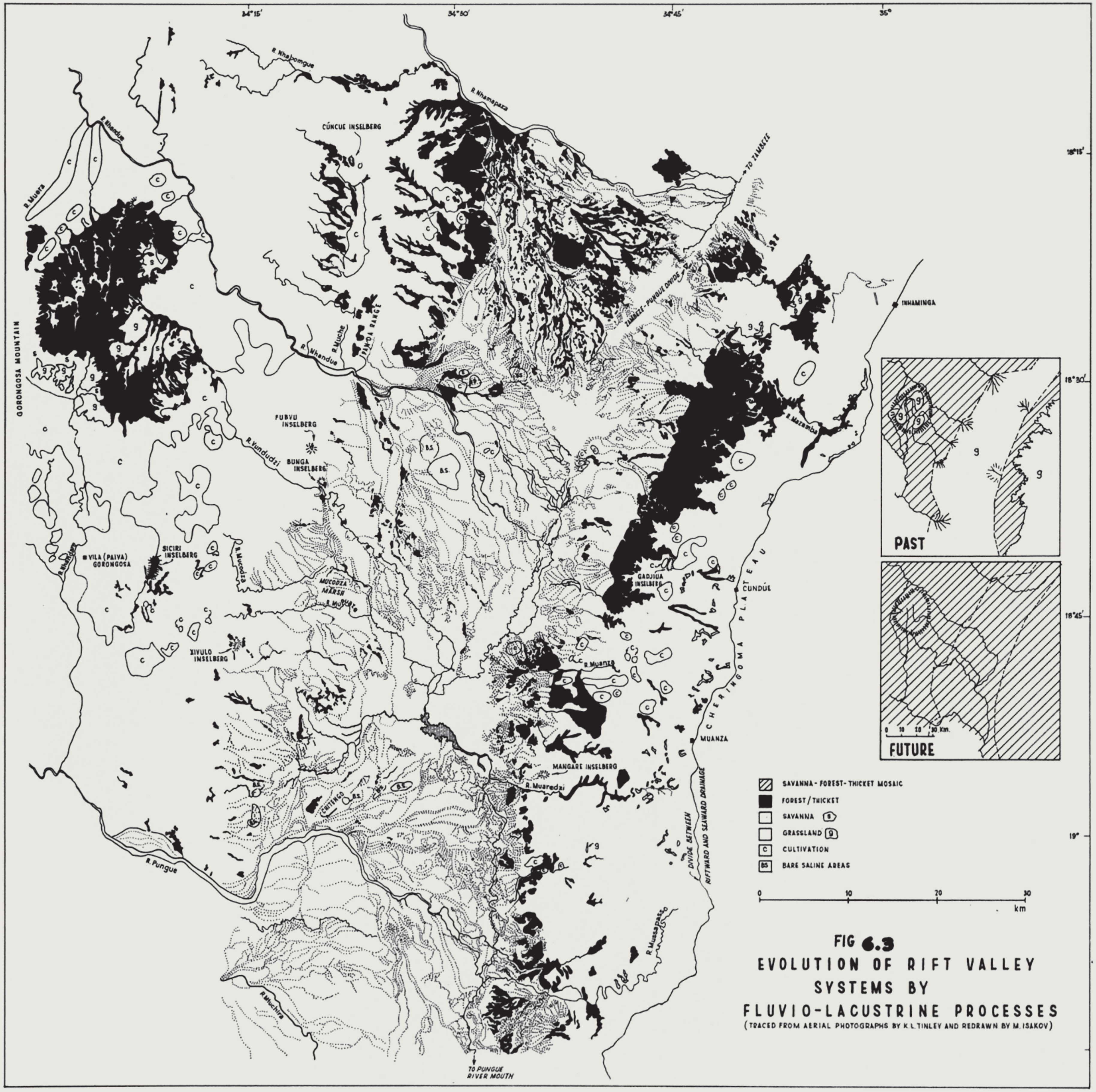


FIG 6.3
EVOLUTION OF RIFT VALLEY SYSTEMS BY FLUVIO-LACUSTRINE PROCESSES
(TRACED FROM AERIAL PHOTOGRAPHS BY K.L. TINLEY AND REDRAWN BY M. ISAKOV)

underlying the present Rift Valley plains. One confluent floodplain system probably existed from the lower Chire River to the Buzi, and possibly the Save River. This subsequent drainage was then pinched off at intervals by the growth of alluvial fan deposits derived from both sides of the trough, especially from the larger rivers, which originate inland. Of these, the seasonal Nhamapaza River built up sufficient alluvium across the Rift floor to form a low divide 59 m above sea level, thus effectively separating direct confluence of Zambezi and Pungue waters.

The Nhamapaza, Nhandue, and Pungue rivers, of which only the last is perennial, have formed the most extensive fan areas reaching across almost to the base of the Cheringoma Plateau, as is clearly shown in Fig. 6.3, and becoming confluent in parts with those formed by the inface drainage of the cuesta. That the building of fans is a function of flood periods and sediment availability in the catchment is well exemplified by the seasonal Nhamapaza River, which has formed by far the largest alluvial fan area, only the southern part of which is shown in Fig. 6.3.
Unlike the Pungue and Nhandue, a large part of the Nhamapaza River's catchment area is on extremely friable Continental Cretaceous argillaceous sandstones.

Alluvial fans grow by the repeated lateral shifting of distributary streams as their courses become filled with coarser sandy sediments, to above the level of the surrounding fan. This and their blockage by alluvial deposits, such as splays and bars from colliding flows causes streams to spill over and follow lower courses in the fan surface. All the sediments are water-laid, and excessive seasonal flooding would have maintained floodplain grassland and marshes over the entire Rift floor. By this means, channel fill deposits are aggraded to above excessive flooding, and the lower interdistributary slacks formed by over-bank deposits during floods become the new distributary courses. Distributary courses aggraded to above the general level of their fans are thus the first surface available above flooding for invasion by hill building termites and woody plants. In time, the main river is closed off on all sides by its own alluvial deposits and at this stage floods break through along the lowest part of the fan, trenching into the fan deposits. Once trenching occurs, the braided of anastomosing fan drainage becomes fossil, left high and dry above the reach of river flooding although some of the old un-filled abandoned courses may flow briefly during exceptional floods. The anastomosing channels of braided drainage are separated by channel bar deposits which grow upward, and like the Ievees, can become some of the first surfaces available for woody plant invasion. All these processes are clearly portrayed on the Rift floor.

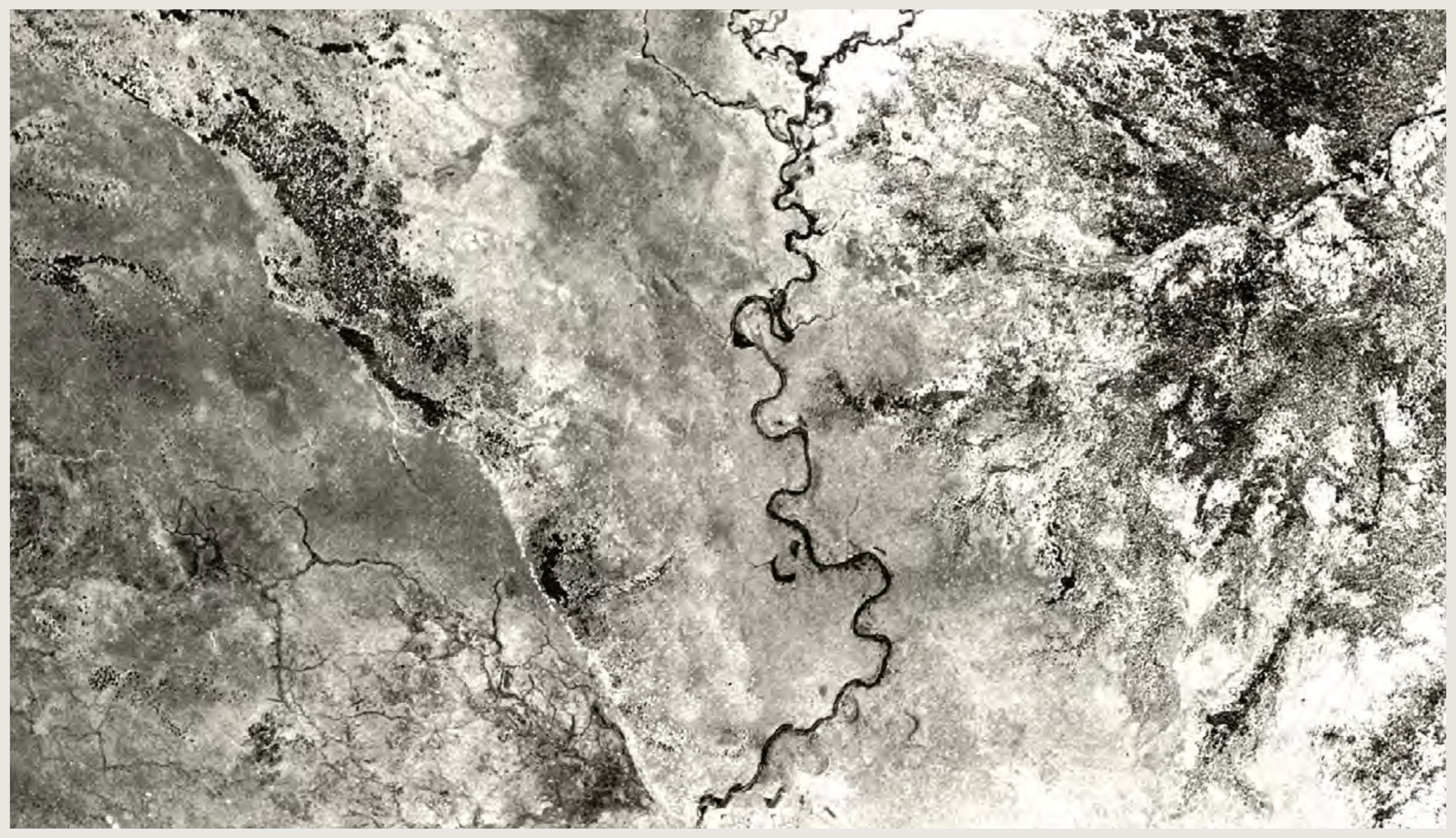
All the fans in the study area have been trenched, and modern sediments are deposited at the junction of the canalized river courses with the major interfan Urema slack, where new fan and slack material is being superimposed over the old in front of the earlier fans. New deposits are also occurring within the slack basin at the head of the Urema Lake, gradually filling in the shallows adjoining the converging delta of the Vundudzi–Mucombezi rivers. The Urema slack basin has also undergone deep drainage incision to over 3 m below the adjacent floodplain surfaces, and active headward donga erosion is in the process of destroying all other slacks or floodplain surfaces.

The extremely small modern fan sediments being formed indicate that the rivers which built the original fan and slack floodplain system either had much larger discharges and sediment loads, or similar discharges as present but with higher sediment load. Leopold and his co-workers (1964, Ch. 11) discuss the relation between rainfall vegetative cover and sediment yield and suggest that in moist areas an increase in precipitation would result in a more complete vegetative cover, thus cutting down the sediment yield, resulting in incision. This implies that lower rainfall with sparser plant cover would lead to greater sediment loads and thus aggradation, but they remark that donga cutting seems to be generally related to aridity (p. 453). Their data do not allow for a definitive answer as equal and opposite effects occur under different conditions of cover and substrate friability in different areas with the same rainfall regime.

The typical floodplain features of levees, splays, meander scrolls, cut-off meanders and backswamps, developed by a meandering river system is shown by the Vundudzi, Mucombezi, Urema and Pungue Rivers. In traversing a flat area, moving water is forced into a deranged course by the irregularities of microrelief, and, by deposition on the inside of curves and erosion of the outside, indefinite drainage is transformed into meanders (Lobeck 1939, p. 227). As the river incises its course, undercutting of the outer curve increases as the slip-off slope deposits grow on the inside of curves, and these processes lead to narrowing of the neck between loops until the river cuts across the neck, shortening the river course and steepening the local gradient. Growth of the pointbar deposits enlarges the meander at the same time as the neck is being eroded. In this way meanders are continually changing their positions, migrating downstream, and leaving

RIGHT:

Typical juxtaposed pattern of fan slack alluviocatena sequences on the Urema Rift Valley floor.



behind cut-off meanders and meander scrolls as evidence of their previous positions (Lobeck 1939; Thornbury 1954).

The deposits formed on the slip-off slope, referred to as meander scrolls or point bars, are typically an arcuate series of alternating ridges and shallow troughs clearly defined by wooded cover on the rises, alternating with grass in the depressions. Levees are formed along the immediate river banks by overbank deposits during floods and, where these are breached, splay deposits are formed by coarser channel fill sediments. The finer material is deposited away from the river in backswamps when the levees are over-topped.

Breached levees are self-sealing by the plug of splay material, if the backswamps are flooded at the time. Where backswamps are drained by incised flood breaches lower down in the course, the splays are cut through and new river channels are formed across the backswamps when they are the lowest part of the floodplain profile. This entire sequence is shown in the Dingedinge tract at the confluence of the Urema and Pungue Rivers (Fig. 10.3). In this example, the Urema has incised its course lower than

LEFT:

Typical juxtaposed pattern of fan slack alluviocatena sequences on the Urema Rift Valley floor—annotated.

the braided Pungue riverbed upstream from their junction, and the inner levees on both rivers have been breached and deeply incised. Through these breaks the Pungue River has formed a new course which cuts across the confluence marshes, and is in the process of rapidly eroding and drying them out. Primary stabilizers of splay deposits are reeds, followed by woody plants.

The distribution of vegetation on the floodplains reflects conspicuously every nuance of deposition and erosion. In particular, it reflects those processes which alter the degree of flooding or waterlogging either by the differential sorting and deposition of sediments, providing a micro-relief of lower and higher surfaces, i.e. by blockage or erosion of alluvial plugs. Thus, the grassland ecosystem and associated grassy marsh areas occur on the following flat, faintly sloping, or faintly concave surfaces: fanfront or interfan slacks, interdistributary slacks, backswamps, abandoned channel fillings, point bar swales or sloughs, and splays. All these are subject to the rule of effective flooding or waterlogging for the maintenance of hygrophilous grasslands. Where this is lost the grasslands are invaded by the two woody ecosystem types. All the faintly convex surfaces such as levees, fan and splay channel bars, point bar ridges, floodplain terraces, and incised surfaces are invaded by one or both of the woody ecosystems. As on emergent fan surfaces, hill-building termites invade all microconvex surfaces, whether depositional, or exposed by increase of drainage. The termite hills are typically the first surfaces to be colonized by woody plants, even on abandoned aggraded river courses, and these island thickets are in many areas the nuclei for woody plant invasion of the intervening ground when flooding or waterlogging is reduced to a tolerable state. The intervening surfaces are also invaded from the apex of fans and the higher colluvial filled margins of the Rift.

Substrate differentiation by sedimentary processes alone has resulted in a complex of alluvio-catenas, mosaics, overlap and interdigitation, made clear by the distinctive vegetation they support. Superimposed on this is the overriding primary control of flooding, the influence of which is directed by microrelief and changes in drainage. As pointed out in the sections on soil (5.7) and soil moisture balance (5.8), excessive flooding or waterlogging results in a hygrophilous grassland made up of a large variety of plant associations, themselves related to soil properties, which in turn are affected by microrelief and duration of

EXPLANATORY NOTES FOR Fig. 6.4

(1) A primary freshwater/brak (brackish) marshland stage in the evolution of Rift Valley communities, characterised by hippo and reedbuck as indicator species of the prevalent habitat (Holocene?). This stage probably followed a shallow sea stage (early Pleistocene?) which must have poured in with the foundering of the 40 Km broad Rift Valley trench. The present lowest part of the Urema basin is only 12 m above present sea level. The alluvial fans shown are the oldest as judged from air photo interpretation and ground study correlations.

At this stage diversity would have been extremely low, despite the possibility of a mosaic of waterlogged grassland types, and an extraordinarily high wild ungulate biomass of a few species as exemplified by the present Zambezi Delta floodplains and marshlands at Marromeu.

(2) An intermediate stage to the present, with the addition of sable antelope to indicate an extensive dambo-woodland mosaic on the aggraded fan surfaces, increasing plant and animal diversity related to the progressive array of substrates being exposed above permanent waterlogging. Note differential growth of alluvial fans from the two sides of the Rift Valley and the pinching off of the Rift floor marshland drainage by their gradual coalescence.

(3) The present stage with maximal substrate, habitat, and biotic diversity, characterised by the addition of impala, bushbuck, and forest mini-ungulates as habitat indicator species. The drainage and erosion of floodplains and slacks, and extensive invasion by woody plants throughout most of these surfaces indicates the probable future stage of the Rift floor systems.

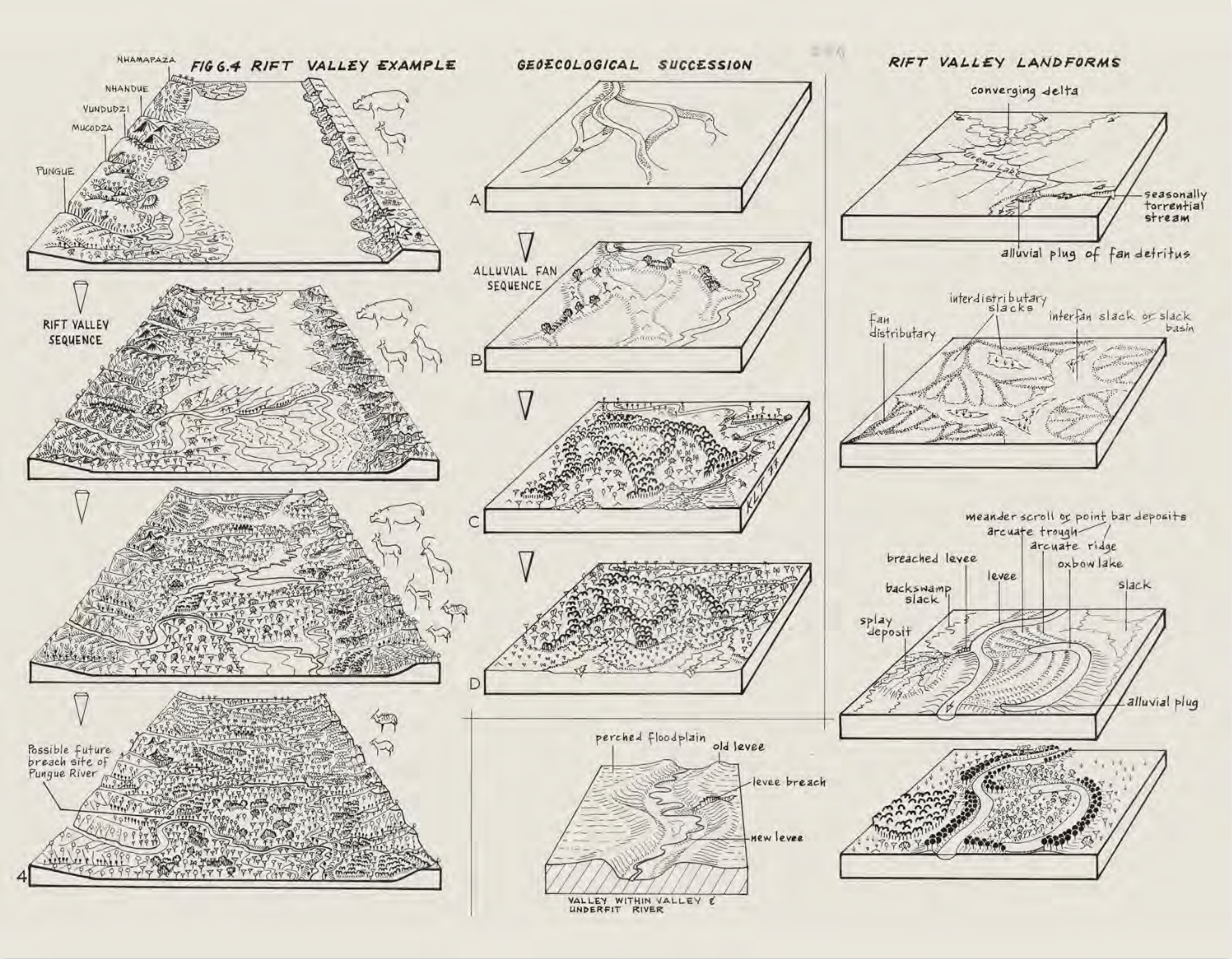
(4) Probable future stage within several decades, when floodplain systems are on the verge of extinction by occlusion of a prevalent cover of savanna, thicket and dry forest mosaic, the latter remaining confined to the duplex sand deposits. Once these have been truncated, dry forest will become extinct and be replaced by scrubby savanna or thicket. This stage indicates a return to a relatively homogenous physiognomy and structure, this time of woody plant dominance. The stages following this will probably remain scrub-dominated as valley side erosion of dongas eat back small scarps and pediments in the alluvia, and slack areas are ever diminishing (see examples A to D of the successional evolution of an alluvial fan).

(A) Anastomosis of distributary courses and of fines deposited as overbank slack deposits. The distributary courses aggraded by coarser sand deposits. First colonization on the aggraded courses by *Macrotermes* hill-building termites, providing the first permanent surfaces for woody plants above excessive waterlogging. Channel courses changed by being blocked off (plugged) by their own bar deposits.

(B) Savanna, thicket and/or forest woody initials on the termite hills, from which the intervening aggraded (convex) and dried out distributary course surfaces are colonized. The main distributaries are forced to break through their own levees due to the bar deposits, and flow along the slacks which are the lowest surfaces in the fan sequence.

(C) Total colonization of all convex surfaces as effective flooding is confined to the lower surfaces and is of progressively shorter duration as these slacks and basins are eroded (C and D).

(D) Lateral coalescence of microvalley sides formed by migrating nickpoints to form a stepped sequence of pediments and microscarps with even-aged woody invasion of each and the progressive contraction of slack communities to the confines of the stream beds.



LEFT: Figure 6.4

Rift Valley example of geo-ecological succession.

flooding. Progressive reduction in excessive soil moisture is the release to habitat diversification, and it is this factor alone that permits invasion of woody plants, the composition and successional tendencies of which express the climo-edaphic properties and changes in these relationships.

Microrelief is developed by disparate vertical and lateral accretion of sediments and by animal activity. Deposits laid by exceptional floods, or through gradual upward growth, are put out of reach of prolonged flooding allowing the invasion of woody plants. Once established, many species can withstand floodwaters of several weeks duration. Levees are an example of surfaces that grow upward, away from flooding and become exposed to erosion and woody invasion. Simultaneously, these irregularities are accentuated by coactive changes in local drainage due to the fluvial processes themselves and their erosion by changing base levels.

In flat, poorly drained terrain, small surface irregularities can have far reaching effects on drainage, and thus on succession and primary productivity. Water movement is, to begin with, hindered by gravity resistance and the edaphic properties of the surface. A faintly concave surface of any dimension forms a marsh covered with hygrophilous grasses which provide green pasture deep into the winter dry season. A gap or furrow, as little as 10 cm depth (such as a hippo path for example), in the sill rimming such a surface, effectively ‘pulls the plug out’ and transforms these marsh surfaces into dry land systems which are then invaded by savanna. Many of these potentially long lasting marsh and pan areas are easily restored by the simple expedient of replugging the outlet with large clods of sod held together by the turf grass *Cynodon dactylon*.

The fundamental function of microrelief and substrate as the determinant of plant zonation in poorly drained areas of low relief is strikingly demonstrated in marshes and estuaries where centimeter differences in level will determine whether a surface dries quickly or forms a drainage channel (e.g. Chapman 1961, 1964; Thorn 1967; Thorn et al. 1975).

Like hill-building termites, hippo are potent geomorphic agents of floodplain change due to their path making habit. Traditionally used paths radiate out from lake and river waters to grazing, and link otherwise discontinuous depressions. During the rains and flood period when sods are soft, constant use of paths makes them into deep channels with levees of mud pushed up on either side. Whilst aiding the dispersal of floodwaters these paths are also the beginning of the end for marshes and pans as rain and floodwater are immediately lost with the ebb. The junctions of deep footpaths made in soft alluvium with hard ground form nickpoints and initiate headward gully erosion. On a microscale the classic (Leopold et al 1964, pp. 448-453) cut-and-fill chain of migrating nickpoints are developed in the canalized footpaths. A deep bare section is developed below the undercut and slumping nick, and lower down deposition of this material forms a small fan within the channel, which is then fixed by grass. The crest of the levee, formed by the animals’ movement when the alluvium is soft, and the sides of the channels are bare eroding surfaces and thus extremely xeric. The radial drainage incision of the floodplains surrounding the Urema Lake is shown clearly on air photographs, and a series of gullies is a feature of most paths. These paths not only canalize rainfall but also rapidly drain off this source of moisture. On a yet smaller scale, faint undulations, as of gilgai soils, on the same floodplain soil determine whether the same species of grass remains green or dries out fast, and large tufted grasses in drainage lines pedicelled by sheet erosion provide sites for woody plant invasion. These features re-emphasize the importance of soil moisture balance at all levels from the micro- to the macro-scale.

A characteristic indicator of new or modified surfaces made available to invasion in the past and more recently, by geomorphic or like action such as cultivation, overstocking, or fire is the presence of even-aged or quasi-even-aged stands of woody plants. New surfaces are invaded according to circumstances of the seasonal or episodic availability and dispersal of plant propagules. On any surface subject to flood and ebb movements of water, propagules are concentrated along contour and microrelief by stillstand, swash and wind action. Patches of even-aged scrub in a dambo or vlei indicate either that the plug has been pulled out of the system, often discernable only after fires have temporarily removed the grass cover to expose the small headward incision responsible, or new sediment has been deposited to above the level of excessive inundation.

In arid savannas, episodic woody invasion of seasonal dambos and vleis may occur during a series of consecutively dry years and be killed off by subsequent exceptionally wet periods. Here soil moisture balance is altered solely by the swing of climate, elsewhere simulated by the cut and fill of geomorphic processes. On almost any landform, sequences of different even-aged stands indicate successive erosion, deposition or altered soil moisture balance. This phenomenon is particularly well illustrated in the study area by the zonation of acacia and palm in even-aged invasions, related to lowering and stillstand of flood regimes in the Urema slack basin. The oldest and tallest stands occur on the highest periphery of the slack basin, with younger groups at successively lower levels toward the present lake area. Similar evidence on many erosional and depositional features of other landforms and physiographic situations testify to the relative ages of surfaces and the sequence or direction of succession. This feature is exhibited by components of all biomes and ecosystems on the subcontinent, particular by fynbos, subdesert dwarf-shrub, acacia, mopane, palm, miombo, mangrove, thicket and forest initials.

The periphery of discontinuous concave surfaces form the temporary base level to each individual depression, and where these are linked by drainage lines the outlet of each depression is its temporary base level. The many Rift Valley (and coast plain) surfaces, all at slightly different levels, are thus controlled by a multiplicity of temporary base levels. The duration of temporary base levels and changes in local moisture input are two salient factors in floodplain ecosystems.

On the macroscale, evolution of systems on the Rift floor has been directed by the interplay of the major rivers entering the Rift from the hinterland. The large alluvial fans of the Nhamapaza, Nhandue, and Pungue, traced from aerial photographs, show clearly in Fig. 6.4. The Urema Lake was probably of much greater extent in the past, fed directly by the Pungue River's now abandoned distributaries. Pungue waters entered the Urema slack basin at different times from the west and along the southern margins. The evidence of the more recent abandoned distributaries shows that Pungue water flowed into the lake at its present exit, at the site of the present alluvial plug formed by the Muaredzi Stream from the Cheringoma Plateau.

The area of the present alluvial plug appears to have been the site of a temporary base level sill during most, if not all, of the Urema slack basin's development. The direction of abandoned distributaries and narrowed lower end of the Urema Lake show that flood sediments deposited by the Pungue River also contributed to forming the convexity of the critical height, now dominated by the Muaredzi Stream. Only when the Urema Lake was filled, did overflow push past the sediment plug into the lower Urema River. This parallels the situation today in the Banhine basin in Gazaland, which is also partially endoreic; outflow down the Changane River only being affected after the basin is filled by the upper Changane and other seasonal drainage. The much larger meandering valley of the Urema River must have been formed at the time when both the Pungue and Nhamapaza Rivers entered the Urema slack basin. Today the underfit, tightly meandering Urema River has incised into the old broader valley (Fig. 6.4 bottom middle diagram). As channel fill and plug deposits sealed off the plug, distributaries of the Pungue River became almost completely separated from the Urema Basin. In the north of the Rift Trough the Nhamapaza River once flowed into the Urema, but it too has blocked itself off by its own deposits and now drains north along the Rift floor to the Zambezi River.

The Urema slack basin, therefore, developed under regimes of much greater discharge and flooding and was beheaded by fluvial processes of deposition and gullying. This has left the Nhandue River as the largest, though seasonal, river entering the basin; the Mucodza and Vundudzi derived directly from Gorongosa Mountain; and the series of small seasonal streams from the Cheringoma Plateau as the sole contributors to the present basin. Of these only the small Vundudzi River is perennial because it rises on the upper catchment of Gorongosa Mountain. This massive cut of water input and sediment load has resulted in the establishment of a cycle of incision affecting the dynamics of the remaining floodplains, particularly through the processes noted above. The remaining floodplains of the Urema slack basin are all deeply incised and are now out of reach of the lake's present flood zone (Fig. 5.11). These surfaces are now perched above the gullied drainage and are thus under an inexorable tendency to change, as they are actually relic systems poised in time and space by the resistance of flatness. On every side these surfaces are being invaded by woody plants of the other two eco-system types and they can only continue to be called floodplain grasslands because the saplings have not yet grown above the grass canopy. In a relatively short time, possibly within twenty years, only part of the lower flood zone of the Urema Lake will remain pure grassland.

Figure 6.4 shows the past, present, and probable future of Rift Valley ecosystem types as shown by present evidence traced through this section. The extinction of floodplain grasslands and their conversion to savanna grasslands, and finally to a thicket-savanna mosaic, is a natural consequence of drainage evolution on the plains, i.e. the lechwe ecosystem is replaced by the impala ecosystem, which in turn will be increasingly invaded by the bushbuck/nyala ecosystem.

The Urema floodplains are the nucleus of the Gorongosa ecosystem and their survival is dependent on two fundamental factors: the water from the mountain, and maintenance of the temporary base level at the outlet of the lake formed by the Muaredzi alluvial plug. The efficacy of the sill formed by the alluvial plug of the Muaredzi stream deposits at its right angle junction with the Urema, in damming up the Urema slack basin, depends on adequate annual sediment replacement to fill the cut made through it by the water running out of the lake and accentuated by hippo movement.

The lowest part of the Muaredzi River is an incised course cut through a channel fan that is formed upstream where the cuesta slopes meet the Rift floor. Headward incision of the lowest part of the course has not yet cut through the well-defined river course 2.5 km upstream from the plug. Inspection of this site shows the formation of a new fan, mostly of sand, which has choked up the incised stream course. Thus most of the sediment is lost to the alluvial plug because it is being deposited further upstream. There is evidence that seasonal road maintenance activities across the Muaredzi course just above the new fan are in part, if not wholly, responsible for these depositional changes. The high river banks just above the fan site are cut down and used as infill to build up a causeway across the sandy riverbed. This river crossing has been repeatedly repaired over a period of some 20 years. With the first rains, build-up of sediments behind the causeway results in breaching of the whole blockage and this excessive load of detritus is dropped at the break in slope some 200 m downstream.

These examples of geo-ecological relations in a fluvio-Iacustrine system emphasize the importance of microrelief changes in controlling geomorphic processes, the ecologic response, and co-relations in the evolution of floodplain landscapes. The poorer drained a substrate, the more important the smallest differences in microrelief, but these lose their significance once the area becomes well drained. Under the former regime the preceding degree of saturation from rain or previous flooding has an important influence on the extent of subsequent inundations.

On the Rift Valley floor, plant succession, and thus change in habitats and their animal components, is primarily determined by edaphic and landform changes wrought by geomorphic processes of accretion and erosion. This induces a continual response to ecosystem and habitat change in dynamic equilibrium with the geomorphic influences, and plant succession within each system occurs during the varying stages of relative quiescence. Substrate diversity and the superimposed control of changing flood levels are thus the determinants of ecosystems and ecotone diversity on the Rift Valley floor. A topographically homogeneous plainsland thus supports a homogeneous ecosystem type at the two ends of its cyclical succession (Fig.6.4).

Initially, there is a grassland ecosystem type in which excessive flooding is the overriding control, well exemplified in the transect of the Cheringoma Coast plain. This is followed by a stage of small scale dissection and incision of temporary base levels reducing the duration of flooding and waterlogging. This allows for the full expression of the soil properties of each substrate in their influence on the kind and variety of plant cover they support. The Rift floor sector of the ecosystem is at this intermediate stage when ecosystem diversity is greatest. The final stage of floodplain dissection, when runoff is greatest, will be a relatively homogeneous cover comprising a mosaic of the other two woody ecosystem types with a predominance of forest/thicket (Figs 6.3 and 6.4), paralleling the situation on the Midlands. Further erosion and sedimentation of valley floors will again increase diversity, followed by a decrease when the valley sides are eliminated and well drained low relief again predominates.

Cheringoma Plateau

The present-day form and cover of the cuesta has been derived from an original broad waterlogged grass plain forming an apron, or piedmont, in front of the interior oldland and subsequently separated from this by the Rift Valley down-faulting. Isolated as a remnant block, the crest of the newly exposed scarp slopes would have formed the new drainage divide along the top of the plateau. Differential erosion of the cuesta scarp and dipslope resulted in the eastward shift of the divide, beheading further all the seaward drainage. The same process continues today and is most active in the central and southern parts.

After separation by trough faulting, the entire dipslope area will have remained predominantly a waterlogged dambo grassland with termite hills as the first invaders of all convex surfaces. The termite hills would have been primary sites of woody plant invasion, unless suitable vleis with flowing water had already provided substrates for swamp forest patches. The Riftward inface would have been invaded by both forest and savanna ecosystem types. Eventually all convex surfaces, including the major divide and interdambo surfaces, were invaded by miombo and forest. The termite hills were major nuclei for invasion of intervening terrain as the soils became better drained. While this process continues today, a more striking process of landsurfaces and ecosystems replacement is taking place on the cuesta where the duplex sands are being rapidly stripped off by natural headward erosion.

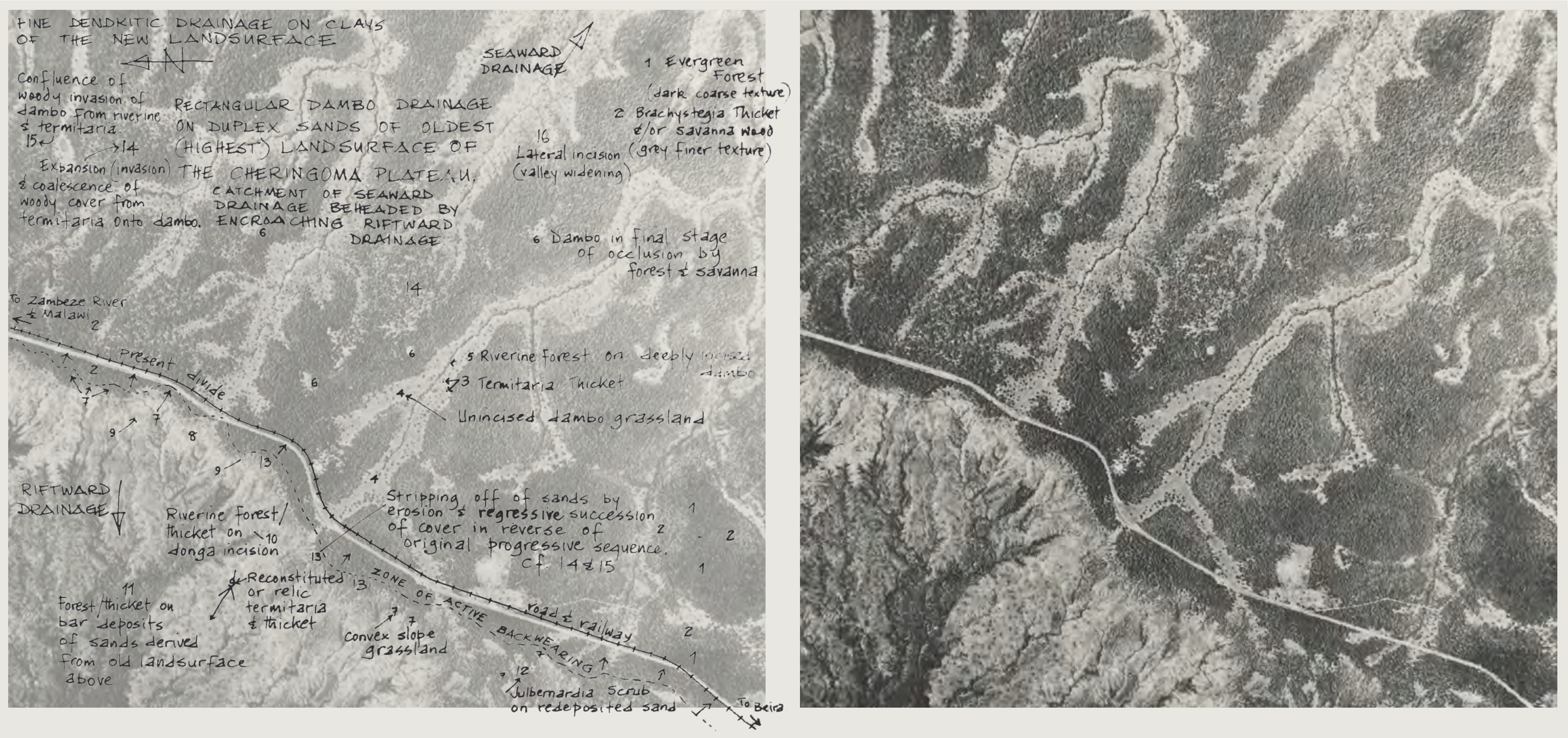
Due to the exposure of alternating bands of hard and soft sedimentary rock, the Riftward inface of the cuesta has been eroded into a series of steps; the hard quartzitic limestones forming a major scarp crest. Above this, another scarp crest is formed by the convex slope of eroding duplex sands and latosols. In the northern and central sectors of the cuesta inface, where hard rock exposures predominate, a fretwork of deep canyon-like ravines have cut back from the Rift into the inface leaving hanging tributary valleys and waterfalls along their sides. The edges of the ravines, their nickpoints, are held up by the white to pinkish-white calcareous sandstone of the Cheringoma Formation. The sandstone weathers into overhangs and steep talus cones are formed below the cliffs. Where the original dambo surface remains on the uppermost sands, tall closed miombo savannas mosaic with dambo grasslands, most of which are now relic in the heads of the inface drainage. Near the ravines these sands and their cover have been stripped off leaving skeletal soils over the sandstone sheets where low scrub now predominates. On the margins of the ravines a band of pure grassland is formed by seasonal lateral ooze of rain water. Where this hard sandstone has been removed by erosion, on the crest of the slopes above the Rift, glauconitic sandstones of the Cretaceous have been exposed, on which an impervious marl soil developed, supporting pure grassland. These now occur as remnants on the rounded landforms of inter-ravine spurs.

By contrast, the weakly cemented calcic-argillaceous sandstone of the Mazamba Formation is exposed and deeply weathered in the central upper catchment of the dip slope and on the inface of the southern end of the cuesta. In these areas where the overlying sands and dambos are being stripped off they are replaced by a badlands topography. It is here where the most pronounced spatial replacement of surfaces and systems is taking place in the transect.

The uppermost sands are a mosaic of deep latosols and duplex sands (with an impervious clay at 1 m to 2 m depth), which mantle the deeply weathered sandy clay material on which badlands develop when they are exposed. On these sands are broadly meandered dambos covered in grass and dotted with thicket islands on termite hills. On the broad convex interfluves are tall closed miombo savanna, and in many areas this has been invaded and replaced by evergreen forest. On air photographs the change in leaf texture from miombo to forest is clearly defined. Thus the savanna ecosystem-type forms a band or zone parallel to the adjacent dambo grassland. Most of the dambos are in the process of stream incision some of which have reached headward to the present divide. These streams which are underfit and tightly meandered are initiating a process of valley within valley development. This, and the beheading of dambo drainage by inface scarp retreat and tributary capture by strong headward eroding streams, has resulted in the drying out and complete obliteration of many dambos by savanna and forest invasion.

Eating into this sand-dambo system, outlined above, is the active headward erosion of deeply incised drainage on the underlying sandy clays. The steeply undulating badlands topography so formed has local relief of a 100 m separating the interfluve crests and the incised stream bottoms. Retreat of the overlying ecosystem occurs along valley sides and around valley heads where a dense dendritic drainage is replacing the broad dambo drainage above. Headward retreat of the friable convex scarp is thus increasing the badlands topography and reducing and eliminating all the upper systems. A drastic immediate result of this is the extinction of perennial vleis and dambos. Where the headwaters of the Musappaso and Musambezl streams abut, for example, interfluve spurs supporting the upper systems have become isolated and are now on their way to being eliminated.

The convex slope of the retreating scarp formed on the sand-clay contact forms new waterlogged surface and here new dambo-type grasslands form. The eroded material is deposited lower down the slope where it is fixed by scrubby miombo or dambo margin trees, which are typical of partially waterlogged soils. The mid and upper courses of the seaward drainage, particularly the Sanga, Zuni, Chinizua and Sambazo rivers, have cut deep valleys in which aggraded flat valley floors have been formed by



RIGHT:

Kinetic multidirectional geo-ecological succession resulting from the differential erosion of a cuesta landform—the Cheringoma example. Active headward erosion of Riftward scarp slope river (the Mussapasso) beheading further the older seaward Plio-Pleistocene (?) dipslope dambo drainage. Resulting in seaward shift or divide, extinction of forest and miombo woodland along the crest and its replacement by waterlogged convex (waxing) slope grassland.

Concurrently, progressive sucession is occurring above and below the zone of active backwearing - riverine forest development in donga drainage, forest invasion of miombo on duplex sands, coalescence of termitaria thickets and occlusion of dambos and oval pans on the dipslope.

the meandering braided courses with the development of typical floodplain landforms such as meander scrolls, levees splays, cut-off meanders, and backswamps. These valleys have been choked by the sand load derived from the catchment and the immediate valley sides where there is active retreat of the duplex sands. Except for the slackwater deposits, all the others noted above are composed of sandy material derived from the stripped duplex sands, and all these are colonized by forest and/or closed miombo savannas. The slackwater areas support sour grass and vlei systems similar to the dambos, all of which are acid substrates.

The forest ecosystem invades up all donga and stream cuts, and where the dendritic tributary heads have incised in close spacing, riverine forest predominates, with narrow strips of scrub covering the intervening narrow ridges. The badlands topography erodes by massive cone-shaped slumping at the heads of the dendritic tributaries on divides and spurs. The donga slumping results in the formation of cirque-like valley heads and the slumped material is deposited immediately below to form a temporary base level; in this way valley-head vleis and dambo grassland pockets are formed. Other dambos parallel to the convex-slope grasslands are formed, occasionally on lower slopes where bands of more compact or durable strata outcrop and cause accretion upward of the blockage.

Investigation of many contact areas between the two surfaces shows that in some parts there is now a period of dynamic equilibrium (quiescence), where the convex slopes are stabilized by grass, and sheet erosion is the main erosive activity. In other areas active donga erosion, slumping, and stripping off of the upper sands is in progress. These low and high intensity geomorphic cycles appear to be related to years of lower than mean rainfall (low intensity erosion) and the years of exceptional rainfall, when profiles are saturated to great depth and slumping occurs.

It is significant that termite hills, which are one of the first sites colonized by woody plants in waterlogged grasslands, become the last sites of forest remnants when the sands are stripped off interfluves, and the intervening terrain, which once supported a closed savanna and forest, is replaced by scrub. Stripping of the sand accentuates the hills to nearly 6 m in height, but eventually these are eroded away as well (Fig 6.5).

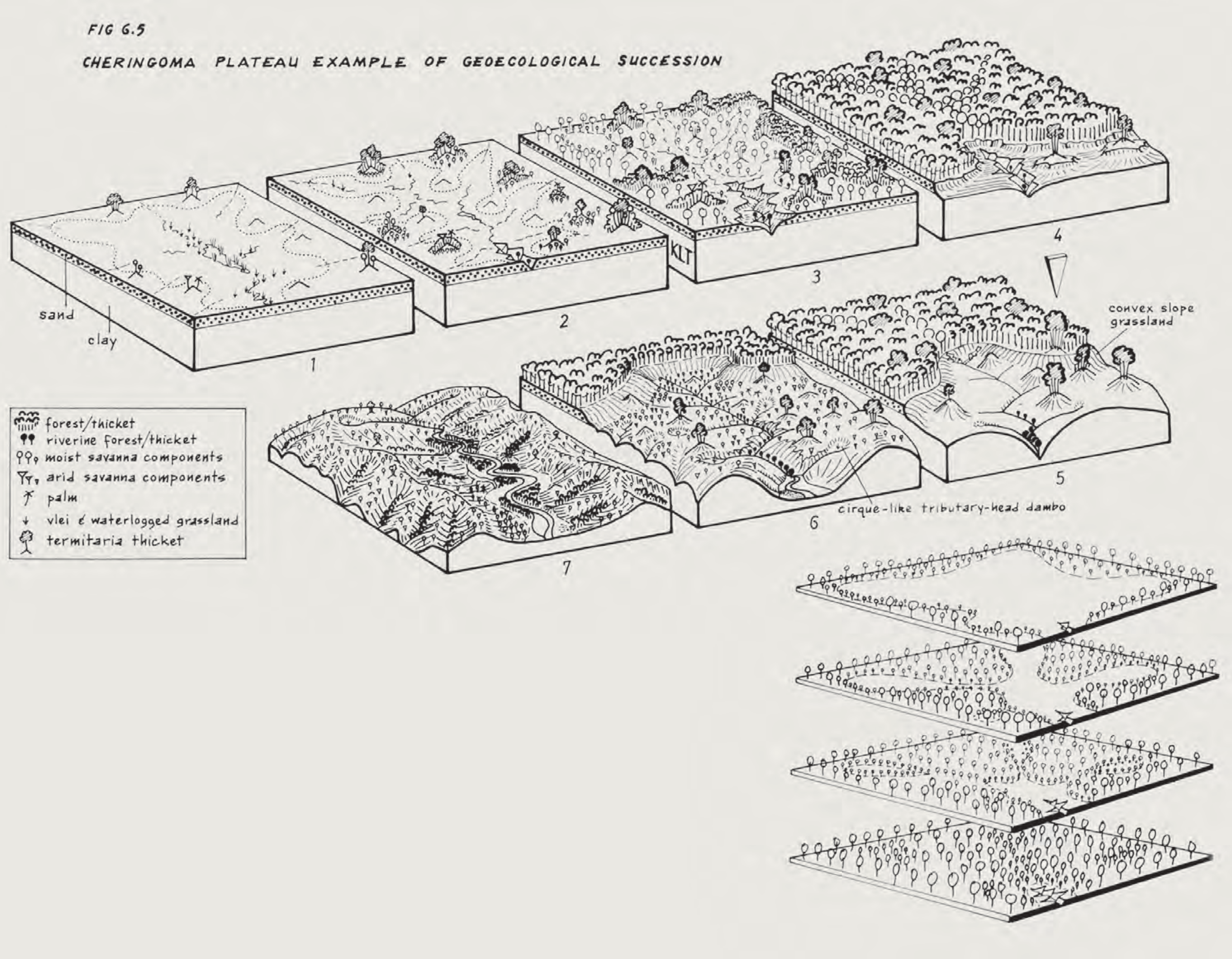
In the southern sector of the cuesta, similar surface replacement has occurred on the upper duplex sands without the deep incision described above. In the upper catchment of the Savane River coast drainage there has been merely a stripping off of the **Bp** sand surface, and exposure of its clay subsoil by sheet and rill erosion. This area has not been studied in the field, but it seems that a much shallower sand cover over the clay has allowed its easy removal. The mature evergreen forests on the convex interfluves are contracting as sands are being eroded away from all sides and no savanna margins remain; the forest on duplex sand remnants meets dambo grassland abruptly on the exposed subsoil clays. The forest breaks down via the same route that it originally invaded and colonized the dambo grasslands, becoming remnant on termite hills and convex surfaces and eventually disappearing from these sites as well. However, as the termite hills are composed of extremely friable subsoil, they are easily waterlogged and eroded when the sands are removed. Thus the most actively eroding zones are around the forest patches on the convex surfaces, where forest is replaced by waterlogged grassland. Further down the slope, redeposition of the sands permits colonization by miombo savanna. Thus, on the one hand the process of surface replacement is immediate and sharp between forest and the grassland that replaces it, as in the badlands example above, or it is a more gradual breaking up of the forest into a pattern of islands on and around termite hills as the sands are thinned off. New forest ecosystems are formed in the incised streams and shelf bar deposits. Although the badlands example of surface and ecosystem replacement is more dramatic, it is merely the incised variant of the more surficial replacement sequence just described.

In the northern sector of the cuesta's coastward dipslope, large areas of dambo drainage with oval shaped pans occur on the original overlying sands, and these are being obliterated by savanna and forest invasion (extension) in response to only lowered soil moisture content of the dambos. No surface replacement, other than narrow incised drainage invading some of the dambos, is evident. The oval and circular pans are all derived from the deeper vlei areas of shallow dambo drainage lines. Oval and round pans related to straight course sectors, and kidney-shaped pans to meander curves and confluences, but all eventually are eroded into an oval shape. The complete story of their origin and eventual extinction is shown in the Cheringoma example. Their origin is similar to that described for the pans in the Lake Chrissie area of the Eastern Tranvaal by Wellington (1955, p. 477). Many originate too from inter-distributary backswamps or slacks as shown where the dipslope fans abut against the delta floodplains. The pans are formed only on areas of duplex sands which is in agreement with Wellington's (1955, p. 475) observation that ' ... the surface is in most places sandy, with a limey substratum an ideal combination of ground conditions for pan formation'. The pans on the Cheringoma have all developed as a result of reduced inflow into the dambos due to river capture and beheading of their catchments by other drainage. This is similar again to that described for the Lake Chrissie area in South Africa. The reduced waterlogging of dambos has released the forests to invade and completely obliterate the shallow drainage courses, leaving the deeper pan areas as a necklace, and then as a line of disconnected depressions completely isolated from one another by the intervening forest. The original links between pans can still be traced in many parts, from the air, by the finer texture of the miombo thicket foliage. The present pans are vlei grassland patches maintained purely by excessive seasonal flooding. Instead of flat or faintly concave floors, some of the pans have islands of higher ground in the centre or along the one side, and these are covered in forest/thicket.

Nowhere are these pans enlarging by deflation (as they do in arid regions) and, except the deepest ones, they are all liable to eventual extinction by forest invasion as the excessive flooding is slowly reduced by evapotranspiration from the margins, and colluvial infill of the weathered edges. Some of the deeper pans have permanent vleis in their lowest parts and others have margins sharply defined by erosion and flooding. The only possible erosive periods are at times of heavy thunderstorm rains, and when the pans are totally flooded some small wind-wave action may cut the western edges. Much of the pan drainage area is in a similar topographic context to those on the Kalahari 'Schwelle' which forms a broad convex critical height in plainsland drainage, and in turn become broad watershed areas when river capture and beheading occurs. The Cheringoma, and similar pans in two other areas of Mozambique, show clearly that lack of evidence of old channels is not proof

RIGHT: Figure 6.5

Cheringoma Plateau example of geo-ecological succession.



EXPLANATORY NOTES FOR Fig. 6.5

(1) Probable pre-Rift appearance of entire Cheringoma Coast plain, with marsh grasslands predominant over laterally coalesced anastomoses of alluvial fans of the rivers from the interior (Plio-Pleistocene). Woody plants, if any, confined to termite hills and highest bar deposits.

(2) Beheading of drainage by down-throw of Rift trough at right angles to the inland drainage (parallel to the coast). Invasion of all convex surfaces by woody plants (savanna, thicket and forest initials). Lowering of primary base level (sea level) contemporaneously with rifting isolated the Cheringoma Coast as an islanded block. Initiation of nickpoints and rapid headward erosion of dambos and slacks of old drainage on friable calcareous sandy clays (weathered Mazamba Formation).

(3) Progressive nickpoint erosion, drainage of waterlogged plains and invasion of woody communities over all faintly convex surfaces by a process of coalescence from the termite hill islands, and along the nickpoint incisions (riverine forest/thicket components with blacked in canopy).

(4) Stage of complete dambo occlusion and forest maturation, with simultaneous destruction of forest and closed miombo savanna by headward erosion of scarps formed from the donga erosion. Resulting in a convex (waxing) slope where the forest-miombo mosaic is being replaced by waterlogged seepage-line grassland (where impervious clay of duplex sands are exposed at the surface)—a sequence of retrogressive succession (in physiognomic and structural terms only). The original woody initial sites on termitaria islanded a second time now by erosive processes. These original communities are shown as cross-hatched areas within the forest canopy.

(5) Further stage in retrogressive succession resulting from scarp retreat and rounding-off of exhumed leached clays.

(6) Colonization of exhumed clays particularly where the upper surface sands have been redeposited as talus or waning slope deposits (i.e. reformation of a duplex substrate with markedly different soil moisture balance to the surrounding inorganic clays). Formation of new cirque-like dambos at heads of dentritic stream network developed on the friable clays. Scarp retreat resulting in further extinction of the mosaic of forest and closed miombo systems. Valley broadening, and aggradation of sandy alluvium deposited in meander belt sequences with new slacks and fan deposits of valley side tributaries, all the convex surfaces colonized by a variety of woody communities including forest, and grassland on concave surfaces and any others that are excessively waterlogged.

(7) Total extinction of the mosaic of forest and miombo woodland and its replacement by scrubby mixed *Acacia* and miombo savanna species. Formation of forest by recombination of upper (now extinct) forest components with riverine components in gullies, on levee and splay deposits of aggraded valley floor, and in-stream head sites where the oval cirque-like dambos have been breached and drained. The Cheringoma example is a fine illustration of the phenomenon of Kinetic, multidirectional, geo-ecological succession.

ECOSYSTEM OCCLUSION

The in situ sequential replacement of dambo and floodplain grasslands by invasion of woody components from the margins as these surfaces dry out progressively from the canalizing effect imposed when the sill responsible for their existence is breached by a nickpoint of any dimension. As these grasslands can be reinstated by the simple expedient of re-blocking the original sill site, the diagram can be read in two directions showing the progressive die-off of woody components as the high water table condition is restored.

that they were not part of an old drainage system. The author's limited experience of both the Kalahari Pans and those in the western Orange Free State indicates that they are all relics of fossil deranged or plainsland drainage systems, now deepened and enlarged mainly by deflation as well as salinization and solution which together are secondary factors. Wellington (1955, p 474-482) and Boocock and Van Straten (1962) show that the Free State and Kalahari pans are all related to fossil drainage systems. Modern workers have either totally ignored any past drainage relations (de Bruiyn 1971) or have thrown out this origin in favour of deflation (Lancaster 1974). The evidence and interpretations given by the older works, and the proof from Mozambique, shows that the origin of pan systems is related to drainage courses whose inflow was cut by the processes of river capture and beheading; the shallow parts becoming choked with sediment and finally obliterated by dry land vegetation.

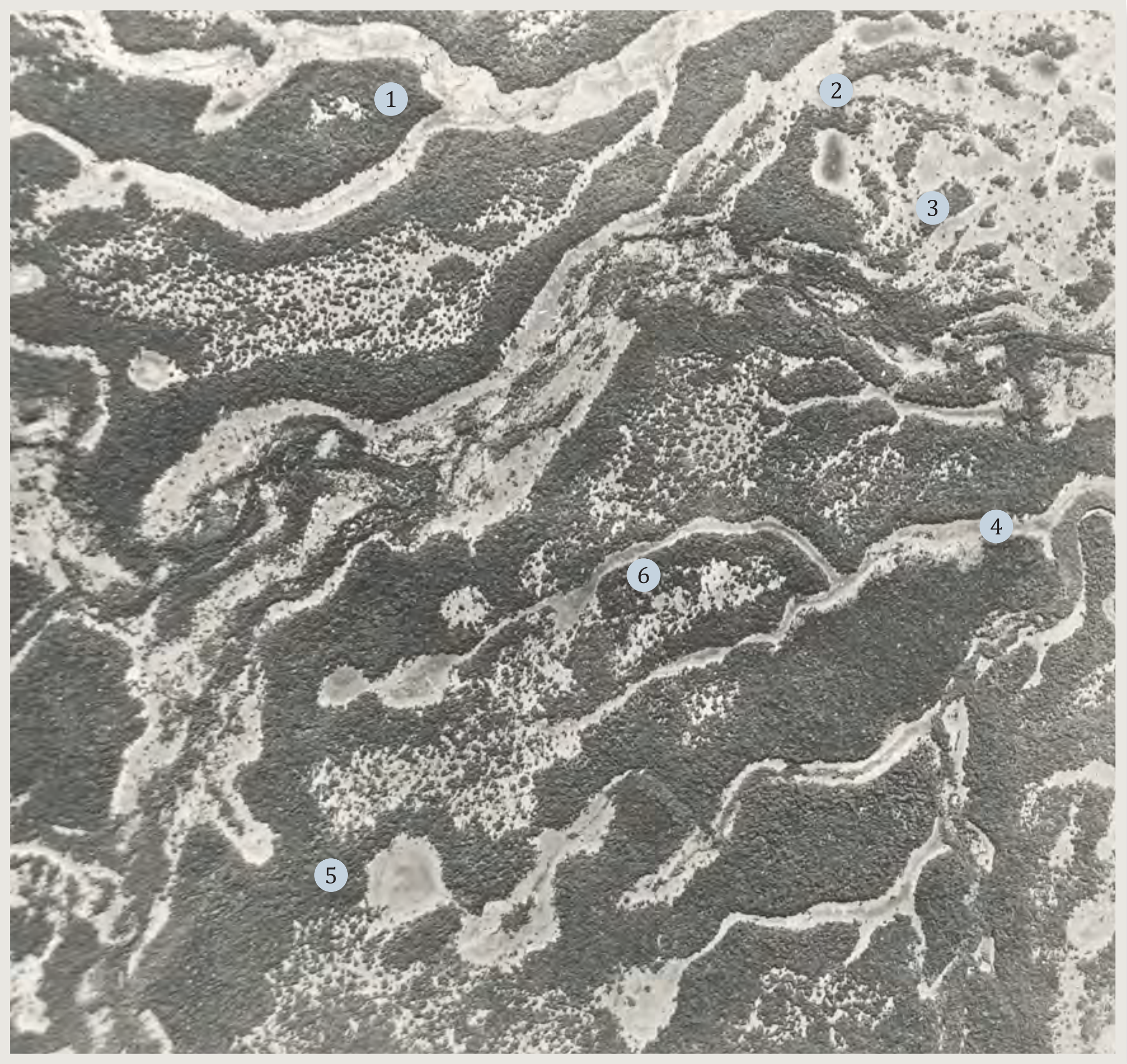
Cheringoma Coast

The Cheringoma Coast comprises four major landforms: (1) alluvial fans of the cuesta's dipslope rivers, (2) arcuate delta floodplains of the Zambezi River, (3) estuary deltas of the cuesta's river mouths and enclosing these on the seaward margin, (4) straight barrier beaches with recurved spits, dune ridges and small parabolic dunes.

The Zambezi Delta deposits, which extend as far south as the Chiniziua River, have been interposed between the cuesta's alluvial fan fronts and an offshore bar. Hence they are a complex of delta alluvium, fan front sediments, and backbar swamp deposits. The fans have built out into these backbar swamps, their original distributaries aggraded to above flood level by sandy, channel fill deposits and covered in miombo thicket and forest. The inter-distributary slacks are waterlogged dambo grasslands covered in large numbers of old and new termite hills. As in the Rift Valley, the ends of the distributary fingers and splay deposits are dotted by island thickets on termitaria. The terminal drainage of the cuesta's rivers have either incised their courses as tortuous meandering streams, tidal in their lowest reaches, or the main river courses have become aggraded with sand fill and further plugs of alluvium have disrupted links with present estuaries. The savanna and forest ecosystem-types have invaded all these abandoned aggraded surfaces and here river water reaches the estuaries only during rains, for the remainder of the season the water disappears into the sands.

Oval pan landscape of the Cheringoma Coast.

RIGHT:



Habitat patterns on alluvial fan anastomosis.

From the top:
① unincised dambo drainage line grassland,
② broad bar deposit (convex surface) with forested margins (cf. islands in the Okavango Delta),
③ central maldrained termitaria thicket islands in the process of coalescence,
④ incised dambo with gallery and swamp forest (pale canopied sinuous line of swamp forest in dambo on extreme right centre of photo,
⑤ various stages in the occlusion of oval pans,
⑥ darker canopied areas are evergreen forest surrounded by paler canopy of seral miombo thicket.

Juxtaposed against the leading edges of these fans is the north–south meander drainage of the Zambezi's old distributary courses. The delta alluvium has been laid almost exclusively from the sequences of abandoned meander courses and their associated landforms of meander scrolls, cut-off meanders, interdistributary slacks, and backswamp deposits. The major part of the area is a mosaic of freshwater and brak swamps, marshes, and grasslands, with papyrus swamps in the deeper abandoned courses. Along only a few of these old distributaries is invasion of convex surfaces (such as levees and meander scrolls) by woody ecosystems into the grasslands. Here too, the dense invasion or colonization of convex surfaces by hill-building termites lends a speckled appearance to all these landforms. The river bar deposits of all types, and marine backbar marshes open to tidal influence, are covered by dense mangrove woods.

The estuary deltas of the cuesta's rivers have been formed by fluvio-marine deposition, and the distributary mouths cut off by channel-fill deposits upstream have been kept open by tidal scouring.

A large part of the estuarine sediments are sequences of terrestrial sands, clays and silts laid down in the summer rains season when high tides dam up floodwaters. In summer, coincidence of high tides and river flooding with on-shore winds is usual on the central coast due to the predominance of the southeast Trades during the day at ground level and storm winds from the south, or east in the case of hurricanes (Tinley 1971). The other deposits are from tidal currents and wave action, by wind erosion and redeposition of sediments by flood and tidal scour involving undercutting and slumping and light deflation of bare salt flats.

On the inner landward margins of mangroves are small to extensive areas of hypersaline bare mud flats. The largest such area occurs in the northern sector of the Zambezi Delta near Quelimane. Within the transect all bare salt flats are of small extent. Thom et al. (1975) describe how these bare flats are derived from an earlier stage covered in mangrove woods, by the process of accretion to above high tide level, and subsequent dessiccation and development of hypersaline conditions killing off the mangroves due to lack of flooding. Examples of dead and dying mangroves on the margins of the flats in the transect uphold their interpretation. These workers suggest that contraction of mangroves to the margins of channels and creeks with maximal extent of salt flats represents a stage of quasi-equilibrium, although they record the presence of shallow gullies (pp. 230-231). The examples from the northern Zambezi Delta show that as soon as the bare flats become incised by spring tide scour and rain into creeks and rills, these surface cuts, extended by typical headward erosion of nickpoints, are invaded by mangroves (typically pure stands of

Oval pan landscape of the Cheringoma Coast.

LEFT:

Oval pans in various stages of occlusion by forest due to drying out of high water table duplex sands from beheading of the seaward (dip slope) dambo drainage. Depicting clearly the origin of oval pans from the deeper parts of dambos, and pinched off by forest invading on convexities in the plainsland of the dip slope.

Avicennia marina). In other sites, these higher flats, many of which are point bar and interchannel deposits, are colonized by dry land communities, or a combination of both, as they become leached of their excessive salt content.

Enclosing these sediments along the immediate shore, is a narrow, low dune barrier composed of parallel dune ridges and fronted by a wave eroded shore with small remnant sections of hummock dunes formed by pioneer strand plants. The dune barrier is cut at intervals by tidal inlets linking the estuaries with the sea, and which are constantly changing position. In other sectors, as between the Zuni and Chiniziua estuaries, the barrier bar has been transported landward and deposited over mangroves and other estuarine and backbar habitats. The process of landward migration of barrier bars is described by Holmes (1965, pp. 828-829). The peats and muds of these habitats and dead mangroves are now exposed within the mid to high tide zone. Closer to the main Zambezi Delta distributaries, the parallel barrier dune ridges curve landward towards an estuary bay forming a system of arcuate ridges covered in thicket and alternating with freshwater or brak troughs. Some of the older recurved beach ridges appear to be related to old breaches to the dune barrier. From the older ridges, small parabolic dunes were formed and these are now covered by dune thicket. A new series of small, active, parabolic dunes have been initiated where the barrier bar has been undercut and slumped by wave action. The younger dune ridges are colonized by strand plants and scrub initials, and the older ridges closer to the backbar marshes are covered in thicket.

Hill-building termites colonize all convex surfaces, except the barrier dunes, to the very edge and into the mangrove swamps where dry islands occur. These sites, as on the flood plains and fans, are one of the first sites of dry land woody plant invasion.

The overlap and interdigitation of land and sea is most intimate and extensive where shallow seas meet low coast plains as on the Cheringoma Coast. Here fluvial and marine processes alternately deposit and erode the same, or incoming sediments, with each tide and with greater or lesser influence seasonally. Superimposed on this are periodic hurricane or frontal storms at sea, and flood rains or droughts inland which interrupt the longer lasting cycles of lower intensity.

These major perturbations disrupt cycles of prograding or retrograding surfaces, and initiate or redirect the surfaces into other landform sequences clearly depicted by the resulting vegetation patterns. Thom and his co-workers (1965, pp. 229-230) conclude from the study of mangroves in northern Australia that geomorphologically induced substrate change, rather than zonation resulting from plant succession per se, is responsible for a dynamic equilibrium between plant cover and habitat change.

A more subtle change, which can have far reaching effects especially on unconsolidated coastland of low relief held in place by plants, is a minor alteration in mean sea level resulting either from world-wide eustatic effects or from more local isostatic changes related to increasing sediment load of the Zambezi Delta on the continental shelf. Important too, are the small but important influences on geomorphic and habitat succession caused by changes in local temporary base levels and changes in distributary discharge, due to catchment changes or plugging and rerouting of river waters in the alluvial fans nearby. Unlike the Rift Valley floodplains, the coast plains are subject to the additional influences of tidal rhythms, wind, waves, alternate flooding by sea and freshwater, and tidal and longshore currents. Like floodplains, seashores most dramatically show the elimination of habitats or alternatively the formation of new land surfaces.

Synopsis of Salient Features

As they are friable surfaces susceptible to relatively rapid change, the Cheringoma cuesta and the floodplain systems demonstrate, in Recent to contemporary time, what appear to be fundamental principles of geo-ecological kinetics. These include the differential flux in intensity and duration of geomorphic processes and the reaction of ecological responses which produce a succession of irregular rhythms of fast and slow tempo. The spasmodic mode of this rhythm results from the interplay of several main chords each made up of two irregular oscillations of different wavelength.

First, the seasonal rhythm of annual cycles within long-term climatic swings. Second, geomorphic succession within larger erosion cycles of geological time scale whose course and tempo is interrupted, and redirected, by diastrophism or base level change. Third, the differential effect of the intensity and duration of these forces on friable and durable surfaces imposes either rapid spatial replacement of ecosystems under the same climatic regime, or the predominance of in-situ edaphic and vegetation change. In situ changes would result from leaching or hardpan formation, and from biotic succession and interactions, tempered by major swings in climate. Though durable substrates arrest landscape development in a Recent context, over geological time these surfaces also undergo inexorable replacement. The resultant complex is a mosaic of geomorphic surfaces and ecosystems of all ages at different stages of kinetic flux, from active to relative quiescence. Fourth, the role of biotic components in accelerating or damping habitat and landscape change (see Ch. 9). Change in density of vegetative cover influences discharge and sediment load (Leopold et al.1964, pp. 457-458), and the far-reaching influences of hippo and hill-building termites in floodplain systems are just a few examples of such interactions.

Process and response must be seen, therefore, as an interacting feedback system where the response and activities of the biotic components are processes in themselves, influencing and modifying geomorphic activity. The examples from friable surfaces, and of hippo eliminating their own aquatic habitat, emphasize the phenomenon of differential sensitivity to change on ecosystem or biome components at every level. The examples of active surface replacement demonstrate how geomorphic processes alone separate, isolate, and eliminate ecosystems or their physiognomic and structural make-up, and provide new surfaces adjacent for recombination of biotic components filtered out by opportunistic availability of propagules and suitability of the new spectrum of landforms. Moreover, these processes also reunite different ecosystem components on new surfaces or extend a whole biome at the expense of another, as demonstrated by the situation in Gazaland, without any change in the climatic regime. Superimposed on this is the differential filtering out of species by dispersal efficiency and distance from source areas, competition, climatic oscillations, and influences such as fire and grazing.

On the Cheringoma cuesta, a pure grassland system replaces forest or closed savanna as headward erosion of scarps contracts the upper, older plains surface. This process, referred to rarely in the literature, is described as retrogressive succession (Cowles 1911), or reversal of succession (Ross 1962, pp. 272-280). Woodworth (1894) realized the ecological significance of geomorphic succession in fluvial processes to organic evolution, and this approach was developed by Adams (1901) and Cowles (1901; 1911). Cowles (1901, pp. 78-82) suggested that there was an order of succession of plant communities related to the order of succession of landforms in a changing landscape. Later he showed that comparable stages of youth, maturity and old age in cycles of erosion were found in cycles of vegetation, with the generalization that deposition influenced progressive succession, and erosion resulted in retrogressive succession (Cowles 1911, pp. 170-171). By progressive, Cowles meant development towards mesic conditions and by retrogressive, the opposite.

The correlations from across the transect, described in this section, showed that there is a succession of habitats and ecosystems related to the provision of new surfaces by denudation and deposition, or merely by change in temporary base level affecting soil moisture balance, and that this succession is kinetic or multi-directional. Succession on sequence of new surfaces is basically one or a combination of three kinds depending on the properties of the substrates: (a) similar species or ecosystems at different stages of development affecting physiognomy and structure only (e.g. age zonation of fever trees on floodplain), (b) different species or ecosystems on contiguous surfaces with similar form (e.g. savanna woodland of the arid savanna biome replacing savanna woodland of the moist savanna biome on exhumed calcic-saline subsoils), (c) different species or ecosystems with different form (e.g. forest replaced by grassland on convex slopes of Cheringoma scarps).

As evolution of ecosystems is the subject dealt with in this thesis, the term retrogressive or reversal as applied to succession needs clarification and restatement to avoid confusion when used in reference to whole systems of any dimension. Cowles' (1911) generalization regarding deposition and progressive succession and erosion and retrogressive succession is not supported by the evidence from the Gorongosa–Cheringoma transect, which shows the most highly developed plant habitat (rainforest) on both depositional and erosional landforms and the simplest habitat, grassland, also on both landforms. Ross (1962, p. 272) defines reversal as the process whereby a community (of plants and animals) of a later successional stage is replaced by one of an earlier successional stage. Ross appears to use the term 'age' synonymously with 'stage' of succession. There is also the implication that earlier or later stages of succession are respectively less or more advanced in an evolutionary context. Such approaches are confusing and mask the real significance of flux in substrate and biotic relations in the field.

Grassland, the simplest terrestrial system in the transect, and forest, the most complex, both occur on the oldest and the youngest land surfaces due to soil moisture balance in different situations. Superimposed on this is the quite opposite relationship of the most complex and diverse wild ungulate associations with grassland and duplex savanna systems, and the poorest with forest. Simplification in physiognomy and composition of the plant habitat by regressive succession, therefore, does not necessarily cause a corresponding reduction in animal diversity, and quite the reverse result holds with the ungulate components. The terms progressive and regressive should thus be applied only to the change of physiognomic complexity of the plant habitat, and not to species diversity of either the plant or animal components. Nor should the use of these terms in a successional context be confused with regressive evolution in organisms, involving loss of functional adaptations characteristic of their ancestors (Allee et al. 1949, p. 672). Both forward and backward, or upgrade and downgrade, succession in physiognomic terms is part of the natural progressive cyclic change of most landscapes and their habitats, not only of estuary and seashore sites where the more ephemeral nature of substrates makes such changes conspicuous.

Many of the surface changes described may seem trivial, but the profound effects they have, especially conspicuous on friable substrates, verify their fundamental importance. The most significant changes are those in base levels of all kinds and nickpoint formation which set in train sequences of landscape and ecosystem change. An outstanding feature of these processes is that, that which happens on the micro scale happens on the macro, the dynamics are essentially the same at all scales.

As pointed out at the beginning of the synopsis, the differential rates of landscape changes, imposed by contrasting properties of the surfaces themselves, result in a spatial spectrum of surfaces of different ages. Some geomorphic processes are, therefore, of geological time scale whilst others are Recent or contemporary. Many more geomorphic events are of contemporary time than is accredited. One such feature, which can be verified by examples from across the whole subcontinent, is the drainage of vleis by nickpoint incision of their temporary base levels resulting in aquatic communities being replaced by savanna within several years (i.e. waterbuck replaced by impala, or duck by sandgrouse). Like the delayed response of plants to rain, the vlei and perched floodplain examples illustrate a basic characteristic of geo-ecological kinetics, the time lag between geomorphic process, landscape adjustment and ecologic response (vide Pitty 1971, pp. 254-257). These lagged responses are also found in many other biotic interactions noted in the following chapters. In certain situations some processes are self-arresting, such as dune blow-outs which become stable when deflation reaches groundwater.

The previous three sections of this book have emphasized the overwhelming importance of soil moisture balance in the evolution of ecosystems and the interaction of their component parts. The invasion of grasslands by woody systems due to changes in soil moisture is probably the most conspicuous, widespread, in situ change in landscapes during contemporary times. Such changes are affected by natural geomorphic processes and biotic activities (e.g. overgrazing) which accelerate these processes or initiate new ones. Alteration of the soil moisture balance to xeric or mesic conditions simulates decrease or increase in the rainfall regimen, as explained for the change in successional tendency in regions above or below the 600 mm isohyet.

These landscape changes require no surface replacement but involve the dynamic of plant succession, resultant on a shift in moisture status of the substrate. Where two contrasting ecosystem types are replacing each other in response to the above edaphic shift, such as forest or closed savanna invading grassland, the grassland areas undergo phases of fragmentation where convex drier surfaces are invaded first, leaving narrow strips linking the larger, wetter areas of the grassland. These larger areas are then islanded off by confluence of the invading woody plants on the drier surfaces. Eventually the isolated larger areas are encroached from all sides and the grassland (or any other habitat) becomes occluded in the manner analogous to the occlusion of a weather front. Fragmentation and extinction, on the one hand, and coalescence and predominance on the other, of biomes, ecosystems or their components, evolves by parallel mechanisms. One such mechanism involves surface replacement (geomorphic succession) and the other, habitat occlusion (biotic succession in response to edaphic change or influences such as fire or overgrazing).

Detailed studies of fluvial (Leopold et al. 1964) and coastal (Steers 1953) processes have shown that the largest percentage of sediment removed is by moderate erosive events which occur relatively frequently and not by catastrophic events. They also point out the tendency for such events to occur in groups, probably related to the persistence of climatic events.

The central importance of coincidence in geomorphic and ecological events is borne out by the flux of different landforms and biotic components, brought together during landscape development, resulting in continued recombinations of contact and mixing. Coincidence of events such as the alluvial plug, responsible for formation and maintenance of the Urema floodplains, and the river capture of the upper mountain catchment by Urema drainage, or simultaneous flooding of rivers with equinox tides and onshore winds, are examples of concurrent events which result in a contrasting diversity of substrates and biotic associations to the prevailing surrounding conditions.

In conclusion, a subject central to the appreciation of succession and climax in an ecological context rather than a purely botanical one, is the concept of a dynamic or moving equilibrium in geomorphology. Such a geomorphological equilibrium refers to open systems where a state of balance or homeostasis is reached between supply and removal of material, resulting in the maintenance of the form or character of the system. A reciprocal multidirectional effect between processes and response operates with each perturbation, resulting in, or tending to restore, a new dynamic equilibrium. In this way an episodic state of flux is maintained, each shift affecting a new balance; in short they are shifts in system kinetics (Strahler 1952; Hack 1960; Chorley 1962; Leopold et al. 1964, pp. 266-268, 274-275). These authors give examples from drainage basins, stream dynamics, hill slopes, coastlines and superposing landscapes.

An analagous relationship is put forward by Allee et al. (1949, pp. 507-508) for ecological homeostasis in biotic communities: ‘Communities are in a condition of flux in all their strata and within each stratum the species populations are in almost continual readjustment to each other and to the varying physical portion of the environment, the result is a biotic balance achieved by complex regulation of community oscillations’. As Cowles (1901) first pointed out, vegetation changes are certain to follow landform changes, but the cover also develops faster to attain a dynamic equilibrium with the environmental controls and its own biotic interactions. The changes in ecosystems and communities, which are correlated with changes in climate and substrate, exhibit different tempos due to the lag in time resulting from the transmission of the changes through the system. Out of unison changes also derive from the independent evolution of levels or components within an ecosystem (Ross 1962, pp. 259-261, 265).

Fundamental considerations in defining which are seral or climax communities are the time scale involved, and the spatial dimension of the system—the smaller units of a system are expected to have quite different orders of temporal equilibrium to the larger units (Mueller-Bombois & Ellenberg 1974, pp.406-408). These authors suggest that a climax community is one which retains its structural and species content over several decades. This definition fits Whittaker's (1953, pp. 183-185) climax pattern concept, but contradicts his (pp. 178-179) and Odum's (1971, p. 251) traditional succession and climax statements, as do the correlations presented here in the last four sections. The field evidence from a diversity of ecosystems across the subcontinent, and the Gorongosa study area in particular, with the discussion above, reaffirms my earlier assertion that all ecosystems and many of their ecotones are at once climo-edaphic climaxes (in kinetic equilibrium), and successional in the short, medium or longterm. It is meaningless, therefore, to recognize climatic or edaphic formations, as both factors work in unison at all times, and are thus climo-edaphic, whether at the community or biome level.

An ecosystem with high physiognomic and biotic complexity, such as forest, does not, therefore, necessarily indicate ecological stability or the culmination of biotic succession, but merely attests to favourable soil moisture balance; the forest in many instances being related to young unstable surfaces which provide a suitable moisture regime allowing for its full development in contemporary time. By contrast, a grassland on a senile planation surface may be far older (more stable) in time and space, yet exhibits a relatively simple structural and biotic plexus. The contrasting make-up of these ecosystems is related simply to climo-edaphic constraints (soil moisture balance), and to the duration of substrate homeostasis available for the development of communities and biotic interactions before a renewed shift in flux asserts another set of changes and combinations, and thus a new dynamic equilibrium, driven by what Ross (1962, p. 336) aptly calls the 'geotectonic machine'.

This analysis of geomorphic and ecological interactions in the Gorongosa ecosystem emphasizes the striking and far reaching impact of geo-ecological succession, and in situ changes in soil moisture balance. Such changes include uplift, valley cutting, river capture, beheading of drainage, and reduction of effective catchment area. Any one of these alone can account for local or regional climo-edaphic changes under a particular macro-climatic regime with persistent temporal oscillations seasonally and in the longterm, rather than the extreme changes in macroclimate interpreted from the field evidence by many disciplines to account for the flux (extinction, predominance or species mix) of flora and fauna in an area or region. The above in situ and replacement changes result in a cyclical sequence of low and high ecological diversity and species content, relative phyto and zoomass ratios, primary productivity and the extension or contraction, mixing and recombinations of communities and biomes or their components.

6.3 GEO-ECOLOGY OF TERMITARIA

Hill-building termites play a vital and unique role in the evolution of landscapes and their ecosystems across the subcontinent—from the southwest Cape, the desertic regions, through the savannas to the moist forests of the east coast. Their impact on the landscape is most clearly seen from the air. The dots of their evenly spaced hills are made conspicuous either by being bare (in desertic areas especially), or covered in thicket clumps; islands in an otherwise pure grassland landscape. These patches in the southwest Cape and Namib Desert have long been an enigma to both scientists and laymen and a profusion of explanations for their origin, ranging from geological phenomena to zebra rolling sites, have been suggested. Some of the current explanations are listed by Van der Merwe (1962, pp. 28-29) and Liebenberg et al. (1976, p. 38). Their origin as termitaria was first put forward by the author in a study of the Etosha and Kaokoveld region (Tinley 1971). Their fairly regular spacing and form are field diagnostic features wherever they occur.

Closer field investigation in the desertic regions shows large numbers of dead 'fossil' mounds of bare hypersaline soils deepened by deflation into the form of round shallow basins (Tinley 1971a), and living termitaria of the same shape but with convex surfaces either within the same area or on the subdesert margin. In southwest Angola (Iona) and the Kaokoveld, 'fossil' termitaria of watchglass form occur in the Namib Desert to within 30 km of the coast on clay flats, hill pediments and in quasi-stable dune areas. Their presence attests to former moister conditions when sub-desert and arid savanna conditions were closer to the coast. These termitaria were built by *Macrotermes* termites, probably *M. mossambicus* and *M. subhyalinus,* which form the large hills across the subcontinent from the Namib fringe to the Gorongosa study area. In the Richtersveld, a similar pock-marked landscape is formed by a mosaic of termitaria, some dead, thus flat or concave, and others living and in convex form. The termite here responsible, collected by the author, is *Microhodotermes viator.* The same species is responsible for the living, and dead, 'heuweltjies' or hillocks of the

Termite hill landscapes of the Rift Valley floor

southwest Cape's Swartland and west coast flats, where an aerial view shows the greener status of crops and other plants due to better soil moisture and nutritional status in the mounds than in the intervening soils. Repeated cultivation of termitaria kills off colonies and this may be the reason for the prevalence of dead or 'fossil' termitaria in the Swartland, rather than change in rainfall regimes suggested above for the northern Namib examples. The pedologist Van der Merwe (1962, pp. 28-30, 114, 306-308) discussed and gave a detailed soil profile description of a 'heuweltjie' and, despite the honeycombed structure recorded between 20 cm - 50 cm depth and other peculiarities, did not recognize it as a termite hill.

A recently published manual on map and air photo interpretation of South African scenery shows many examples, although unrecognized as such, of termite hill landscapes, the prevalence of which emphasizes their edaphic and ecological importance (Liebenberg et al.1976, Photos 4, 9, 15, 18, 31, 38, 42, 46, 48, 51, 62, 66, 72) The ecological role of termites in other regions is detailed by Lee and Wood (1971) and for Africa in a brilliant paper by Trapnell et al. (1976). Detailed studies on termites in southern Africa have been made by Dr. W. G. H. Coaton and his co-workers at the Plant Protection Institute, Pretoria (e.g. Coaton et al. 'National survey of the Isoptera of Southern Africa' series in Cimbebasia).

In the Gorongosa transect, six termite genera were collected: *Amitermes, Ancistrotermes, Cubitermes, Grallatotermes, Macrotermes* and *Odontotermes*, of which *Macrotermes mossambicus, M. subhyalinus* and *Odontotermes* are hill-building species. *M. mossambicus* appeared to be the most common across the study area. The *Cubitermes* construct rounded mounds of soil up to 50 cm high, glued together with faecal matter, and occur characteristically on the dambo grasslands of the Cheringoma cuesta. *Grallatotermes africanus* construct arboreal nests, also glued with faecal matter, on tree trunks 10 m or more

RIGHT:

Termitaria thicket (archipelago-like) on a convex surface of the floodplain grasslands. Note incised game paths radiating from the termitaria thicket area draining the convexity further.

above the ground, and occur mainly in the miombo savannas south to about the 22° latitude in Mozambique.

The fundamental geo-ecological role of hill-building termites in the evolution of floodplain and high watertable landscapes has been detailed in the preceding sections on soil development, soil moisture balance, and geomorphic and ecologic dynamics. In these examples, illustrated by photographs, profiles and block diagrams, the emphasis has been on the multiplicity of influences brought about by formation of a hill landform of subsoil built above the surroundings. But this is only part of the story; a further array of influences is generated by the erosion of termite hills, in areas with high densities of browsing ungulates.

The development of a termite hill, as opposed to a mound, often results in the formation of an annular depression around part of the base of the hill due to either slight subsidence resulting from removal of subsoil for the formation of the hill, or to rain swash action, or to both. On the microscale these resemble the basal annular depressions formed by rainwash off inselbergs in desert. These annular depressions around termitaria hold water during the rains and are initial sites of pan development by enlargement through the wallowing action of wild ungulates. The initation and development of pans by wallowing is recorded by many authors (e.g. Young 1970; Weir 1960; Jarman 1972; Hall-Martin 1972; Flint & Bond 1968 and personal data) including pans formed by gemsbok in Namibia. The annular depression is perfectly preserved in areas where wild ungulates are rare. In areas of intermediate population the annular depression is enlarged and eroded to an irregular oval shape immediately at the base of the hill.

A unique phenomenon, apparently unrecorded, is the development of pans on the actual sites occupied by termite hills, a process of landscape reversal by biotic and geomorphic interactions. In areas with a high ungulate browsing population density, as on the Rift floor in Gorongosa, the hills are replaced by oval pans. The cyclical evolution of

Termite hill landscapes of the Rift Valley floor

FAR LEFT:

Mature thicket on termite hill with associated rain-filled pans and aquatic communities adjacent.

TOP LEFT:

Bare arcuate depression around the base of a termite hill (covered by thicket on right) in an area lightly stocked by wild ungulates.

BOTTOM LEFT:

Bare, invasive stage of *Macrotermes* hills in drying sectors of the converging delta area at the head of the Urema Lake.

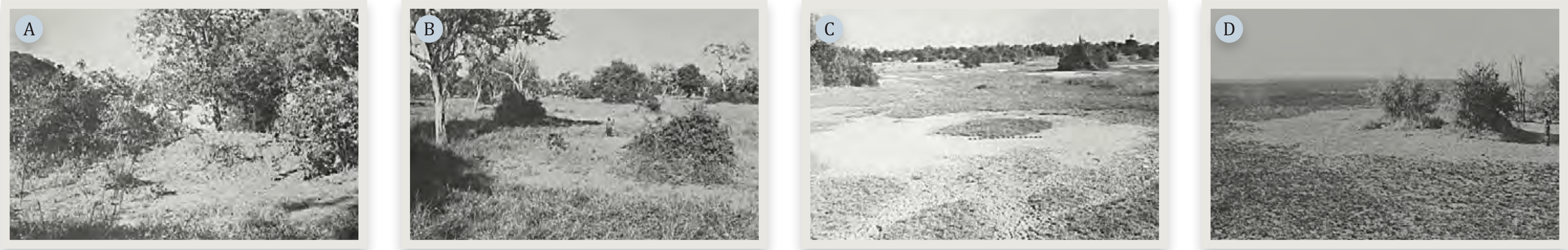
‘termitaria pans’ follows the sequence outlined by Fig. 6.6.

In open plainsland termite hills become centres of attraction to all forms of life as perches, observation posts, or refuges from flooding or fire. Seeds are concentrated here; deposited by the animals attracted to these sites. The ensuing thicket growth is, therefore, composed of almost all the species whose fruits are most favoured by birds and mammals (see Chapters 8 and 9). The cover and rich browse available is then used by all browsing ungulates, and because these sites are islands in a sea of grass or in savannas composed of other species, they are under disproportionate utilization pressure which results in destruction of the cover and the break up of the surface by trampling (plus digging and eating salt-rich soil in some areas) which promotes rapid erosion. The hills are worn down primarily by hoof action and rain, and once hollow they are enlarged, chiefly by species such as warthog and elephant. As the main hill is truncated, new hills are formed beneath the protection of remnant thicket or scrub patches on the periphery and grow upward as the pan develops on the original termite hill site. These satellite colonies may originate by fragmentation of the original colony.

The significance of this micro-landform evolution by interacting biotic and geomorphic processes is the proliferation of diverse substrates, communities and resources. On the one hand, convex surfaces above excessive flooding are enlarged or initiated by hill building activity of the termites, and these coalesce by erosion and radial deposition of material extending the areas of dry land communities at the expense of flood dependent communities. The pattern formed by multiple hill areas is closely related to the template of microrelief developed during floodplain sedimentary processes, and also to the convexities left by former colonisations made during periods of consecutive low flood years and killed by subsequent excessive flood. At the same time there is the multiplication of pans, and thus a wider reticulation of water and seasonal aquatic communities (including seasonal fish such as *Nothobranchius rachovii*). The increase in number of termite hills per unit area proliferates the amount of island thicket habitats, ecotones and the concentration of preferred food plants they support.

If wild ungulates disappear from an area, for one or other reason, pans become filled in by sediment washed from the surroundings and they go through a stage of senescence and eventual extinction. If, however, there is a dense plant cover and no ungulates, especially if the hill is on duplex soils, the annular depressions or their enlarged forms may remain for the duration of the termite hill’s life.

In sum, termite hills increase arid biome substrates in moist areas by bringing saline subsoils to the surface which act as ‘stepping-stones’ for arid elements between separate arid biomes. In areas with non-saline subsoils the hills carry forest or moist savanna biome elements into, and through, extreme arid or upland areas. They also carry savanna biome elements through the Cape Fynbos region, and link them with the west coast desert biome (pers. obs.). In the evolution of landscapes, termite hills provide initial or relic sites for the forest-thicket ecosystem type, and multiply seasonal aquatic communities by the combined action of rainwash and the eroding activities (trampling and wallowing) of ungulates where they occur in high density. The degree of impact expressed by termite hills in different landscapes depends on contrasting properties of the subsoils brought to the surface and/or to their contrastIng soil moisture balance with the juxtaposed intervening ground.



RIGHT:

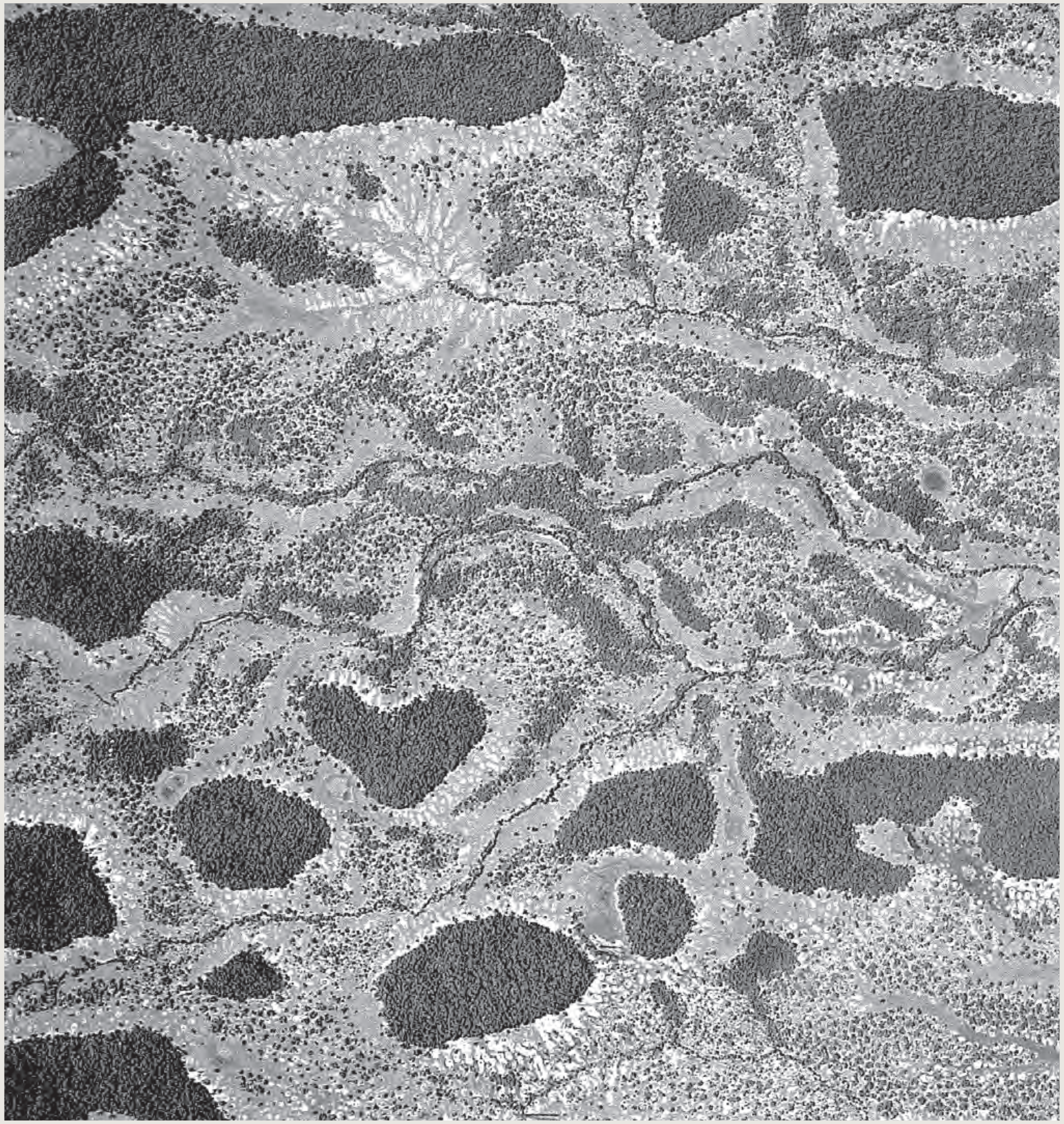
Eroded termite hills and natural firebreaks.

A Flat-topped (mesa-stage) of termite hill erosion. Thicket now confined to hill slopes.

B Later dome stage with thicket relic prior to being eroded flat. Note tree-base thicket in backgound.

C Primary development of a pan on the original termite hill (watch glass stage). Seasonal hygrophilous grass in the centre (next to 3 m measuring rod) and bare rim. Note heavy utilisation by wild ungulates.

D Natural firebreak of lawn grasses on change of soil of termite hill pediment protecting the thicket cover. In other sites a similar ring is formed by the trampling of browsing ungulates feeding on the thicket.



FAR LEFT:

Termite hill landscape of the Cheringoma Coast

Natural sheet erosion of friable white duplex sands in the plains headwater catchment of the Sambazo River. Note (1) large black area of mature evergreen forest contracting as sands are stripped off the underlying leached clays (white margins to forest and white dots of dead termitaria), (2) incised dambos with active headward and lateral erosion, (3) dark dots are termitaria thickets, coalescing in zones of redeposition of sands on the waning slopes.

TOP LEFT:

Oblique air view of the 50 m broad termitaria on white duplex sands. The white soil is from erosion of friable leached subsoil clay brought to the surface by the termites.

BOTTOM LEFT:

Young *Parinari curatellifolia* tree on microrise of *Cubitermes* termite mound in an otherwise flat, waterlogged dambo.

RIGHT: Figure 6.6

Cyclical evolution of termite hills to pans.

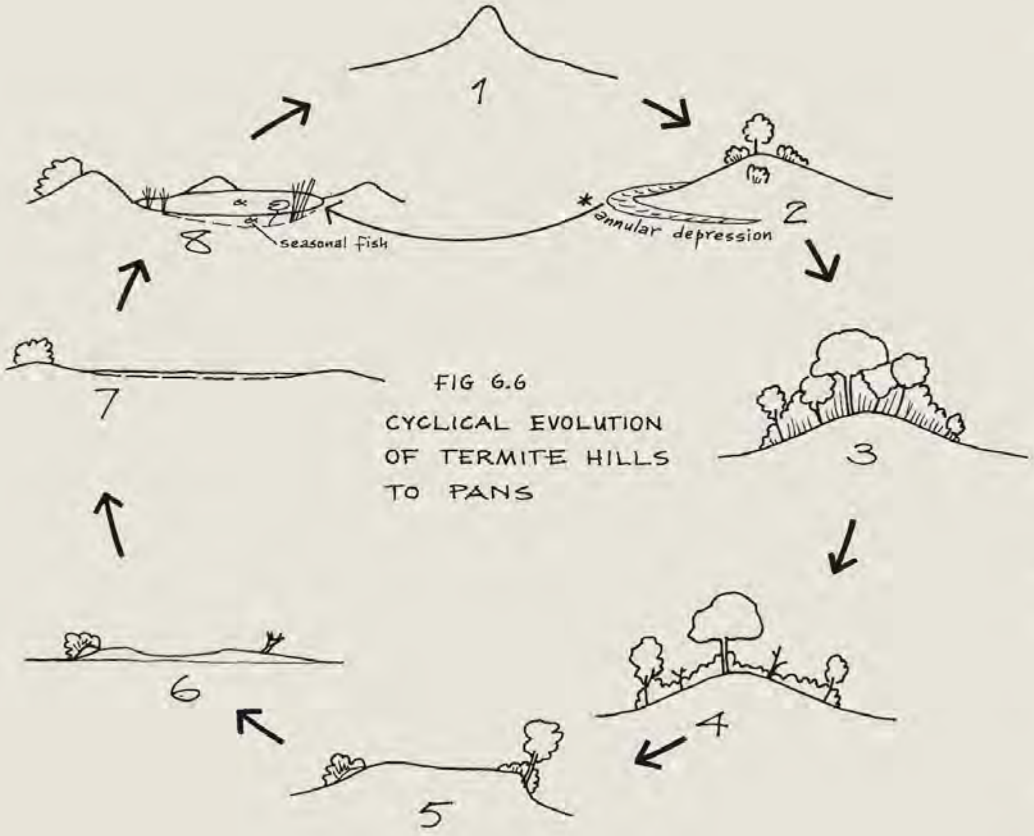


FIG 6.6

CYCLICAL EVOLUTION OF TERMITE HILLS TO PANS

1 Growth of termite hill above surrounding flat ground. Enlargement of hill by termite building activities, erosion & radial deposition of material forming a pediment apron. Conical prominence attracts seed dispersing animals (birds, primates, ungulates), which use it for perching & resting, or as a look-out, & defaecation here concentrates seed accumulation.

2 Annular depression formed around base of termite hill.* Growth of plants, particularly woody species, cover the hill & provides new habitats – food, cover & edge effect, reinforcing the hill's attractiveness to animals. Increased input of drupe-fruit woody species by animals & from parent plants. Typical development of single large tree (primary colonist) on apex of hill. Increasingly attractive to browsing ungulates.

3 Maturation of thicket on termite hill.

4 Over-utilization of thicket by browsing ungulates opens up the cover & breaks up the surface by trampling which promotes rapid erosion.

5 Lowering of the termitarium (mesa stage), the remnant thicket or scrub patches, under which termite building activities are protected & continue, become confined to the convex edge of the hill.

6 Penultimate stage of erosion. Hollows often formed on chamber within the termitarium.

7 Faintly concave (watchglass) oval depression formed with the rim breached by footpaths & rainwash. Primary deepening to level of surrounding ground by scouring (mostly by rain & a little by deflation). Growth of one or more satellite termite hills on the rim of the depression.

8 Final stage of pan formation, further deepening & enlargement due solely to wallowing & trampling action of wild ungulates. Entire sequence can be initiated again on one or other of the new termitaria resulting eventually in further enlargement of the depression.

* In areas of medium to low ungulate density the annular depression can be enlarged to form a pan without involving the mature thicket covered termitarium.

REFERENCES / CORRELATION PROCESS AND RESPONSE

Adams, C.C. 1901. *Base leveling and its faunal significance.* Amer., Nat., vol. 35, pp. 839-852.

Allee, W.C., Emerson, A.E., Park, 0., Park, T. & Schmidt, K.P. 1949. *Principles of animal ecology.* W.B. Saunders Co., Philadelphia & London.

Astle, W.L., Webster, R. & Lawrence, C.J. 1969. *Land classification of management planning in the Luangwa Valley of Zambia.* J. Applied Ecol., vol. 6 (2), pp. 143-169.

Boocock, C. & Van Straten, O.J. 1962. *Notes on the geology and hydrogeology of the Central Kalahari region Bechuanaland Protectorate.* Trans. Geol. Soc. S. Afr., vol. 65 (1), pp. 124-171.

Cain, S.A. & Castro, G.M. De Oliveira 1959. *Manual of vegetation analysis*. Harper & Bros, NY.

Chapman, V.J. 1961. *Salt marshes and salt deserts of the world.* Leon HiII, London.
—1964. *Coastal vegetation.* Pergamon Press, London.

Chorley, R.J. 1962. *Geomorphology and general systems theory.* U.S. Geol. Survey Prof. Paper, No. 500-B.

Chorley, R.J. (ed) 1969. *Water, Earth & Man: a synthesis of hydrology, geomorphology and socio-economic geography.* Methuen, London.

Clements, F.E. 1916. *Plant succession.* Carnegie Inst., Washington, Pub. No. 242.
—1928. *Plant succession and indicators.* Wilson, NY.

Cole, M.M. 1960. *Cerrado caatinga and pantanal: distribution and origin of the savanna vegetation of Brazil.* Geographical Journal 126, 168-79.
—1963. *Vegetation and geomorphology in Northern Rhodesia. An aspect of the distribution of the savanna of Central Africa.* Geog. J, vol. 129 (3), pp. 290-310.

Cowles, H.C. 1901. *The physiographic ecology of Chicago and vicinity. A study of the origin, development and classification of plant societies.* Bot. Gaz., vol. 31 (2), pp. 73-108.
—1911. *The causes of vegetative cycles.* Bot. Gaz., vol. 51 (3), pp. 161-183.

De Bruiyn, H. 1971/2. *Pans in the western Orange Free State.* Ann. Geol. Survey, No. 9, pp. 121-124.

Drury, W.H. & Nisbet, I.C.T. 1971. *Inter-relations between developmental models in geomorphology, plant ecology and animal ecology.* General Systems, No. 16, pp.57-68.
—1973. *Succession.* J. Arnold Arboretum , vol. 54 (3), pp. 331-368.

Flint, R.F. & Bond, G. 1968. *Pleistocene sand ridges and pans in western Rhodesia.* Geol. Soc. Amer. Bull., No. 79, pp. 299-314.

Hack, J.T. 1960. *Interpretation of erosional topography in humid temperate regions.* Amer. J. Sci., vol. 258, pp. 80-97.

Hall-Martin, A.J. 1972. *Aspects of the plant ecology of the Lengwe National Park, Malawi.* M.Sc. Thesis, University of Pretoria.

Holmes, A. 1965. *Principles of physical geology*. 2nd edn. (revised), Thomas Nelson, London.

Jarman, P.J. 1972. *The use of drinking sites, wallows and salt licks by herbivores in the unflooded middle Zambezi Valley.* E. Afr. Wild. J., vol. 10, pp. 193-209.

King, C.A.M. 1959. *Beaches and coasts.* London.

King, L.C. 1963. *South African scenery: a textbook of geomorphology.* 3rd edn. (revised), Oliver & Boyd, London.

Lee K.E. & Wood, T.G. 1971. *Termites and soils.* Academic Press, London & NY.

Lancaster, I.N. 1974. *Origins and development of the pans of the southern Kalahari.* Botswana Notes & Records, No. 6, pp. 157-169.

Leopold, L.B., Wolman, M.G. & Miller, J.P. 1964. *Fluvial processes in geomorphology.* Freeman & Co., San Francisco.

Liebenberg, E.C. Rootman, P.J. & Van Huyssteen, M.K.R. 1976. *The South African landscape: exercise manual for map and airphoto interpretation.* Butterworth & Co, Durban.

Lobeck, A.K. 1939. *Geomorphology: an introduction to the study of landscapes*. McGraw-Hill Book Co., NY & London.

Michelmore, A.P.G. 1939. *Observations on tropical African grasslands.* J. Ecology, vol. 27, pp. 282-312.

Mueller-Dombois, D. & Ellenberg, H. 1974. *Aims and methods of vegetation ecology.* Wiley, NY & London.

Odum, E.P. 1969. *The strategy of ecosystem development.* Science, vol. 164 (3877), pp. 262-270.
—1971. *Fundamentals of ecology.* 3rd edn. (revised), W.B. Saunders Co., London.

Parris, R. 1976. *A study of the major components of the Kalahari pan ecosystem.* M.Sc. Thesis, University of Pretoria.

Partridge, T.C. 1973. *Geomorphological dating of cave openings at Makapansgat, Sterkfontein, Swartkrans and Taung.* Nature, vol. 246(5428), pp. 75-79.

Pitty, A.F. 1971. *Introduction to geomorphology.* Methuen, London.

Ross, H.H. 1962. *A synthesis of evolutionary theory.* Prentice-Hall, NJ.

Shimwell, D.W. 1971. *The description and classification of vegetation.* Sidgewick & Jackson, London.

Small, R.J. 1972. *The study of landforms.* Cambridge University Press, London.

Smith, J. 1949. *Distribution of tree species in the Sudan in relation to rainfall and soil texture.* Sudan Ministry Agric. Bull., No. 4.

Steers, J.A. 1953. *The sea coast.* Collins, London.

Strahler, A.N. 1952. *Dynamic basis of geomorphology.* Bull. Geol. Soc. Amer., vol. 63, pp. 923-938.

Thom, B.G. 1967. *Mangrove ecology and deltaic geomorphology, Tabasco, Mexico.* J. Ecology, vol. 55, pp. 301-343.

Thom, B.G., Wright, L.D. & Coleman, J.M. 1975. *Mangrove ecology and deltaic-estuarine geomorphology: Cambridge Gulf-Ord River, Western Australia.* J. Ecology, vol. 63 (1), pp. 203-232.

Thomas, M.F. 1974. *Tropical geomorphology.* Macmillan, London.

Thornbury, W.O. 1954. *Principles of geomorphology.* Wiley, NY & London.

TInley, K.L. 1971a. *Etosha and the Kaokoveld.* Afr. Wild., vol 25 (1), Supplement .
—1971b. 'Determinants of coastal conservation: Diversity and dynamics of the environment as exemplified by the Moçambique Coast' in *Nature conservation as a form of land use.* Proceedings SARCCUS Symposium, pp. 124-153.
—1975. *Habitat physiognomy, structure and relationships.* Mammal Research Institute 1966-1975, Symposium proceedings, University of Pretoria Pub., New Series No. 97 pp. 69-77.

Trapnell, C.G., Friend, M.T., Chamberlain, G.T. & Birch, H.F. 1976. *The effects of fire and termites on a Zambian woodland soil.* J. Ecology, vol. 64 (2), pp. 577-588.

Van Der Merwe, C.R. 1962. *Soil groups and subgroups of South Africa.* 2nd edn. (revised), Gov. Printer, Pretoria, Science Bull. No. 356.

Weir, J.S. 1960. *A possible course of evolution of animal drinking holes (pans) and reflected changes in their biology.* Proc. 1st. Fed. Sci. Cong., Salisbury, Rhodesia.

Wellington, J.H. 1955. *Southern Africa: a geographical study.* Vol. I, Cambridge University Press.

Whittaker, R.H. 1975. *Communities and ecosystems.* 2nd edn., Macmillan, London & NY.

Woodworth, J.B. 1894. *The relation between base leveling and organic evolution.* Amer. Geol., No. 14, pp. 209-235.

Young, E. 1970. *Water as 'n faktor in die ekologie van wild in die Nasionale Krugerwildtuin.* D.Sc. Thesis, University of Pretoria.

* * *

PART 2

CORRELATION

Chapter 7

Human

Human

© Jeffrey Barbee

This section on human influences in the Gorongosa ecosystem is interposed here between the earth and life components since human activities result in both geomorphic and biotic changes in a landscape.

Large-scale bulldozed clearance of wooded country for agricultural purposes is striking. As profound over the long term, are the more subtle, cumulative selective changes imposed by primitive cultivating cultures. The impact of shifting cultivation, and previously the iron-smelting cultures which required hardwoods for their furnaces and for hut construction, on the present day appearance and composition of the vegetative cover over various areas is probably far greater than is generally realised.

7.1 HISTORICAL

Hunting in the Gorongosa region must have gone on since at least Bushman times and increasingly with the arrival of the Sena (Karanga–Shona) tribes from the north, who replaced the iron age people, about 1,130 B.P. (Fagan 1965, p. 120). As populations built up, this hunting pressure increased. The real impact on wildlife probably began with the advent of Indian and Arab trade (12C-14C) and the Portuguese (early 1500s to 1600) who specialised in ivory (both elephant and hippo) and slave trade in the entire area between the Zambezi and Save Rivers. This region lies between the seaports which served the Monomotapa and Zimbabwe kingdoms of the interior Mashona plateau, which were the main suppliers of gold from about A.D. 600 (Summers1969). Access to the interior was both upriver along the Zambezi, Chiri, Pungue, Buzi, and Save (only in summer) as well as on foot routes up these valleys (and others such as the Mazoe), and on interfluves through the saddles in the Great Escarpment on the Mozambique–Zimbabwe border (Balsan 1970; Summers 1969; Axelson 1973). Prior to Portuguese control, trade from Central Mozambique was with East Africa, Somalia, the Persian Gulf, and India, and to a lesser extent between the people of the interior and Madagascar (Kent 1968 a & b; 1969). Summers (1969) remarks that ivory and leopard skins were probably East Africa's oldest exports since about 1,500 B.C. The gold trade came to an abrupt end in about 1825 when

© Paul Dutton

LEFT:

Vasco Matondo—a former elephant hunter who became my tracker, friend and right hand man. He assisted me in the field; writing notes, pressing plant specimens and helping to dig soil profiles. He also kept a sharp eye out for curious lion, buffalo or elephant who may be attracted by the sound of digging! Vasco was a master Mbira (thumb piano) player and his playing often made light of hot mosquito infested nights.

RIGHT: Figure 7.1

Background to human influences on Mozambique landscapes.

Study area.

the Nguni chiefs Zwangendaba, and later Mzilikazi in 1840, destroyed these kingdoms (Summers 1969).

Thus up to the time of the proclamation of Gorongosa as a national park, the region had since time immemorial been subjected to intensive hunting pressure, particularly of tuskers.

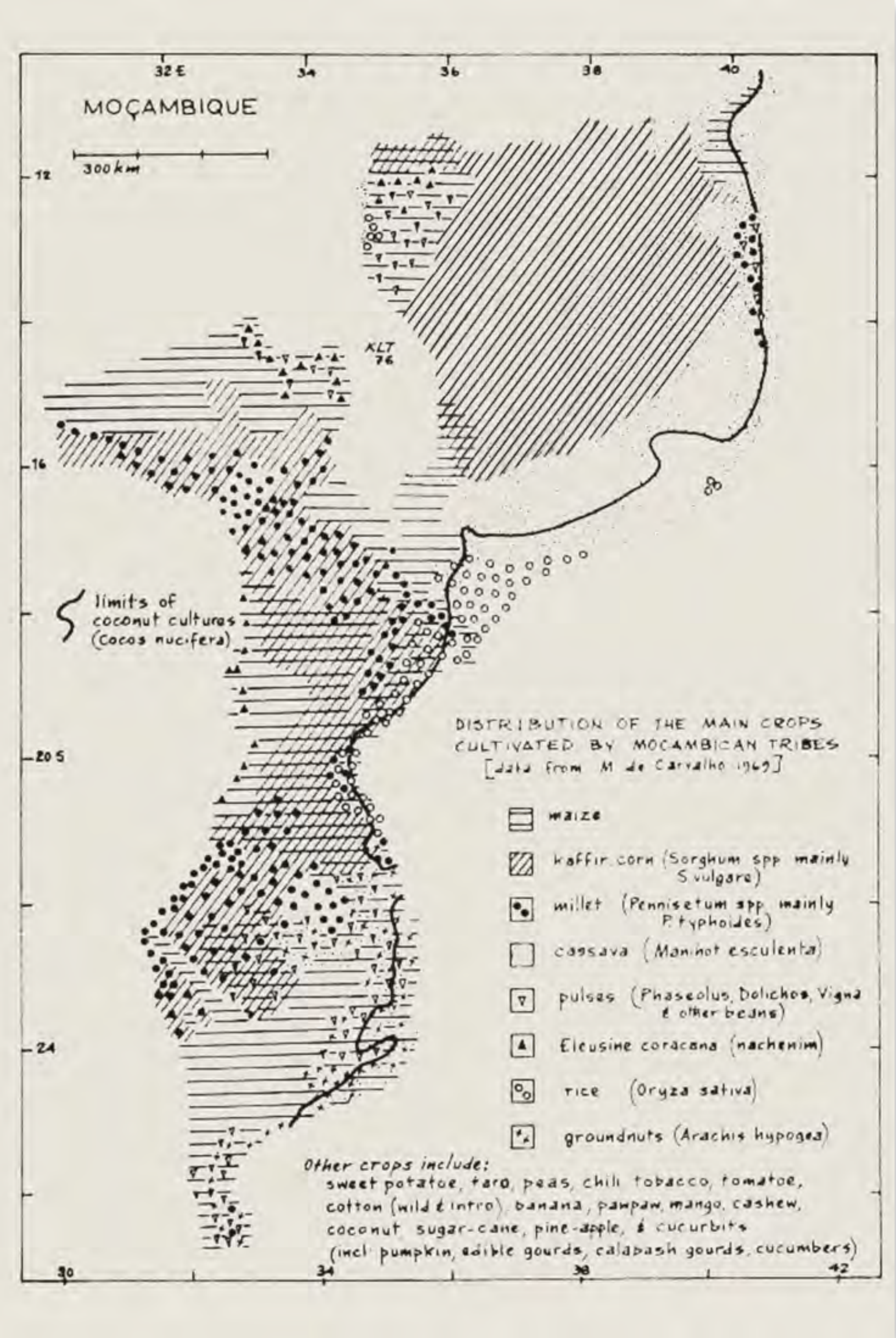
It is probable, therefore, that overall, the wildlife populations recorded in the early 1970s, during the period of this study, represent some of the greatest concentrations ever to occur in the recent history of Gorongosa as the 1963-1973 decade saw the best attempt at strict conservation measures. However, according to the signs of old bark damage of baobabs by tuskers, and the eroding of hippo paths, plus early photos of vast hippo numbers, it is possible that elephant and hippo populations may have been greater in earlier times.

In the more recent past, intensive hunting for trophies and meat continued outside the park boundaries so that most of Central Mozambique, except for Gorongosa and Marromeu in the Zambezi Delta, has extremely decimated wildlife populations, although sufficient in patches to support safari hunting. This general emptying of wildlife and natural resources from the landscape around the park is the main reason for the present subtle invasion of the park by the local tribespeople.

Relatively modern innovations and facilities such as trading stores, timber extraction, cash crops, roads, railways and safaris have resulted in depletion of wildlife as a food resource. Increased pressure on the remaining stocks is occurring from tribal cultivators who, despite extensive well-watered and unoccupied areas of similar miombo with forest patches suitable for cultivation in every direction away from the Park, are concentrating along riverine sites into the park area. With each succeeding reduction of the park boundaries to keep the invading human populations on the outside, there is a fresh invasion of cultivators along riverine areas, and workers for safari, timber and cotton companies who operate yet deeper into the park area.

7.2 PRESENT POPULATIONS AND DISTRIBUTION

The tribal people in the Gorongosa ecosystem are Sena with three main dialect groups: the Chegorongosa on the west of the Rift and the Cheringoma and Bangue on the east of the Rift. They are primarily shifting cultivators using mapira (sorghum corn) as the major crop as this can



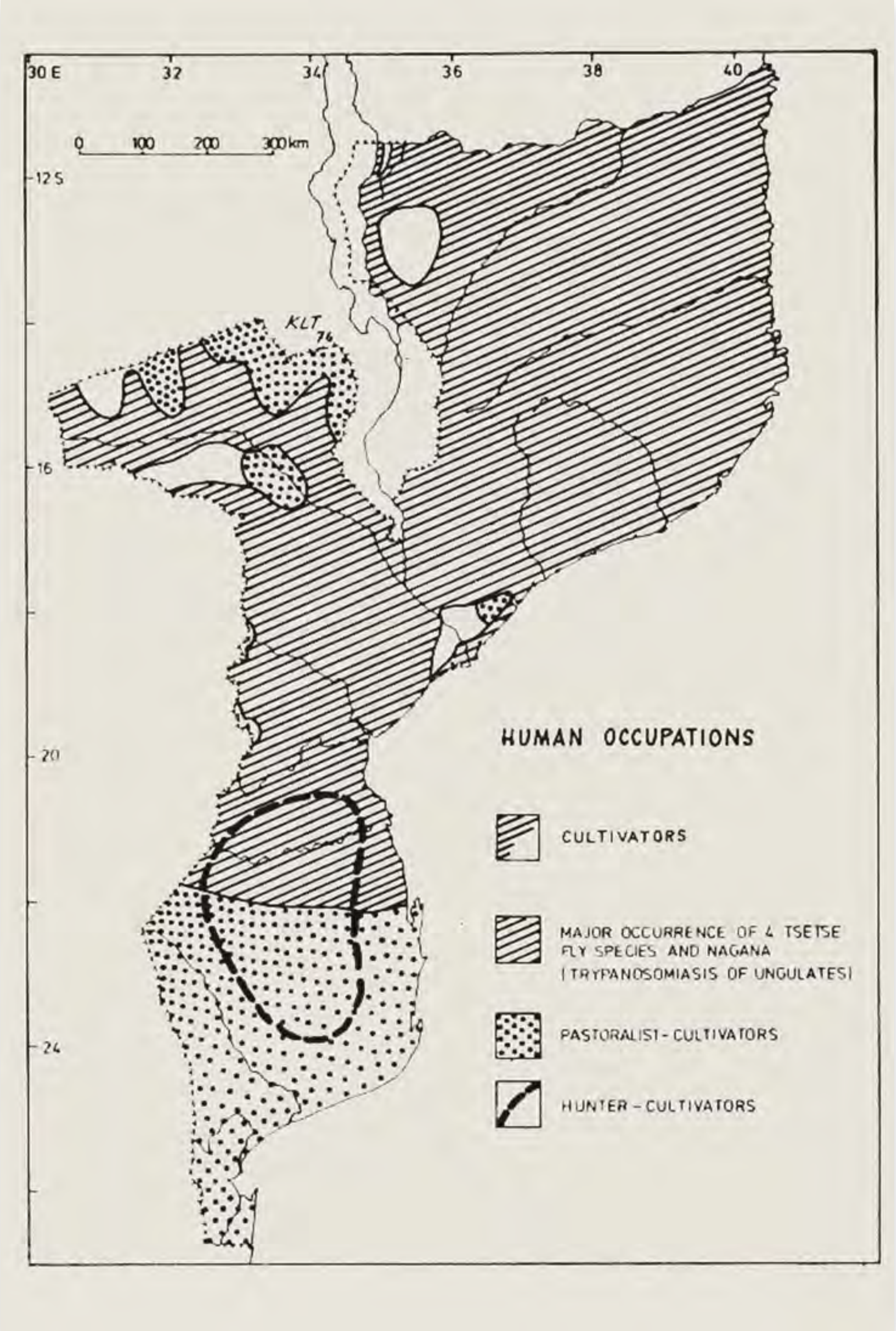


Figure 7.1 *Cont.*

Background to human influences on Mozambique landscapes.

FAR LEFT:

Distribution of the main crops cultivated by Mozambique tribes.

LEFT:

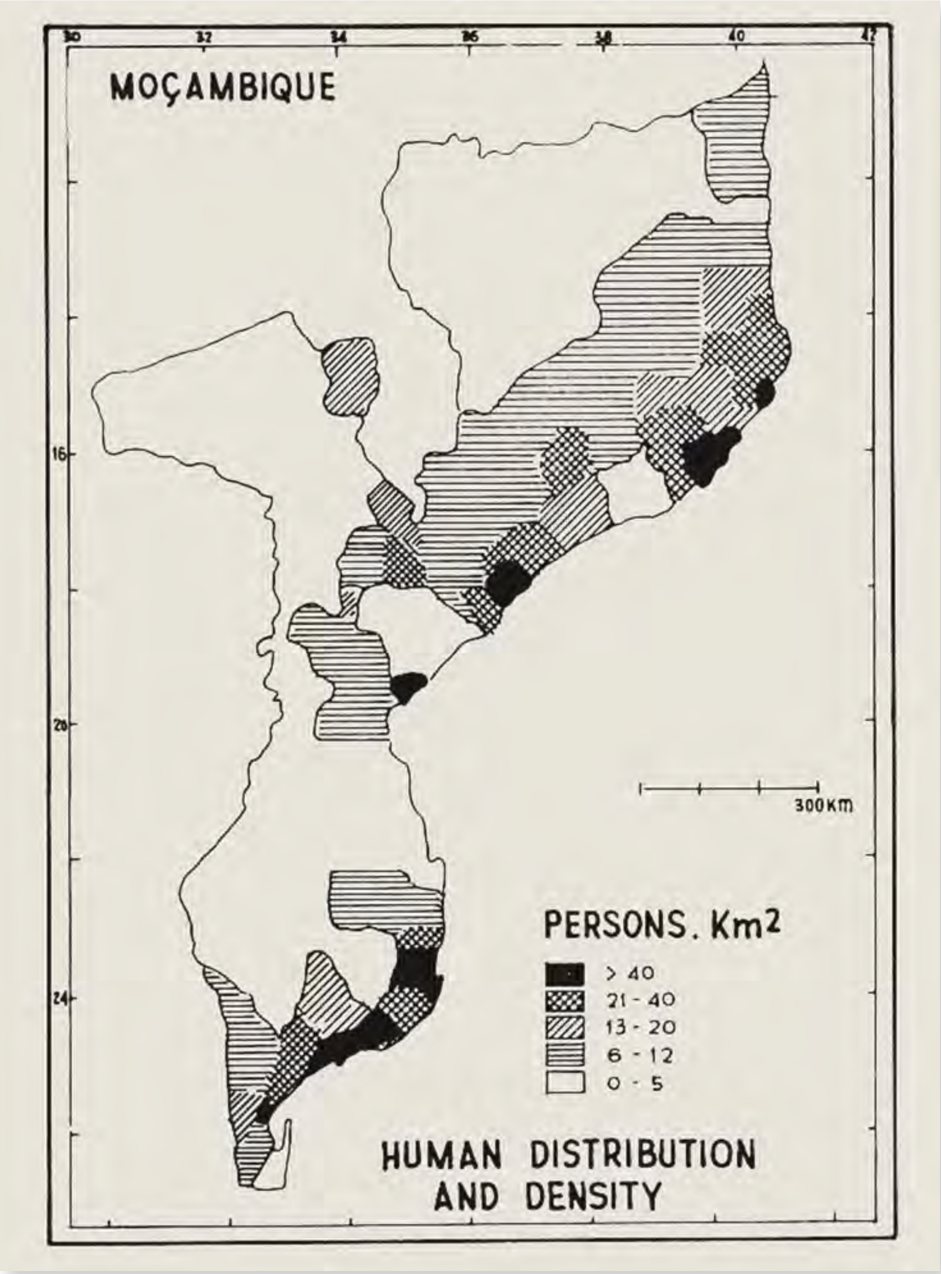
Human occupation.

RIGHT: Figure 7.1 *Cont.*

Background to human influences on Mozambique landscapes.

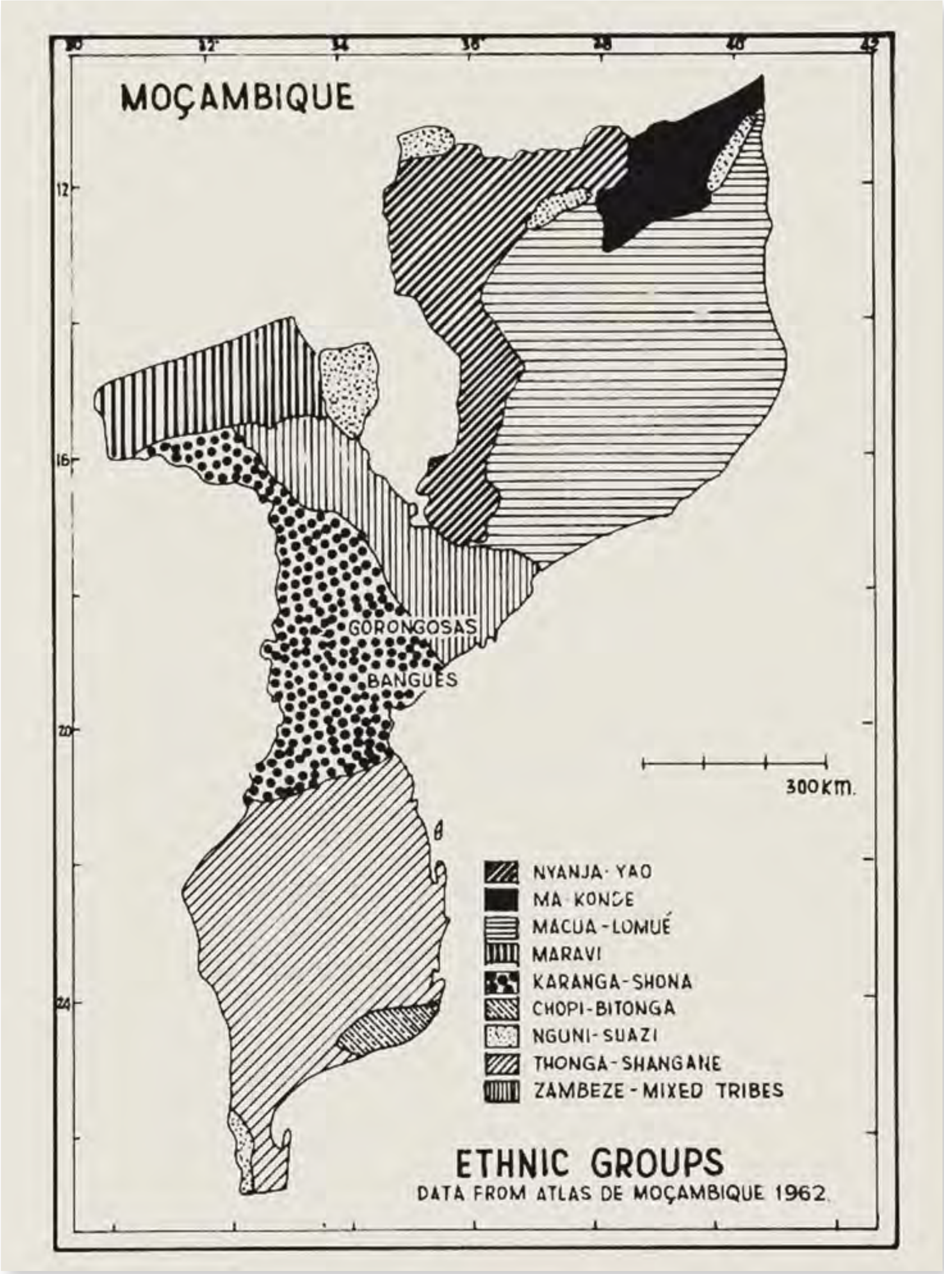
RIGHT:

Human distribution and density.



FAR RIGHT:

Ethnic groups.



withstand the occurrence of midsummer droughts and general predominance of poor sandy soils. Maize is of second import, or the major crop locally where more fertile pockets of soil occur. Other crops include ground-nuts, pumpkin, cassava, sweet-potato, *Colocasia* (taro) and various beans. In drought years the ripe grains of indigenous grasses are gathered, especially *Panicum maximum*, a robust 3 m tall form which is abundant in pure swards on certain Rift alluvia in the shade of *Piliostigma thonningii* and *Acacia sieberiana* savanna woodlands and on the heavier black soil patches in *Brachystegia* riverine areas. *Urochloa mossambicensis, Echinochloa* and wild sorghum are also important grain foods at such times.

Certain families specialize in bee-keeping for which undisturbed miombo savannas are a pre-requisite. There is thus a friction between the cultivators and beekeepers as one displaces the other. Land hunger pressures due to population increases or cash crop demands cause the remaining undisturbed woodlands to be utilized and the bee-keepers are then forced to move. No cattle are kept, and goats only rarely, due to the prevalence of trypanosomiasis (nagana), thus the region has escaped the ravages of overstocked pastoralism (Fig. 7.1).

The daily and seasonal life requirements of tribes-people that can be obtained from the land include: veld (bush) foods, plant medicines, construction materials, famine foods, animal foods, honey, wax, thatch, firewood, binding materials (twine, rope) weaving materials, cosmetics, oils, dyes and tannins, gums and resins, spices, spinaches, and hunting materials including poisons. Prior to 1950 the tribes-people living on the Rift Floor bartered game meat, fish or salt for grain from the people of the higher rainfall plateaux on either side of the Rift, especially when midsummer or extreme dry seasons occurred in the Rift. Salt was gathered from the salt rings which form around the bases of termitaria in the areas of saline vertisols on the floodplains.

Under primitive conditions the spatial distribution of tribal cultivators is controlled by that of perennial water, suitable soils and social ties. Such patterns would be temporarily disrupted at intervals by invasion of warring tribes. At these times the cultivators hid away in sites of seclusion such as Gorongosa Mountain, which was used by the Chegorongosa during the invasion of the Maconde from the north.

The present distribution and abundance of tribal cultivators in and around the park is shown in Fig. 7.2. The striking feature of their present concentration patterns is their relation to roads (e.g. along the old main road to Inhaminga), stores, and lumber camps, all of which bear no relation whatsoever to the spatial distribution of soils most suitable for cultivation. Other patterns are more significant and fundamental as they relate directly to water and optimum soils, for example those on alluvial fans and the red clay loams associated with dolerite dykes (locally referred to as 'matakamashaa'). Part of the past distribution (Fig. 7.2), as obtained from local headmen, shows one striking contrast with the present pattern and which is the result of perhaps the most ironic affair in the chequered history of changing park boundary limits.

Until the 1950s the Rift Floor area between the Pungue River and the Urema Lake, and between the floodplains and the western slopes of the Rift Valley, supported the greater part of the human population now shown on the dissected midlands between the Rift and the eastern base of Gorongosa Mountain. There were, therefore, only rare tribal cultivators in the area between the mountain and the Rift Valley, and shifting cultivation with large cotton cash crop production took place in the Rift Floor areas noted above. At this time the main concentrations of wildlife were on the floodplain areas north (Macoreia) and northeast (Guinha) of the Urema Lake. In the 1950s the human population on the Rift Floor area was moved out of the Park and settled in the area around the base of Gorongosa Mountain as no one in authority realized that the entire park ecosystem and about 12,000 tribes-people south of the mountain were dependent for their perennial water solely on the water flowing off Gorongosa Mountain. The addition of a large population to the eastern base of the mountain resulted in encroachment of the catchment and riverine areas on which all life depends.

7.3 CULTIVATION

Shifting cultivation can decrease the area of forest, replacing it either with open communities or with thicket, and spread the increase of thicket in savanna areas when left fallow for long enough. Not only are there far reaching changes in the physiognomy and composition of the vegetation due to selective felling and clearing, but new erosion cycles (especially nickpoints) are initiated and older processes are accelerated, and in this way soil moisture regimes are changed. These changes are greatest, or most permanent, where forest and savanna systems interdigitate in tension zones of ecological instability.

Apart from alluvium and soils derived from basic rocks, the soils of the Gorongosa region are predominantly poor and sandy. Thus over the greater part, cleared land is only occasionally used for semi-permanent cultivation, i.e. for periods of up to 12 years without respite. The indicator plants used by the tribal cultivators to discern the best soils are the trees *Piliostigma thonningii* and *Acacia sieberiana* and the grasses *Pennisetum purpurem*, first and foremost, then *Panicum maximum* and *Hyparrhenia rufa*.

The cultivators quite naturally prefer to use sites where the least work is required. Thus in mountain and flatland, the margins of grassy drainage lines are used first,

RIGHT: Figure 7.2

Distribution and numbers of tribal kraals in the Gorongosa system.

FIG 7.2

DISTRIBUTION AND NUMBERS OF TRIBAL KRAALS IN THE GORONGOSA SYSTEM
(DATA FROM AIR COUNT BY K.L. TINLEY 1971)

although seasonal waterlogging requires mounding of the soils on which the crops are planted. Next in preference are savannas, and lastly thicket and forest which require the most work in clearing. Some of the savanna and riverine areas covered in *Pennisetum* require an inordinate amount of work to remove the large tough tufts of this grass, but it is well worth the effort as these soils are amongst the most productive. It is significant that areas of savanna replaced by thicket only require half the usual 15 to 20 year fallow before they are used again. The reason for this is probably a faster build-up of humus under thicket than in secondary savanna where annual fires burn each year's leaf-fall supply. The report by tribesmen of the rejuvenating effects of secondary thicket on soils, as opposed to secondary savanna, is supported by the findings of Gillman (1945) in the Maconde thicket cultivation system near the Rovuma in Tanzania (Tanganyika).

In wooded areas clearing begins in midwinter; the trees are felled at waist height and left where they have fallen until October. Everything is then burnt, leaving a dense ash over large parts of the clearing. First rains arrive in November and planting begins just before their arrival. In the Gorongosa region one hectare is the general size cleared and planted per year by a family. Sorghum and maize are planted, the former only being reaped in May to June. In the second year, hoeing of the same clearing is required to remove grass and weeds, these are then thrown into small piles and burnt.

Preparation in the second year is only begun in September and October. Sorghum and cassava are planted, and in the third year mostly cassava, as the soils are at their poorest. Depending on the type of secondary cover which re-invades during the subsequent fallow, the area is not used again for a period of 10 to 20 years. A grass scrub replacement requires the longest fallow period and scrub thicket the shortest. On the slopes of Gorongosa Mountain crops are planted behind boulders because of the steep slopes (30°) on areas that once supported rain forest. As most of the perennial streams born on the mountain are small, cultivation and burning of their catchments results in their permanent destruction as perennial flows, and running water is thereafter confined to each occurrence of rain. These effects force families to move along the contour to undamaged sites with perennial water. The greatest tragedy of all is that a relatively few tribal people are thus responsible for destroying their own water resource and affecting thousands of their own people downstream, as well as jeopardizing the park ecosystem as a whole.

In riverine areas two, or even three, crops a year are obtained as the river water recedes. The bottom lands are planted with maize and beans in the autumn, then again in mid-winter giving harvests in August and October before the rains arrive in November.

7.4 BEE-KEEPING

In common with most of the tribes occurring in the miombo savannas of Africa, those on either side of the Rift Valley practice bee-keeping. This form of husbandry is practiced throughout Mozambique in the miombo areas as far south as the Limpopo River. Many individuals own more than 20 hives (up to 50 reported) which makes this a full-time, specialist occupation.

The hive is made from a bark tube removed from the basal 2 m of a living miombo tree. *Brachystegia boehmii, B. spiciformis*, and *Julbernardia globiflora* are particularly used. From the two latter species bark is removed in the mid-rains period when it strips off most easily. However the first species strips cleanly throughout the year and is, therefore, the most valuable. This feature is well known by elephant, who strip the bark of *B. boehmii* throughout the dry winter season ignoring the other species until summer.

The tube is made by cutting around the trunk of the tree at two ends, one longitudinal slice is cut between them so that the bark can be peeled off in one piece. Wooden pegs are driven through the now overlapping longitudinal slit and the ends closed with coils of palm leaf or grass. The bark tube is then lodged in a tree as high as possible so as to be conspicuous to swarms or scout bees passing over the canopy (Guy 1971). In the hot dry period prior to the first rains in November, when swarming occurs, the general leaflessness of the trees renders the hives more obvious. Lodging the bark tubes as high as possible also protects the hives from the honey badger and from veld fires, which in 3 m tall grass scorches trees to a high level. A more recent innovation to foil honey badgers is a thin metal sheet attached around the base of the tree which acts as an effective skid. The propolis of stingless bees is used to bait new bark hives. Honey is removed mainly in the autumn and early winter, and the wax is moulded into blocks and sold at trading stores.

The phenology of the miombo and Rift Valley system is described in Chapter 8, and

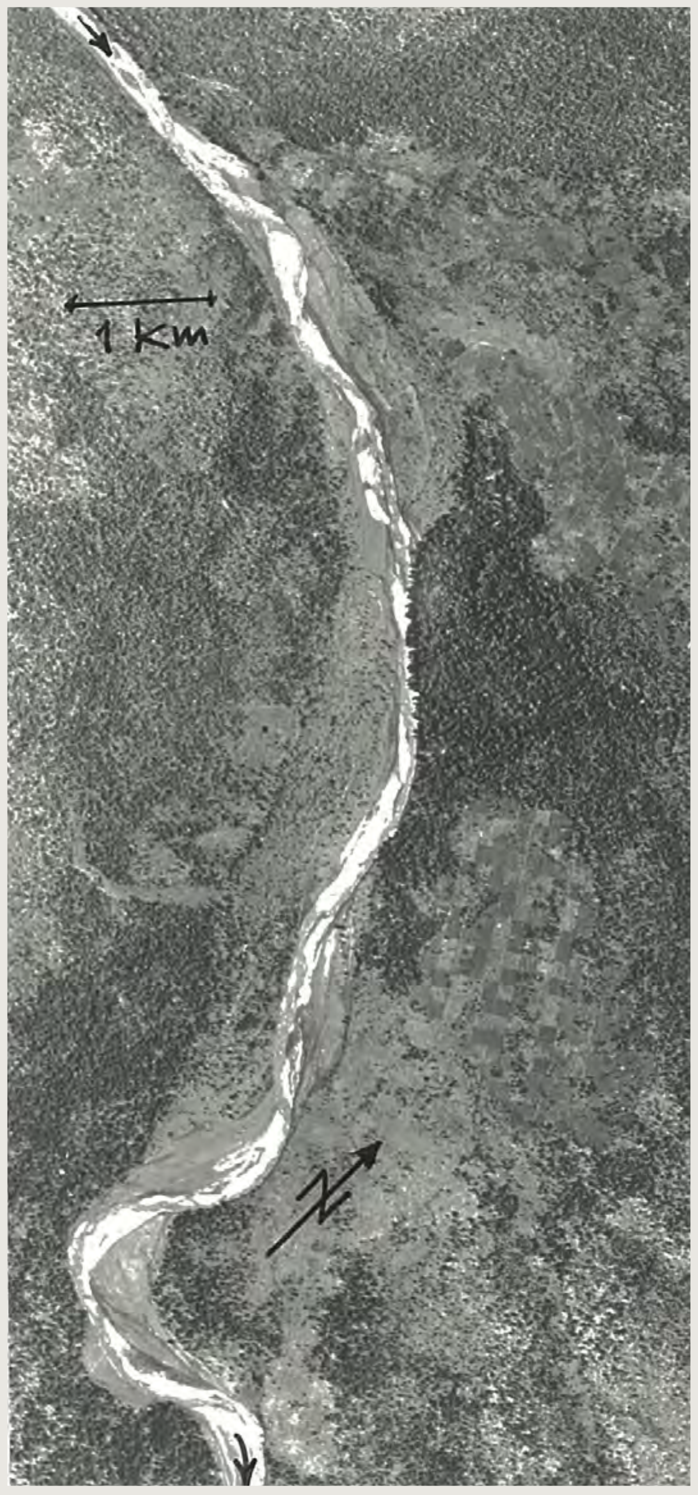
Mapira (sorghum) cultivation in cleared miombo savanna woodland of the Midlands

LEFT:

Nhandue River, from a Midland catchment, where it enters the Rift trough near Canganetole. A tall big-timber riverine forest remnant of *Khaya nyasica*, *Milletia stuhlmanii* and *Sterculia appendiculata*. Note invading shifting cultivation from both ends.

RIGHT:

Shifting cultivation on shallow sandy soils developed on crystalline migmatitic granite-gneiss (2 to 3 year use with 15 to 20 years fallow). Photo: J. L. P. L. Tello



shows the seasonal peaks and sequences of flowering in closely related species in the same system and between the different ecosystems. Bees are active throughout the year in the region and in March, bees have been recorded in the canopy of mopane woodland, for example, actively collecting propolis from the sweet resin secretions of the leaves and new bark of the terminal branchlets. Bees also collect grass pollen much more than is generally realised. This activity occurs in the early mornings whilst the pollen is moist and sticky. *Cynodon dactylon* and *Echinochloa* species appear to be the most important. As the primitive bee-hive smokers are made of a bundle of green, and partially dry, grass which are abandoned as soon as they catch alight, the bee-keepers are major culprits in setting fire to the countryside in the autumn.

The ravages of cultivating on water catchments.

TOP LEFT:

Before—perennial rainforest stream on southwest slope of Gorongosa Mountain.

BOTTOM LEFT:

After—the same stream several kilometres below the preceding photo, near the base of the mountain where riverine forest has been cut and burnt in stages upstream for cultivation.

7.5 FISHING

Various fishing methods are practiced by the tribespeople in both the floodplain areas and in the small streams of the uplands. Reed barriers with valved baskets are used in seasonally flooded plains, similar to those described for southern Mozambique and Tongaland (Tinley 1964). The thrust baskets are similar in construction to those of the upper Zambezi and Okavango (Maclaren 1958), which have an extension of wattles past the upper hand opening to form a handle. Plant poison is also used in fishing, chiefly in the upland areas including Gorongosa Mountain, and when applied indiscriminately some streams become fished out. This is tragic, not only as a waste of a resource, but as the little scientific collecting done here has shown the presence of newly described endemics such as *Parakneria mossambica* (Jubb & Bell-Cross 1974); unique biotic elements can be lost before they are known.

The plant poisons are derived chiefly from the pounded stem and root-bark of trees and shrubs such as *Strychnos potatorum, Mundulea sericea,* and *Albizia versicolour*. In the drier areas of the Zambezi and Save Valleys, bark of the riverine tree *Croton megalobotrys* is important. The large-tubered *Neorautanenia mitis*, with annual aerial parts, is a potent fish poison used from coast to coast between the 15^0 and 20° latitudes where it occurs on compacted sands or calcareous sandy clays. The tuber is cut up into small pieces, pounded, and then sown into the water in the normal way. The roots of an unidentified shrub known as *nyakorakota* and a cultivated plant *mutika* (*Tephrosia sp.*) are also used as fish poisons.

Prior to the use of manufactured string, fish nets were made of fibre from baobab bark and *Sansevieria*. The nets were then preserved by soaking in boiled bark chips of tannin-rich species such as *Euclea, Ficus, Piliostigma, Lannea* and *Acacia.* On the coast, the bark from mangroves such as *Bruguieria gymnorrhiza* is used. Most of the baobabs in the Urema Trough have large rectangular scars where sheets of bark were cut out for making cord, including nooses strong enough to snare animals the size of wildebeest and sable.

Barbless spears are also used for fishing. The spear shafts are generally made from the solid-stemmed bamboo *Oxytenanthera abyssinica* common in the higher rainfall savannas on either side of the Rift. The bamboo is of course used for many other purposes including the construction of huts and grain stores.

7.6 CASH CROPS

In addition to the unfortunate but inevitable industrially orientated grid (Tinley 1971) imposed on the land and people, by roads, trading stores etc. (Figs. 7.2 and 7.4), perhaps the greatest iniquity was the introduction of a cash crop economy to shifting cultivation cultures. As noted above, shifting cultivation is a means of obtaining the highest productivity from a poor substrate, by the process of alternating cultivation with long periods of fallow. Thus any clearing of land required above the annual food-growing requirements of a family means that the bank of land for future use is expended for a cash return.

Cotton is the main cash crop which is grown around and, until the early 1950s, inside the national park on the Rift floor north of the Pungue River. Cotton growing by each family requires opening up three to four times the area required for food over the same shifting cultivation cycle. In this way, land hunger under relatively low population concentrations develops and causes a typical chain reaction. Pressure to return to fallow areas too soon results in diminished yields and stunted crops. This then forces the clearing of riverine and forest vegetation resulting in damaged catchments and spring areas. Politically, grave problems then arise as the tribal people, who have never directly benefited from the park they surround, demand park land to make up the shortage caused by cash crop cultivation.

The latest intrusion in the Rift Valley on a grand scale is the cultivation of sugar, which requires heavy irrigation in the winter due to the extreme Rift Valley dry seasons and the added problem of salinization then arises. The Pungue plains, crossed en route to Beira, are now under sugar but were reported to have been covered by tremendous herds of buffalo, similar to the Zambezi Delta, in the 1940s.

The cash crop agriculture in Mozambique was merely shifting cultivation on the large scale, as after three years the soils became exhausted and it was uneconomical to fertilize such large areas. Thus a new wooded area would be cleared and used for the next three years. In this way vast areas were rendered useless to tribal cultivators, forcing them into larger concentrations and resulting in devastation of water catchments, riverine areas and invasion of the specially protected forest reserves and national park areas.

Under such inexorable pressures it is surprising that any areas retain their pristine conditions. It is also clear that authorities can seldom resolve this problem as they tackle the results and not the primary causes. The irony of this successional process of land devastation, and the disruption of tribal social life and their precarious balance with the land resources, is that this is the procedure adopted by the industrial approach to 'development' of a country.

7.7 TIMBER EXTRACTION AND CHARCOAL BURNING

In addition to cash crop pressure, the invasion of timber extraction companies, with each company vying to take out the most in the shortest possible time, has caused widespread damage to virgin forest and savanna woodland areas. The temporary establishment of timber extraction stations or sawmills sets in train another typical succession. Access roads made into uninhabited areas, and bulldozed tracks through forests to extract the largest timber, provide ready made clearings for shifting cultivators. Temporary lumber camps and sawmill sites are also responsible for new human settlements in otherwise uninhabited country. Once the timber supply is exhausted from an area the companies move on, leaving nuclei of cultivators where trading stores have become established.

The traders then set up their own systems of barter, especially in drought (famine) periods, when meal is supplied in exchange for animal pelts. To obtain animal pelts, more and more ingenious snaring methods are employed until the habitats become cleaned out. Thus the wildlife meat resource is reduced to near extinction levels long before company bulldozers come to open up new wooded country on the large scale for the production of cash crops.

The main timber species extracted from the mosaic of forest, miombo and riverine areas on either side of the Rift Valley include the following:

Adina microcephala	(for railway sleepers)
Brachystegia spiciformis	(for railway sleepers)
Burkea africana	(for railway sleepers)
Cassipourea gummiflua	
Chlorophora excelsa	
Erythrophleum africana	(for railway sleepers)
Erythrophleum suaveolens	
Khaya nyasica (mbaua)	
Millettia stuhlmannii	(panga-panga)
Pterocarpus angolensis	(mbila)

In more recent times the expanding threat to both the Miombo woodlands and forests of all kinds is by the depradations of charcoal burners. Unless they are helped to grow their own woodlots of fast-growing timber, such as eucalypts for example, this degradation of wooded land will continue.

7.8 SELECTIVE INFLUENCES ON HABITATS

Selection is on several fronts, and all influence the differential success of species in recolonization and succession according to the efficacy of their dispersal mechanisms. Useful trees which provide edible fruit or perennial shade are often left standing by man and they eventually come to dominate the landscape. An example of this type of selection is the cultural-savannas in the Macia area, as seen from the main road between the lncomati and Limpopo Rivers in southern Mozambique. Those woody species most useful as wattles for hut construction are changed by overcutting to a more productive multiple-stemmed growth form, or are eliminated from an area. Other multiple-use species such as baobab *Adansonia digitata* are either planted around kraal sites, or grow from the refuse heaps where the unused parts of edible fruits and seeds are thrown. On the Rift Valley plains for example, islands of baobabs on mounds are generally associated with old hearths and masses of pot sherds now being exhumed by the incisional erosive phase of the plains. Secondary growth on fallow fields is composed of weeds (usually alien plants), primary invader species, and coppicing of some of the woody species from the original mature woody cover. These regrowths typically form even-aged stands, sometimes of one or several species paralleling the appearance of primary savanna invasions of floodplain areas. Fire, used excessively (twice a year) to clear secondary growth or tall coarse grass cover, also has a selective influence.

Removal of these selection pressures by movement of people to another area provides a mosaic of different aged stands at different stages of succession. Although edaphic controls may still determine the species composition in different sites, these disruptions can confound or make a mockery of naive approaches to explain pattern and process purely by physical environmental factors alone.

The impact of peasant cultivators, accelerated by new pressures and controls of industrially orientated cultures, has thus had far-reaching implications in influencing the appearance and composition of many present-day ecosystems.

The part played by shifting cultivation, pastoralism, timber extraction and other forms of landuse, in moulding the cover and surfaces of present-day landscapes, is thus essential for meaningful interpretation and analysis of many present geomorphic processes and biotic systems.

REFERENCES / CORRELATION

HUMAN

Allan, W. 1965. *The African husbandman.* Oliver & Boyd, Edinburgh & London.

Axelson, E. 1973. *Portuguese in south-east Africa 1488-1600.* Struik, Cape Town.

Balsan, F. 1970. *Ancient gold routes of the Monomotapa kingdom.* Geog. J., vol. 136 (2), pp. 240-246.

Carvalho, M. De 1969. *A agricultura tradicional de Moçambique.* Lourenço Marques, Missao de Inquerito Agricola de Moçambique.

Dickinson, R.W. 1975. *The archaeology of the Sofala coast.* S. Afr. Archaeol. Bull., vol. 30, pp. 84-104.

Dumont, R. 1966. *False start in Africa.* Andre Deutsch, London.

Fagan, B.M. 1965. *Southern Africa during the Iron Age.* Thames & Hudson, London.

Garlake, P.S. 1967. *Seventeenth century Portuguese earthworks in Rhodesia.* S. Afr. Archaeol. Bull, No. 21, pp. 157-170.

Gillman, H. 1945. *Bush fallowing on the Makonde Plateau*. Tanganyika Notes and Records, 19, pp. 34-44.

Guy, R.G. 1971. *Moçambique (beekeeping in)*. S. Afr. Bee J., vol 43 (5), pp. 11-19.

Huffman, T.N. 1974. *The linguistic affinities of the Iron Age of Rhodesia.* Arnoldia (Rhod.), No. 7 (7).

Jubb, R.A. & Bell-Cross, G. 1974. *A new species of Parakneria Poll (1965) (Pisces, Kneriidae) from Moçambique.* Arnoldia (Rhod.), No.6 (29).

Kent, R.K. 1968a. *Madagascar and Africa I*. J. Afr. Hist., vol. 9 (3), pp. 387-408.
—1968b. *Madagascar and Africa II.* J. Afr. Hist., vol. 9 (4), pp. 517-546.
—1969. *Madagascar and Africa III.* J. Afr. Hist., vol. 10 (1), pp. 45-65.

Leisegang, G. 1972. *Archaeological sites on the Bay of Sofala, Azania.* vol. 7, pp. 147-159.

Livingstone, D. 1857. *Missionary travels and researches in South Africa.* Ward, Lock Co., London.

Maclaren, P.I.R. 1958. *The fishing devices of Central and Southern Africa.* Occ. Papers Rhodes-Livingstone Mus., No. 12.

Mansard, W. 1974. *Tropical agriculture*. Longman, London.

Monod, T. (ed) 1975. *Pastoralism in tropical Africa.* I A I Oxford University Press, London.

Rita-Ferreira, A. 1958. *Agrupomento e caracteristicas etnicas dos indigenas de Moçambique.* Junta de Investigação do Ultramar, Lisboa.

Selous, F.C. 1893. *Travel and adventure in south–east Africa.* Rowland Ward, London.

Summers, R. 1969. *Ancient mining in Rhodesia.* Museum Mem., No. 3, National Museums of Rhodesia, Salisbury.

Tinley, K.L. 1964. *Fishing methods of the Thonga tribe in northeastern Zululand and southern Moçambique.* Lammergeyer, vol. 3 (1), pp. 9-39.
—1971. 'Determinants of coastal conservation: dynamics and diversity of the environment as exemplified by the Moçambique coast' in *Nature conservation as a form of land use.* Proceedings SARCCUS Symposium, Govt. Printer, Pretoria, pp. 125-153.

Vasse, W. 1909. *Three years' sport in Moçambique.* Translated from the French by R. and H.M. Lydekker, Pitman, London.

Vaughan-Kirby, F.V. 1899. *Sport in east central Africa.* Rowland Ward, London.

PART 2

CORRELATION

Chapter 8

Vegetation

OPPOSITE:

Large baobab west of Urema Lake near mopane.
Photo Greg Reis

Vegetation

8.1 INTRODUCTION

The vegetation of the Gorongosa ecosystem and the transect across the Cheringoma Plateau to the sea comprises a stepped sequence of moist and dry formations related to the physiography and climate. Mountain rain forest and arid saline grasslands of the Rift floor are juxtaposed within a distance of 22 km. Rain forest covers the greater part of the Gorongosa massif with montane grassland patches and heath on the summits. The Midlands support moist, closed *Brachystegia* (miombo) savannas; the Cheringoma cuesta a mosaic of moist, closed miombo savanna, extensive groundwater forests and dambos. Separating the two miombo areas is the Rift Valley trough with a mosaic of mesic savannas, dry forest, thickets and floodplain grasslands.

The major biomes represented are: moist savanna, forest and the aquatic biomes and, to a lesser extent, Afro-temperate arid savanna and the marine littoral (terms after Tinley 1975, Fig. 3). In the phytochorological terms of Monod (1957) the plant formations belong chiefly to the Angola–Zambezian Domain of the Sudano–Angolan Region (comprising chiefly the *Brachystegia* system), the Eastern Forest Domain of the Guineo–Congolian Region, the Montane Region and are in close proximity to the Southern Subgroup (**Bl Bb**) of the arid Sahelian Type in the Zambezi Valley and Gazaland. Unfortunately the more recent phytochorological treatments of Africa by White (1965; 1971) and Chapman and White (1970) have made a fundamental error in combining the southern Sudanian and Sahelian sub-types as one phyto-region, i.e. equivalent to grouping the Moist and Arid Savanna Biomes as one biotic and climoedaphic system.

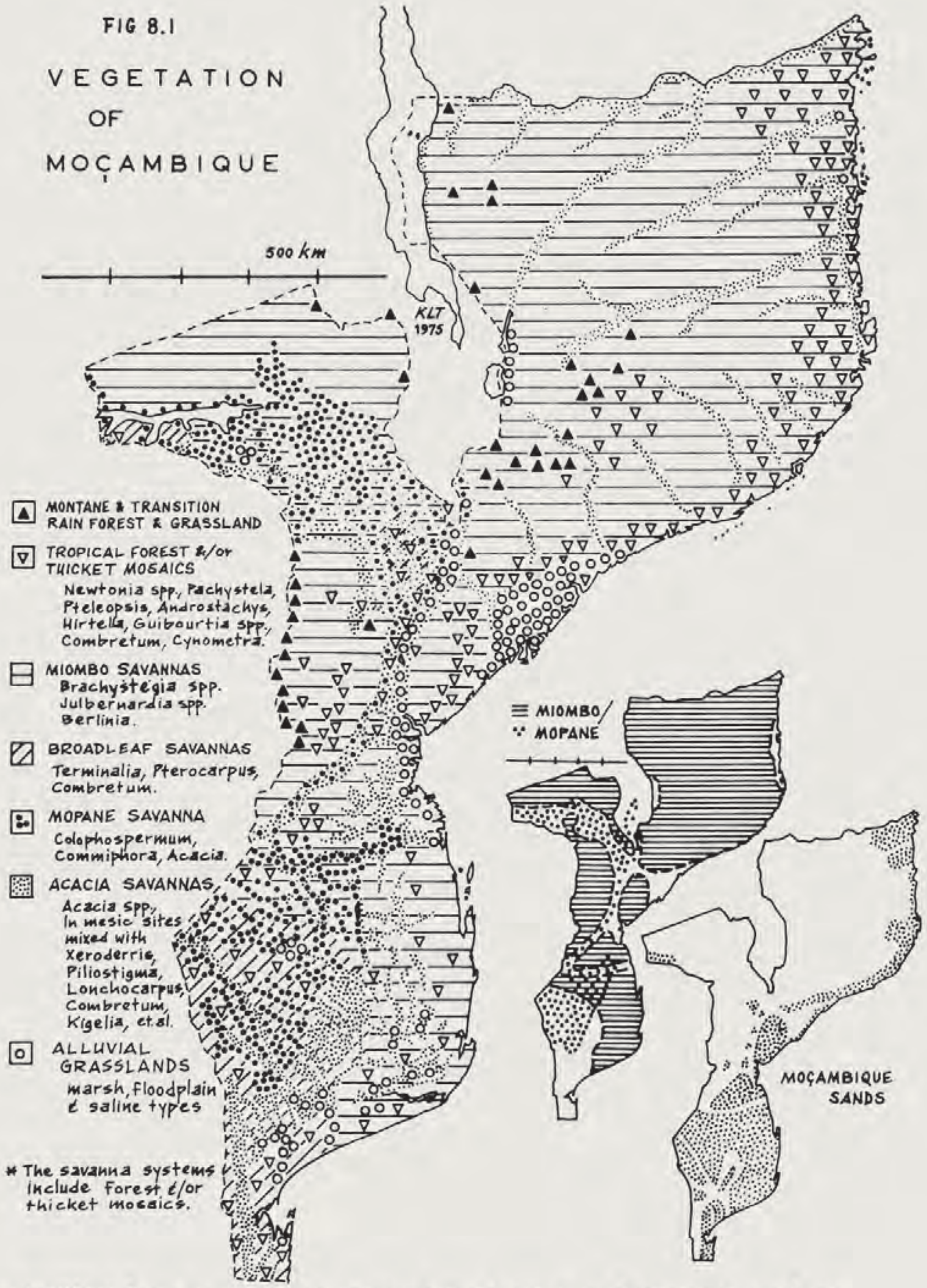
The vegetation map of Africa (AETFAT/UNESCO 1959) at a scale of 1:10 million shows five types in the Gorongosa–Cheringoma transect: montane (No. 3), forest savanna mosaic on the coast (No. 9), *Brachystegia* woodland (No.18), undifferentiated dry types (No. 20) in the Rift Valley, and mangroves (M). The 1:2 million vegetation map of Mozambique by Pedro and Barbosa (1955) and the 1:2.5 million vegetation map of the Flora Zambeziaca Area by Wild and Barbosa (1967) show 14 vegetation types. A number of this complexity of types are, however, merely a change of species dominants, or aspects of the same formation, and the present author has simplified these by means of air and ground studies to produce a more accurate depiction of spatial relations and boundaries of the major vegetation types in Mozambique and Map 2 in Smithers and Tello (1976).

In 1965 the botanist José M. de Aguiar Macedo completed a four month survey of the vegetation of both Gorongosa National Park (Macedo 1966) and Gorongosa Mountain (Macedo 1970a, 1970b). Unfortunately a vegetation map with explanatory text was made for the mountain area alone (Macedo 1970b). His preliminary report on the vegetation of the national park contains 11 schematic profiles and sections dealing with conservation, especially of the mountain forests.

In the absence of high relief, the normal climatic gradient on the central and southern coasts of Mozambique is in belts parallel to the coastline with the highest rainfall, humidity and damped temperature extremes closest to the land-sea junction. Low rainfall with high extremes and variability occur inland. This sequence superimposed on edaphic controls is responsible for the zoned nature of vegetation in the broad plains region, known as Gazaland, between the Save and Limpopo Rivers. In the Gorongosa-Cheringoma transect, a stepped physiographic sequence parallel to the coast has resulted in a stepped or disjunct climo-edaphic sequence with moist formations near the coast, dry to arid formations in the Rift Valley trough, and a repeat of moist formations on the Midlands west of the Rift. The abrupt rise of the isolated Gorongosa massif above the

FIG 8.1

VEGETATION OF MOÇAMBIQUE



simplified from the vegetation maps of Moçambique by Pedro & Barbosa (1955), & Wild & Barbosa (1967). Modified by K.L.Tinley from air & ground studies of the territory (1968–1973).

LEFT: Figure 8.1

Vegetation of Mozambique.

Riftward margin of the Midlands results in the development of orographic rains which provide rain forest conditions on its confines.

The physiognomic terms used here follow Tinley (1975). Attention must be drawn to the persistent misclassification in the literature of the *Brachystegia* (miombo) formation as open forest ('foret claire') or woodland as opposed to savannas. As the analysis in this section will show, miombo forms the moist end of the savanna or wooded grassland climo-edaphic cline between the equatorial rain forest and the deserts. Botanists seem keen to separate miombo from other savannas apparently on the criterion of their closed canopy habit. However, mopane and certain acacias also show the closed canopy habit over large areas in many situations, and the floral and faunal constituents of miombo are savannoid.

Savanna and veld are duplex systems composed of one or more woody strata, of greater or lesser density, with a nearly continuous grass groundlayer. By contrast, grasslands and forest or thicket are either almost purely herbaceous or woody; they are therefore uniform formations though they show horizontal stratification.

The subject of misapplication of successional terminology has been covered under Process and Response (Chapter 6). However, it should be re-emphasized that the separation of climatic (climax) and edaphic communities is misguided, as all communities are climo-edaphically controlled whether they are influenced or not by factors such as fire, frost, cultivation or herbivores.

The greater part of Gorongosa Mountain is covered in rain forest, and this meets grassland on the slopes, in valley heads, and on the summit areas abruptly, with little to no ecotone except where rock outcrops support thicket and scrub.

The Midlands exhibit the greatest area of a single unbroken community; that of closed miombo savanna, and thus ecotones are minimal and narrow. This contrasts with the Rift Valley floor where plant communities of diverse physiognomies and flora are juxtaposed, providing a multiplicity of both sharp and broad ecotones. A similar situation pertains on the Cheringoma Coast. It is significant that where distinct plant communities such as forest or grassland become reduced to relics, the ecotone of mixed components on transitional soils broadens to become the major plant formation or ecosystem. In this way, on the macroscale, transitional biomes can become new biomes and the original types are left as ever decreasing remnants, or they disappear entirely, though many of their components survive in new combinations.

The plant communities recognized in the montane to mangrove transect are distinguished by their contrasting physiognomic, structural, and floristic properties. Composites of these and substrate criteria circumscribe the communities on aerial photographs where they are expressed as changes in texture and tone. These properties were used as controls against one another to ensure that a community was not divided into separate types simply on height, density or canopy spacing alone. Most of the communities are closely correlated with distinct soils and/or soil moisture gradients. It is appreciated, however, that whilst conspicuous relations are exhibited between communities and climo-edaphic features, not all species distributions are incurred by these factors alone, but are also due to competition, shade, dispersal, fire and biotic influences such as grazing and human activities. A clear example, which is due to grazing pressure, are the ‘hippo lawns’ of *Cynodon* and *Digitaria* on the Urema Plains which occur on similar vertisol profiles as tall *Setaria* and *Vetiveria* grasslands.

Due to the close juxtaposition of quite different plant communities, such as dry forest on sand and mopane savanna on clays, from contiguous alternation of alluvio-catena; few communities are ‘pure’ due to the overlap of certain components on ecotonal intrusions. Thus not all species in a particular community can be regarded as typical or characteristic. The plant communities recognized are therefore associations of species having similar requirements and tolerances, implying coincidence of communal and ecological affinities, and interspersed with intrusives or colonists.

8.2 METHODS AND DATA RECORDED

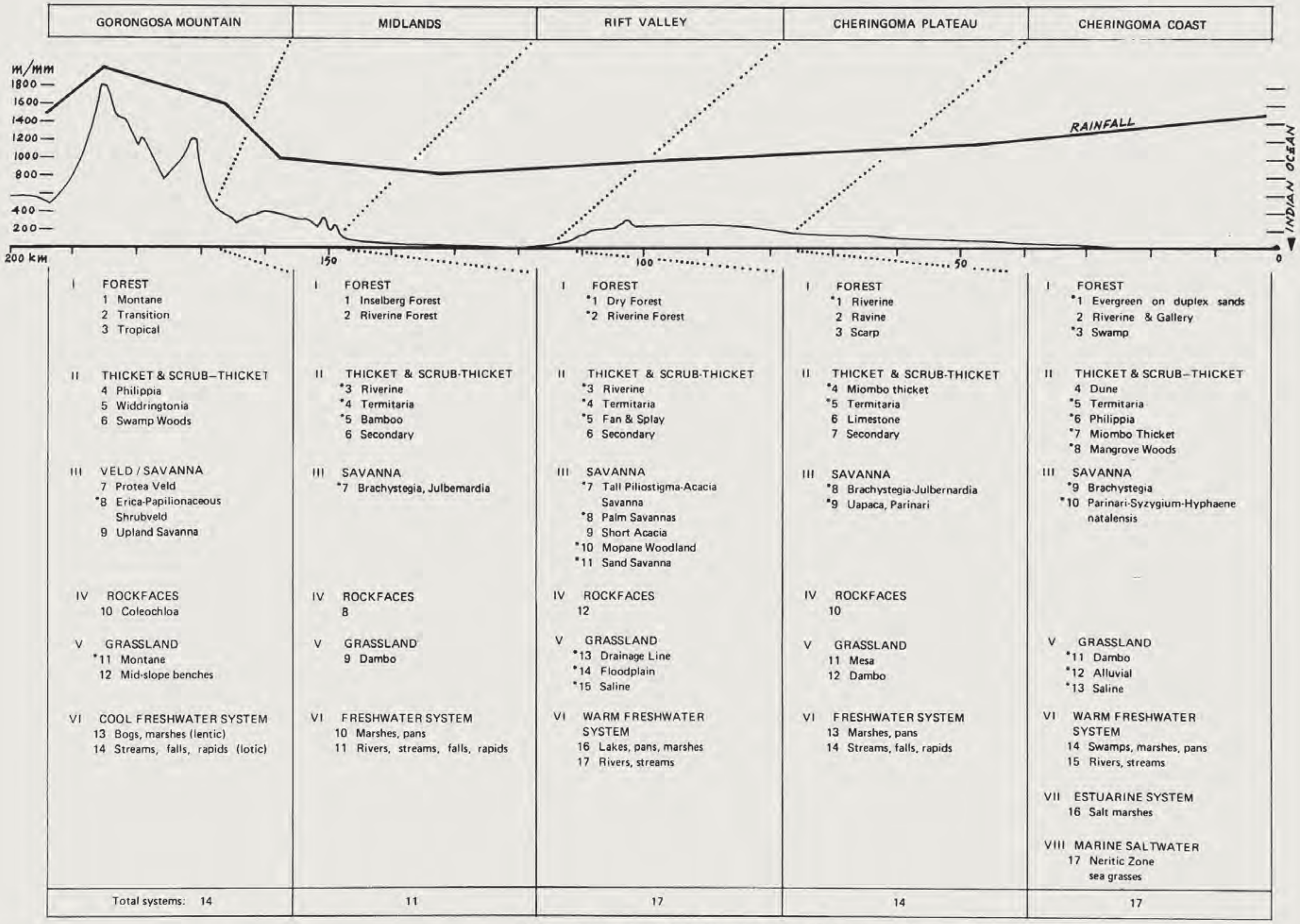
Sampling

It was originally planned to complete representative quantitative analyses at a one percent sampling level of the areas occupied by at least the major plant communities in the ecosystem. This approach had already been initiated on the floodplain grasslands of the Rift Valley, which are the key pasture areas for the majority of the large wildlife concentrations. However at this stage armed conflict in the area required a jettisoning of the ideal quantitative approach for one which would provide examples only of a variety of communities.

With the unique occurrence in the transect to the coast of a full spectrum of systems, and the closure of the western and northern sectors by active warfare, it was decided to obtain quantitative examples of the plant communities seaward of the Gorongosa ecosystem. No quantitative samples were therefore made of communities on Gorongosa Mountain, the northern sector of the ecosystem, and the ravine forests of the Riftward drainage on the Cheringoma Plateau. Those sampled are marked by an asterisk on Fig. 8.2.

Prior to the initiation of area-based sampling, a large number of methods were tested in the field, primarily to determine greatest returns for minimal time spent in view of the fact that the study area consisted of 8,700 km^2, and the transect to the coast, 100 km. These trials were aided by the guidance of Dr. Brian Walker (Botany Department of the University of Rhodesia, Salisbury) whose method of recording feeding utilization of plants by large herbivores was used throughout the sampling of all communities. The field tests showed that the quadrat and belt transect method, as described by Curtis and Cottam (1962) for example, was the most suitable sampling method as a large area was covered in each sample within a reasonable time. The point quarter method (Curtis and Cottam 1962) was the most suitable if only woody plants taller than the field layer were sampled.

Also tested in the field were the merits and demerits of using either random or systematic sampling in a 12,000 km^2 area. Random sampling, even with the aid of aerial photographs was found to be totally impractical due to the inordinate amount of time wasted in determining where each point was. Systematic sampling was thus practiced throughout, and though the first point may have been subconciously chosen, those that followed were inevitable and thus unbiased.



GORONGOSA MOUNTAIN	MIDLANDS	RIFT VALLEY	CHERINGOMA PLATEAU	CHERINGOMA COAST
I FOREST 1 Montane 2 Transition 3 Tropical	I FOREST 1 Inselberg Forest 2 Riverine Forest	I FOREST *1 Dry Forest *2 Riverine Forest	I FOREST *1 Riverine 2 Ravine 3 Scarp	I FOREST *1 Evergreen on duplex sands 2 Riverine & Gallery *3 Swamp
II THICKET & SCRUB–THICKET 4 Philippia 5 Widdringtonia 6 Swamp Woods	II THICKET & SCRUB-THICKET *3 Riverine *4 Termitaria *5 Bamboo 6 Secondary	II THICKET & SCRUB-THICKET *3 Riverine *4 Termitaria *5 Fan & Splay 6 Secondary	II THICKET & SCRUB-THICKET *4 Miombo thicket *5 Termitaria 6 Limestone 7 Secondary	II THICKET & SCRUB–THICKET 4 Dune *5 Termitaria *6 Philippia *7 Miombo Thicket *8 Mangrove Woods
III VELD / SAVANNA 7 Protea Veld *8 Erica-Papilionaceous Shrubveld 9 Upland Savanna	III SAVANNA *7 Brachystegia, Julbemardia	III SAVANNA *7 Tall Piliostigma-Acacia Savanna *8 Palm Savannas 9 Short Acacia *10 Mopane Woodland *11 Sand Savanna	III SAVANNA *8 Brachystegia-Julbernardia *9 Uapaca, Parinari	III SAVANNA *9 Brachystegia *10 Parinari-Syzygium-Hyphaene natalensis
IV ROCKFACES 10 Coleochloa	IV ROCKFACES 8	IV ROCKFACES 12	IV ROCKFACES 10	
V GRASSLAND *11 Montane 12 Mid-slope benches	V GRASSLAND 9 Dambo	V GRASSLAND *13 Drainage Line *14 Floodplain *15 Saline	V GRASSLAND 11 Mesa 12 Dambo	V GRASSLAND *11 Dambo *12 Alluvial *13 Saline
VI COOL FRESHWATER SYSTEM 13 Bogs, marshes (lentic) 14 Streams, falls, rapids (lotic)	VI FRESHWATER SYSTEM 10 Marshes, pans 11 Rivers, streams, falls, rapids	VI WARM FRESHWATER SYSTEM 16 Lakes, pans, marshes 17 Rivers, streams	VI FRESHWATER SYSTEM 13 Marshes, pans 14 Streams, falls, rapids	VI WARM FRESHWATER SYSTEM 14 Swamps, marshes, pans 15 Rivers, streams
				VII ESTUARINE SYSTEM 16 Salt marshes
				VIII MARINE SALTWATER 17 Neritic Zone sea grasses
Total systems: 14	11	17	14	17

FIG 8.2 ECOSYSTEMS & PLANT COMMUNITIES IN EACH PHYSIOGRAPHIC UNIT OF THE GORONGOSA – CHERINGOMA TRANSECT

LEFT: Figure 8.2

Ecosystems and plant communities in each physiographic unit of the Gorongosa-Cheringoma transect.

Presence, Density, Frequency

The quadrat and belt transect method described by Curtis and Cottam (1962) was used to analyse the various strata of all plant communities, from grassland to forest, so that results would be comparable.

Trees

All trees taller than 3 m were counted in plots of 1 ha in savanna, or in 500 m^2 subplots in forest and thicket. Total counts were made of island communities such as termitaria thickets.

Data recorded

Species, height, diameter breast height (dbh at 135 cm above ground level), and degree of utilization by ungulates (0 to 5). The latter data will be elaborated in Section 9.5.

Results

Expressed as: (a) no. of each species
(b) relative density (total of one species/number of total species)
(c) total basal area in cm^2.

Shrub or field layer (50 to 300 cm in height)

Sampled by means of total counts in four (1 m x 25 m) belts across subplots in forest and thicket (total area of 100 m^2). In the savanna plots of 1 ha, the field layer was sampled by means of five (5 m x 20 m) equidistant belts in dense cover and five (10 m x 20 m) in open cover.

Data recorded

Species, height, and degree of utilization.

Results

Expressed as: (a) number of each species
(b) relative density %.

Grass or herbaceous stratum

Sampled by a minimum of 10 (1 m^2) quadrats per 300 m^2 subplot in forest or thicket. and by 30 (1 m^2) quadrats per hectare at 20 m intervals in savanna and grassland. In relatively homogenous grasslands 15 (1 m^2) quadrats were used in one hectare or half hectare plots. Where two well-defined layers occur within this stratum, two sets of readings were made, e.g scrub invasion within a taller grass sward, or tall weeds in short grassland.

Data recorded

Species, dominants (in cover-abundance), height and degree of utilization.

Results

Expressed as (a) number of quadrats of occurrence
(b) relative frequency % (out of total number of occurrences).

Physiognomy

Physiognomy and floristic composition were recorded by means of profile diagrams drawn to scale onto graph paper along belt transects (Davis & Richards 1933) using measuring poles for horizontal distance between individual trees, and for the height of lower storey components. Canopy tree heights were measured by triangulation and cross-checked against windthrown or elephant-felled trees. Belt transects were 5 m x 60 m in forest and 10 m x 60 m (up to 200 m) in savannas and across ecotones.

Bisects of thicket were 5 m or 10 m wide and for scrub thicket (e.g. heath) 1 m or 2 m in width. Sample size was adjusted to the density of cover. In addition, visual estimates were made to construct cover-stratification diagrams as shown in Cain & Castro (1959, 223).

Phenology

Over a period of three to four years the phenophases of woody plants were recorded on the Midlands and in the Rift Valley, and to a lesser extent on the Cheringoma Plateau. The phenology of the highest summit grassland and its associated forbs on Gorongosa Mountain was made once a month over a two year period. Phenonophases recorded for woody plants included mature leaf (mt), leaf fall (lf), bare (ba), new leaf (nl), flowering (fl), fruiting (fr). The occurence of different stages on separate trees, or on the same plant is indicated in the tables by the concurrence of symbols in a month. A minimum of five specimens of each species in a particular phase was required for recording a positive occurrence. Rare or inconspicuous species would have been underscored. Although these data were noted whenever I was in the field, road traverses of 100 km were made once a month, latitudinally across the ecosystem as far as the Cheringoma divide.

No data were collected on the following aspects: (1) the number of species in different phenophases per unit area, (2) quantitative records on similar species in different situations, and (3) the pollinators. Phenological data will be included under the plant communities of each physiographic feature and then compared under a separate heading. Plant foods and cover availability for animals through the annual cycle is the complementary aspect of plant phenophases.

Dispersal

To obtain even a rudimentary understanding of the interrelations and dynamics of succession and evolutionary tendencies in the development of ecosystems, a knowledge of the part played by dispersal agents in different plant communities is fundamental.

Methods of dispersal of a large number of plant species were observed but many others have had to be arbitrarily designated according to their seed morphologic characteristics. Thus all drupe, berry and arillate seeds are designated as animal dispersed, plumed or winged seeds and pods as wind dispersed, and those with explosive dehiscing pods or capsules as active ballists. It is appreciated, however, that many of these are polychorous, being disseminated by several methods according to circumstances. Where this is known, all agents will be included without attempting to determine the most important agent. Examples of polychory include the wind-blown pods of *Colophospermum mopane,* which are also carried by sheet and rill wash during rains and deposited on ebb lines along microrelief features. They can also be dispersed by animals such as elephants. The succulent tree euphorbias have explosive capsules which can throw the seeds several metres from the mother plant. These seeds are avidly eaten by doves and voided from perches resulting in these species becoming major components of thicket clumps. Acanthaceae which have explosive capsules are in addition dispersed by birds once the seeds have been thrown, and are also found germinating in buffalo dung. Other species with berries may have to rely on wind dissemination once the berries have dried out. With these limitations in mind, the woody plant components have been used in an attempt to characterise various plant communities. The data are illustrated in comparative compound diagrams showing percent occurrence of dispersal types, and the importance of such methods in each community, by adding the relative density of frequency of the species involved where these have been determined. The dispersal classes have been determined from personal observation and guidance from published data and the books by Ridley (1930) and Van der Pijl (1972). The classes are noted by capital letters in brackets after each species and are open to additions or corrections by other workers: Z =animal-dispersed (zoochory), V =by weight (barochory), Y =water (hydrochory), W =wind (anemochory), X =by explosive dehiscence and seeds thrown (active autochory or active ballists). A question mark after any of the symbols means that the case is uncertain.

The succeeding chapters will show the salient part played by the various dispersal types in coaction with the animal components in influencing succession and landscape evolution.

Soil Properties and Edaphic Features

Soil pits and auger samples were made in every plant community and quantitatively analysed by the Soil Science Department, University of Pretoria for pH (H_20), salinity R (ohms) and percent effervescence of free carbonates $CaC0_3$ (using dilute HCl).

Layout

Due to the influence of contiguous surfaces on succession and system interactions, and the influence of adjacent communities on the floristic relations of a community, the vegetation types of each physiographic feature are dealt with together, following the same procedure used in previous chapters. Within each feature, however, communities with similar physiognomy are placed together in order of relative complexity, from herbaceous communities to forest. The subheadings used within each physiognomic group include:
(a) physiognomy, structure, composition,
(b) dispersal,
(c) phenology/availability,
(d) environmental factors,
(e) succession.

A final section will synthesize the chapter by means of comparative analyses and floristic relationships of the communities.

8.3 GORONGOSA MOUNTAIN

With its greater axis longitudinal, the oval form of Gorongosa Mountain rises steeply from the Midlands between 400 m and 500 m to over 1,800 m. This presents two major faces to the elements, a northern and western xerocline comprising equator-facing rain shadow (lee) slopes, and a southern and eastern mesocline of poleward-facing and rain-ward (windward) slopes. A northeast-southwest diagonal marks the transition from one to the other. This has resulted in aspect and altitudinal

Summit and Slope Aspects of Gorongosa Mountain

asymmetry of the rain forest lower margin: from 500 m on the mesocline to the 1,200 m contour on the xerocline where the lower margins extend down stream gorges linking with the riverine strips of the Midlands and Rift Valley. Dry savannas, more typical of the valleys and drier areas of the miombo system occur in the xerocline, with thickets on colluvium or talus materials of mixed composition. The mesocline savanna and thickets meet the lower margins of the rain forest usually abruptly, accentuated by past and present shifting cultivation. The upland savannas on the mesocline comprise the moister end of the miombo system and thus contain species typical of skeletal soils plus others found nowhere else in the region.

The rainshadow effect caused by the mountain mass is most marked at the base, and immediately west of the mountain just outside the ecosystem limits. Here, savanna species typical of the hot low-lying Rift Valley are mixed with miombo or alternate on the mosaic of sands and clays, the latter supporting the valley species. On the mesocline, forest is rapidly confined to riverine situations below the 500 m contour and the tall miombo, not yet disturbed by cultivation, contains a woody field layer in its grass stratum of forest margin and understorey species.

While only the highest summits above about 1,700 m can be defined as montane, some of the thicket constituents and proteas of this zone also occur on the lower forest margins and stream slopes of the mesoclines between 800 m and 900 m. The summit grasslands are entirely separated from those of the lowlands by rainforest except at one small site on a west-facing spur immediately adjacent to Gogogo, the highest peak. Only on this one narrow spur can veld fires from the Midlands occasionally ascend and ignite the highest summit grassland. Otherwise summit grasslands are burnt by tribal hunters or possibly by lightning induced fires.

Gorongosa Mountain is unique in that the greater part is covered by rainforest and the least proportion by grass or tree veld, the converse of most African mountains. If areas modified by shifting cultivation on the footslopes are avoided, a large series of profile transects can be obtained showing altitudinal and aspect gradients of moisture, physiognomy and species replacement. The main path to the highest summit area of Gogogo enters the lower margin of rainforest on the mesocline at about the 800 m contour where tall, large-boled trees form a canopy between 25 m and 30 m high. As one ascends the spur in the cool shade of the understorey, the canopy level gradually becomes lower and other tree species appear which are mixed with those most common on the highest forest margins. The montane forest of the highest parts rarely exceeds 10 m in height, and the canopy leaves appear smaller than those of the lowland forest below. The midslopes are thus a transition zone of mixed forest flora and fauna, the bird components being the most conspicuous. The upper montane forest is generally festooned with *Usnea* lichens and epiphytic orchids and ferns, indicating the zone wreathed longest by cloud.

RIGHT:

Gogogo summit area with the highest point on the mountain on the left (1,863 m. alt.). Depicting montane grassland with montane thicket around the base of rock outcrops. *Cyathea* tree-fern in the foreground. Zombue summit discernable below fern fronds.

FAR RIGHT:

Gogogo summit under orographic cloud (guti drizzle) with montane grassland and scattered *Protea gazensis* shrubs.

The exit from montane forest to the summit grasslands is generally abrupt or through a margin of heaths and cedars. Where the change from forest to grassland is sudden the impact on the observer is greatest, from humid cool shade with the scent of leaf litter and the sounds of bird calls to crisp clear air infused with the faint aromatic perfume of everlastings and a riot of flowering forbs amongst the grasses. From the dark humidity of the forest one comes out into a chill wind in bright sunshine with mist creeping over nearby peaks and breathtaking vistas of the lowlands and distant mountains. Such an experience is at once a balm and a rejuvenation to the whole being for any who live in the adjacent oppressive steaming heat of the coast lowlands.

From the Gogogo summit plateau on clear days the towering peak of Mhanda Inselberg can be viewed, and beyond to the west the Inyanga Mountains of Rhodesia, the archipelago of inselbergs towards Tete in the northwest, and the Chimanimani end of the Great Escarpment in the southwest. To the southeast the Urema Lake and surrounding flood plain grasslands on the Rift floor are distinct, and in the northeast the isolated Morrumbala massif at the junction of the Chire and Zambezi Rivers.

Aquatic Herb Communities

Open water

The submerged rooted and floating aquatics of the cool lotic or lentic waters on the mountain are unrecorded, but contain a number of species in common with the bog community described below. Herbaceous species on stream margins in the upper reaches, attaining 100 cm in height, include: *Aeschynomene* sp., *Cyperaceae*, *Dissotis* sp., *Melastomastrum* sp., *Restio* sp., *Rhynchospora rugosa* and ferns (Macedo 1970a). A single seasonal tarn or pan occurs on a flat plateau interfluve grassland in the central part of the mountain east of Zombue summit just above the 1,600 m contour.

Summit and Slope Aspects of Gorongosa Mountain

LEFT:

The 100 m high Murombodzi Falls on the southern slopes of the mountain.
A perennial tributary of the Nhandare River flanked by riverine high forest.

BOTTOM LEFT:

Rock outcrop communities — arborescent *Strelitzia nicolai* clumps, and the sedge *Coleochloea setifera*, with hair-like foliage on otherwise bare rock faces.

RIGHT:

Aerial view southwards of Gogogo summit above the inland-facing west slopes.

TABLE 8.1
Acid bog herb communities of mountain summits and coast high water table sands

GORONGOSA MOUNTAIN SUMMIT		CHERINGOMA COAST
Peat Moss	*Sphagnum* sp.	
Club Moss	*Lycopodium carolinianum*	*Lycopodium carolinianum*
Grasses	*Agrostis continuata*	● *Andropogon eucomis*
	● *Andropogon eucomis*	● *Ischaemum arcuatum*
	Coelachne africana	*Oxyrhachis gracillina*
	● *Ischaemum arcuatum*	*Panicum dregeanum*
	Sacciolepis luciae	*Panicum parvifolium*
		Panicum subalbidum
Sedges	*Bulbostylis densa*	*Bulbostylis contexta*
	Costularia natalensis	*Bulbostylis pilosa*
	Cyperus holostigma	*Cyperus tenax*
	Cyperus leptocladus	*Fimbristylis dichotoma*
	Ficinia filiformis	*Fuirena umbellata*
	Fimbristylis hygrophila	*Kyllinga pauciflora*
	Fuirena stricta	*Rhynchospora candida*
	Pycreus macranthus	● *Rhynchospora rugosa*
	● *Rhynchospora rugosa*	*Rhynchospora triflora*
	Scirpus fluitans	
Yellow-eye grass	*Xyris sp. (KLT 2223, 2293)*	*Xyris straminea*
Pipewort	*Eriocaulon sonderanum*	*Eriocaulon subulatum*
Rush	*Juncus lomatophyllus*	*Juncus kraussii (or J. maritimus)*
Forbs	*Anagallis gracilipes*	● *Drosera burkeana*
	Cynorkis anacamptoides	*Drosera indica*
	Cyrtanthus tuckii	*Gentianaceae (KLT 2917)*
	Dierama pendulum	*Lapeirousia erythrantha*
	● *Drosera burkeana*	*Lindernia sp. (KLT 2913)*
	Helichrysum adenocarpum	*Lobelia erinus*
	Laurembergia repens	*Mesanthemum africanum*
	Lobelia intertexta	*Platycoryne pervillei*
	Senecio auriculatissimus	*Polygala capillaris*
	Senecio inornatus	*Sauvagesia erecta*
	Utricularia appendiculata	● *Utricularia livida*
	● *Utricularea livida*	*Utricularia subulata*

KEY
● = species in common

Proportional Composition

MOUNTAIN SUMMIT BOG		COASTAL BOG
Mosses	2	1
Grasses	5	6
Sedges	10	9
Sedge-like herbs	3	3
Forbs	12	12

Bogs and Vleis

Around valley heads and on stream margins in the summit grasslands are springs and oozes which support perennial low herbaceous bog communities, generally less than 50 cm in height. Some are peat bogs dominated by patches of *Sphagnum* moss mixed with sundews and many small mat-forming herbs of rhizomatous, stolaniferous and tufted growth form. The more seasonal bogs support pure patches of the 150 cm tall pedestaled sedge *Costularia natalensis*. The bogs are extremely acid (pH 4) and are closely related floristically in species, or species equivalents, to the acid coastal bogs on high water table podsolic sands. Their compositional proportions of mosses, grasses, sedges, cyperoids and forbs are also very similar. Sedges and small forbs predominate in each. For this reason the components of the montane and lowland bogs are listed together for comparative purposes (Table 8.2). No saline waters are known to occur on the mountain.

Phenology

The majority of the bog and vlei components on the highest summit area of the mountain show a midsummer and autumnal peak in flowering. Some species such as *Lobelia intertexta*, which also occurs in the adjacent grasslands, flower throughout the year. The spread of the reproductive period of bog herbs may differ annually, depending on the incidence of precipitation, frost, and fire. In two years of monthly visits to the Gogogo summit area, the red fire lily *Cyrtanthus tuckii* was only recorded once,

TABLE 8.2
Reproductive periods of bog and vlei herbs on the Gogogo summit plateau of Gorongosa Mountain from 1,700 m-1,830 m (recorded from 1969 to 1972).

		J	A	S	O	N	D	J	F	M	A	M	J
Poaceae	*Agrostis continuata*									●	●		
	Andropogon eucomis							●	●	●			
	Coelachne africana									●			
	Ischaemum arcuatum					●	●	●	●	●			
	Sacciolepis luciae									●	●		
Cyperaceae	*Bulbostylis densa*									●			
	Costularia natalensis						●	●	●	●	●		
	Cyperus holostigma										●		
	C. leptocladus						●	●					
	Ficinia filiformi						●	●					
	Fimbristylis hygrophila					●	●	●	●	●	●		
	Fuirena stricta										●	●	
	Pycreus macranthus						●	●					
	Rhynchospsora rugosa						●	●	●	●	●		
	Scirpus fluitans						●	●	●	●	●	●	
Xyridaceae	*Xyris* sp. (KLT 2223. 2293)				●	●	●	●	●	●	●		
Eriocaulaceae	*Eriocaulon sonderanum*						●	●	●	●			
Juncaceae	*Juncus lomatophyllus*				●	●							
Orchidaceae	*Cynorkis anacamptoides*			●	●	●				●			
Amaryllidaceae	*Cyrtanthus tuckii*									●	●		
Haloragaceae	*Laurembergia repens*						●	●	●				
Primulaceae	*Anagallis gracilipes*									●	●		
Lentibulariaceae	*Utricularia appendiculata*									●	●		
	U. livida									●	●		
	Genlisea hispidula						●	●	●	●			
Campanulaceae	*Lobelia Intertexta*	●	●	●	●	●	●	●	●	●	●	●	●
Compositae	*Helichrysum adenocarpum*									●	●		
	Senecio auriculatissimus	●	●	●	●	●	●						
	S. inornatus								●	●			
99 total occurrences		2	2	3	5	7	14	14	11	20	16	4	1

in a consecutive period of three months, following a fire which had burnt off both grassland and vlei areas.

Environmental factors

Fires are not an annual event on all the summit grassland and vleis of the mountain. Some areas are only burnt once in two or three years. If the Gogogo summit area escapes early or midwinter fire started by tribal hunters, fire from the lowlands only reaches past the narrow spur late in the dry season (September or October) or is extinguished by orographic rain before it ascends as far as the uppermost slopes.

Frost occurs at night during the midwinter months on flat and concave terrain of the grasslands, but no data are available on frequency or intensity. At the same altitude in the Inyanga Highlands, 100 km west of Gorongosa, frosts are recorded only in June and July (Rhodes Estate records).

Succession

Natural headward erosion by migrating nickpoints of streams, or more usually by pipe erosion and the development of sink holes, indicated by lone or clumped tree ferns *Cyathea dregei,* result in the slow elimination of bog and vlei areas. The process is slow due to the coherence of the peaty soils bound by a dense root mat, thus vlei areas remain as perched systems on either side of deep narrow streams which originated as subsoil drainage. This substrate sequence results in a plant succession which shows the following stages on the mountain:

(a) bog (perennial)
(b) vlei (seasonal)
(c) riverine suffrutex stage
(d) shrub stage
(e) forest.

The sequence can go from vlei directly to donga erosion, which is then invaded by woody forest components. Similar gradual or more rapid successions are shown in the development of herb vlei to swamp forest.

TABLE 8.3
Flowering periods of montane grassland components on the Gorongosa summit area of Gorongosa Mountain (1,700 m–1,800 m) (recorded from 1969 to 1972).

		J	A	S	O	N	D	J	F	M	A	M	J
Poaceae	*Agrostis continuata*										●		
	Andropogon eucomis								●	●			
	Andropogon schirensis							●	●	●	●		
	Andropogon flabellifer		●					●					
	Aristida recta				●	●							
	Digitaria apiculata				●	●	●	●	●	●	●		
	Elionurus argenteus		●	●	●	●	●	●					
	Eragrostis racemosa							●					
	Eragrostis volkensii				●	●	●	●	●	●	●		
	Eulalia villosa				●	●	●	●	●	●	●		
	Festuca abyssinica	●	●	●						●	●	●	●
	Festuca costata						●	●	●				
	Koeleria capensis		●	●	●								
	Loudetia simplex							●	●	●	●		
	Merxmuellera davyi				●	●	●	●					
	Microchloa caffra		●					●					
	Monocymbium ceresiiforme								●	●	●		
	Panicum ecklonii			●				●			●		
	Panicuma inaequilatum				●	●	●	●	●	●			
	Rhynchelytrum rhodesianum		●					●					
	Setaria anceps				●	●	●	●	●	●	●		
	Setaria sphacelata						●						
	Sporobolus mauritianus							●					
	Sporobolus subtilis				●	●	●	●					
Cyperaceae	*Bulbostylis schoenoides*						●	●					
	Bulbostylis macra						●	●	●	●			
	Pycreus macranthus					●	●	●					
	Schoenoxiphium sp. IKLT 22891						●	●					
Commelinaceae	*Commelina africana*							●					
	Commelina diffusa									●			
	Cyanotis barbata										●		

Cont.

		J	A	S	O	N	D	J	F	M	A	M	J
Liliaceae	*Albuca kirkii*				●								
	Aloe rhodesiana				●	●	●	●					
	Dipcadi longifolium				●								
	Kniphofia linearifolia									●			
	Ledebouria revoluta				●	●	●	●					
	Urginea nyasae				●								
Amaryllidaceae	*Cyrtanthus* sp. (KLT 2201)				●								
Hypoxidaceae	*Hypoxis dregei*							●	●				
lridaceae	*Gladiolus* sp.									●	●		
	Dierama pendulum				●	●	●	●	●	●			
	Moraea spathulata									●			
Orchidaceae	*Satyrium neglectum*									●	●		
	Satyrium chlorocorys									●	●		
Proteaceae	*Protea gazensis*									●	●		
Santalaceae	*Thesium scabridulum*				●						●		
	Thesium sp. (KLT 2526)										●		
Caryophyllaceae	*Silene bruchellii*						●	●					
Ranunculaceae	*Knowltonia transvaalensis*				●								
Crassulaceae	*Crassula alsinoides*									●			
Papilionoideae	*Aeschynomene nodulosa*				●								
	Argyrolobium rupestre									●			
	Crotalaria gazensis										●		
	Eriosema buchananii						●	●	●	●			
	Eriosema burkei						●	●					
	Eriosema lebrunii						●	●					
	Indigofera cecilii	●			●			●	●	●	●		
	Indigofera setiflora										●	●	
	Kotschya scaberrima	●									●	●	●
	Lotus wildii	●	●	●	●						●		
	Rhynchosia clivorum	●	●										
	Vigna nervosa									●			
Geraniaceae	*Geranium incanum*	●					●	●	●	●	●	●	●
Polygalaceae	*Polygala ohlendorfiana*		●				●	●	●	●	●	●	●
Apiaceae	*Alepida longifolia*				●								

Cont.

		J	A	S	O	N	D	J	F	M	A	M	J	
Apiaceae cont	*Pimpinella* sp. (KLT 2076, 2101)									●	●	●		
Gentianaceae	*Sebaea leiostyla*	●	●							●	●	●		
Lamiaceae	*Acrocephalus chirindensis*									●	●			
Scrophulariaceae	*Alectra sessiliflora*										●			
	Nemesis montana									●				
	Sopubia mannii									●	●			
	Sutera carvalhoi	●									●	●	●	
Dipsacaceae	*Scabiosa austroafricana*						●	●	●	●				
Campanulaceae	*Cyphia mazoensis*										●			
	Lobelia chamaedryfolia				●						●			
	Lobelia intertexta		●	●	●									
	Wahlenbergia virgata				●	●	●	●						
Compositae	*Athrixia rosmarinifolia*				●									
	Conyza subscaposa		●	●	●									
	Gerbera ambigua				●	●	●	●						
	Senecio erubescens						●	●						
	Senecio swynnertonii		●				●	●						
	Tolpis capensis		●					●	●	●				
	Vernonia natalensis						●	●						
	Helichrysum adenocarpum										●			
	Helichrysum buchananii										●	●		
	Helichrysum cephaloideum									●				
	Heliochrysum gazense	●	●									●	●	
	Helichrysium odoratissimum	●												
	Helichrysum nitens			●	●	●								
	Helchrysum nudifolium				●	●	●	●						
	Helichrysum pilosellum							●						
	Helichrysum setosum										●			
Total occurrences		10	15	8	31	17	30	44	18	36	36	10	6	260
%		4	6	3	12	7	12	17	7	13	14	4	2	
		99 total occurrences												

Rockfaces

Communities

The rounded granite rock faces are covered in radial lines of pure stands of the pedestalled sedge *Coleochloa setifera* which attains 100 cm in height and has hair-like foliage. In greater or lesser abundances, either on the pedestals themselves or in mats, are associated lichens, ferns, orchids, *Aloe arborescens, Crassula argyrophylla, Hypoxis* spp., *Vallozia* sp., and others. A cycad, *Encephalartos* sp., is reported from rock outcrops on the northern rim of the mountain near Inhantete summit.

Phenology

The flowering of three components was recorded: *Aloe arborescens* (April to July), *Coleochloa setifera* (January to March) and *Crassula argyrophylla* (October to November). The aloe also occurs as a component of montane thicket and as an epiphyte on tree trunks of the forest margins.

Environmental factors

In some sites *Coleochloa* is sufficiently dense to be burnt off by veld fires, otherwise rock faces are never burnt. Most outcrops occur in exposed sites and are excessively drained and experience a contrasting sequence of precipitation from mist, direct high insolation, and strong wind.

Succession

The isolated tufts of *Coleochloa,* whilst not initiating the confluence of root mats, allow such a process to take place. The more horizontal rockfaces become completely covered by root mats and dense shrub stages of succession occur, comprising most of the species described under 'Montane Thicket'. On steeper faces the plant mass can exceed the angle of repose and slumping occurs in patches. In isolated sites the sequence is: herb mats — suffrutex and shrubs — scrub thicket gravity slide — bare rock — repeat of sequence. No sites were found where the woody cover had attained a forest dimension.

Grassland

The mountain grasslands comprise three main types: montane (> 1,700 m) and submontane (1,400–1,600 m) treated together, and upland (800–1,400 m). The last occurs as pure swards only on the benches of the southwest slopes of the mountain, elsewhere the slopes are wooded to a greater or lesser degree and form part of the moist extreme of miombo savanna.

Montane grassland

The montane grassland of the Gogogo summit plateau above the 1,700 m contour is composed of a dense sward of tufted perennial grass species, with an average height of 40 cm in the vegetative state and 80 cm when in inflorescence. The striking feature which separates montane grassland from all the lowland types, except the dambo or high water table grasslands on sands, is the abundance of associated forbs and suffrutices. The large tussocks of *Merxmuellera davyi* (= *Danthonia davyi*) also contribute to the distinctiveness of montane grassland physiognomy. The most important grasses in the Gogogo summit area are *Andropogon schirensis, Eragrostis volkensii, Festuca abyssinica, F. costata* and *Merxmuellera davyi*. The most important associated forbs are composites (*Helichrysum* spp.) and papilionaceous legumes.

Macedo (1970a, 1970b) reports that the grasslands at a lower level, between 1,400 and 1,600 m on rounded relief of the valley heads in the centre of the mountain, are dominated by *Monocymbium ceresiiforme* and *Loudetia simplex*.

Twenty four grass species and 69 forb species representing 23 families were collected over a two year period at monthly intervals from the Gogogo summit grassland. Of the latter, composites made up 23%, and papilionaceous legumes 17% of the total. Nine of the 16 composites were *Helichrysum* species. The montane grass–forb association can therefore be defined as *Festuca–Helichrysum–Pailionoideae* grassland. The total list of 93 species appears under the following section (Table 8.7).

It is significant that high grass species diversity per unit area, and rich forb and suffrutex floras, are associated only with acid leached grasslands as exemplified by montane, upland and moist savanna (e.g. miombo), and high water table (podsolized) sands in lower rainfall and coastal situations. This contrasts with the low grass species diversity per unit area, and relatively poor forb flora of grasslands on heavier acid or alkaline base saturated soils.

Phenology

Conspicuous mass flowering of one or several species at different times of the annual cycle is a feature of montane grassland. The succession of aspect dominance on

Gogogo summit comprises:

Compositae:	*Helichrysum nitens*	OCTOBER
Liliaceae:	*Urginea nyasae*	OCTOBER
Poaceae:	*Festuca costata*	JANUARY
Poaceas:	*Andropogon schirensis*	MARCH
Liliaceae:	*Kniphofia linearifolia*	MARCH
Orchidaceae:	*Satyrium neglectum*	MARCH
Compositae:	*Helichrysum cephaloideum*	MARCH
Compositae:	*Helichrysum buchananii*	APRIL–MAY

Greatest mass flowering of four species occurs around the time of the autumnal equinox in March. In the lower grassland in the centre of the mountain, both grass dominants *Monocymbium* and *Loudetia* showed aspect dominance in the late summer and early autumn.

Flowers of some species such as *Geranium incanum* are to be found in almost every month of the year except when veld fires have occurred. Sedge components of the grassland are all in full inflorescence in midsummer, and the grasses and composites show a trimodal peak at the time of the equinoxes and summer solstice, i.e. October (vernal), December–January (aestival) and April (autumnal). The papilionoids also show three peaks, in July (hibernal), January and April. Forbs that flower only during the winter season include *Helichrysum gazense, Helichrysum odoratissimum, Kotsehya scaberrims, Sebaes leiostyls* and *Sutera carvalhoi*. The three main peaks coincide closely with the two radiation peaks near the equinoxes, caused by high cloud cover values over the intervening summer period, and with the summer solstice at the peak of the rains and with daylength. A lesser August peak is caused by the occurrence of fire in the late winter.

The effect of veld fires in stimulating the unseasonal or earlier flush of grassland and savanna is well known in Africa (e.g. Phillips 1965, West 1965, and their bibliographies). However, fire-induced flush of grasses only occurs where there is sufficient soil moisture; in the arid savannas of Botswana and South West Africa grasslands may remain bare for several months after fire until the advent of the first rains (Tinley 1966). Out of phase, early flowering of certain grass and forb components was recorded in August 1971 after a fire at the end of July had burnt the greater part of the Gogogo summit area. Pioneering specimens confined solely to the burnt areas included the grasses *Andropogon flabellifer, Elionurus argentens, Koeleria capensis, Michrochloa caffra, Rhynchelytrum rhodesianum*, and the forbs *Indigofera cecilii, Polygala chlendorfiana* and *Tolpis capensis*. *Senecio swynnertonii,* however, was flowering equally abundantly in both burnt and unburnt grassland at the same time (Table 8.3).

Bayer (1955) suggests that fire stimulates early flowering in grassland components by heating up the ground, which simulates the increase of soil temperature in the spring. Bayer points out, too, that a large proportion of spring-aspect forbs have underground storage organs or have greater ability to obtain moisture and are thus independent of the first rains on which the grass components generally rely. Due to these features and contrasting seasonal influences, the response of vernal and autumnal forbs is quite different; the former are stimulated by fire and the latter are generally suppressed. Bayer concludes that the whole behaviour of the spring aspect plants points to the antiquity of lightning fires as a normal periodic event in the ecology of grasslands (see also Komarek 1964, 1965). Lemon (1968) describes the increase of vigour after fire of certain grassland forbs on the Nyika Plateau in Malawi.

Environmental factors

No climatic data are available from the summit grassland areas, thus the frequency and intensity of features such as precipitation fog, drought, and frost are unknown. The summit areas are subject to frequent orographic fog and drizzle (guti) throughout the year, especially in spring, summer and autumn, occurring on more than 14 days per month, and least in May (8 days), as judged by data from the Great Escarpment on the frontier (Fig. 4.12). The increased cloudiness and humidity, resulting in decreased light intensity and temperature is strikingly expressed by the abundance of ephiphytes on the crowns and trunks of the montane forest trees near the summit. Judging by the Inyanga records, frosts can be expected in the summit grasslands in June and July.

Fire occurrence has been dealt with above in relation to bog and vlei communities. The influence of fire on flowering of both grasses and the associated spring-aspect forbs has been noted above.

Intensity of fire is directly dependent on the distribution of precipitation in any one year. The mountain summits are generally at their driest in September and hot fires can then extend from the grasslands into the forest margins and through montane thicket. The only clear evidence that veld fires are reducing forests on their margins in the entire transect is in the summit areas of Gorongosa Mountain. It seems contradictory that fire in relatively short grasslands in a humid regime should have devastating effect on forest, when in the dry lowlands fire in medium to tall (3 m–4 m) grasslands has little or no retarding effect on the long term configuration of existing forests, or in suppressing thicket and forest extension on the coast. The disproportional impact of fire may be more closely tied to the soil moisture balance regimes in the different sites rather than abundance of grass fuel or severity of the dry season. This aspect seems to have been little studied in the detailed longterm investigations on fire in various parts of Africa, and thus the whole subject remains an open question.

Succession

Over most of the summit areas montane grasslands and forest meet abruptly without any ecotonal shrub margin. In the heads of the valleys in the central part of the mountain, grassland is replacing forest as fires burn back their edges. On valley slopes a scrub zone, of varying width, comprising mainly bracken *Pteridium aquilinum* and *Smilax kraussiana*, separates pure grassland from the riverine forest strips. In this scrub, forest precursors such as *Trema orientalis, Maesa lanceolata, Harungana madagascariensis, Dombeya burgessiae*, and tall ginger plants *Zingerbaceae* are to be found.

In the summit areas where boulder outcrops occur, tall thickets of pure or mixed *Philippia benguellensis* and *Widdringtonia nodiflora* are interposed between the grassland and forest, and these are burnt out at intervals long enough to allow regeneration to a canopy height of 10 m.

The progressive and retrogressive succession of these zones appears to vacillate with the occurrence of consecutive years of high rainfall or of drought, the devastation by fire being greatest in the latter. The eroding surfaces are generally being invaded by forest or scrub thicket seral to forest, and grassland is extending on the stable rounded topography.

Upland grassland

On the southwest slopes of the mountain, dense swards of tufted perennial grasslands cover bench plateaux between the 800 m and 950 m contours. These are generally taller than the montane grassland, averaging 80 cm in height in the vegetative state. Main components include *Loudetia superba, Themeda triandra, Trachypogon spicatus* and *Tristachya hispida*. On forest margins *Cymbopogon validus* becomes dominant and on savanna margins *Hyparrhenia filipendula, H. tamba, H. variabilis, Panicum maximum* and other species common to the miombo. In most sites on latosols or on old cultivation sites the grasses *Pennisetum purpureum* and *Melinus* sp. form extensive dense clumps up to 4 m in height.

Environmental factors

The pure upland bench grasslands occur on what appear to be soils which are excessively waterlogged after the occurrence of rains and which subsequently become extremely dry. They are avoided by subsistence cultivators. On the slopes of the Nhandare River the benchlands have been broken up by mass slumping which indicatesa deeply weathered profile on the gabbro geology.

Veld fires burn these grasslands almost every year except when well distributed rains occur. At one time a thriving beef ranch was maintained on the southwest slopes of the mountain and one of the most important pasture grasses was *Cymbopogon validus*. Under heavy grazing this tufted species, which attains 3 m in height, assumed a prostrate growth form and became more vegetatively productive.

Succession

These grasslands are climax cover on the bench plateaux, with tension zones against forest or thicket in moist sites on valley slopes and streambanks and against savanna in stoney sites and areas of old cultivation and overgrazing. Slopes and small scarp areas which may have supported forest in the past, and could be re-invaded by forest under a regime of fire protection, are indicated by the bracken fern *Pteridium aquilinum* with a mixture of *Smilax kraussiana, Vernonia* spp. and low scrub with isolated savanna trees such as *Dalbergia nitidula*.

Upland savanna

Upland savanna is an altitudinal tailing off of the surrounding Midland miombo and mixed acacia and broad leaf savannas of the valleys, up the sides of the mountain. The former on the mesoclines, and the latter, which relate to the Rift Valley vegetation, extend up the xeroclines. At the same time the uplands have woody savanna species which are found nowhere else in the ecosystem and are confined to the mesocline slopes. These include:

WOODY SAVANNA SPECIES

Acacia karoo
Cussonia spicata
Dalbergia nitidula
Erythrina lysistemon
Faurea sp.
Syzygium cordatum

The savanna of the uplands is typically comprised of pure species savanna patches of even age, separated by grassland or mixed in a mosaic with the thickets. Its appearance is thus quite different to the continuous even spacing (except where cleared for cultivation) of the surrounding Midland miombo. Although the mesocline and xerocline upland savannas are clearly different in species composition, at each extreme they overlap on transitional aspects and slopes of the mountain, i.e. on a single spur mesocline species occur on the poleward aspect and xerocline species on the equatorward face.

Mesocline savanna

A patchwork of wooded grasslands, generally single layered, up to 12 m in height but generally shorter, of evergreen and deciduous species. Woody components include:

WOODY COMPONENTS

Acacia karoo (W? Z)
Albizia adianthifolia (W)
Brachystegia glaucescens
  (ex *B. tamarindoides*) (X)
Cussonia spicata (Z)
Dalbergia nitidula (W)
Erythrina lysistemon (Z)
Faurea sp. (W)
Ficus vogelii (Z)
Heteropyxis natalensis (W)
Parinari curatellifolia (Z)
Pericopsis angolensis (W)
Strychnos spinosa (Z)
Syzygium coroatum (Z)

KEY
W = wind (anemochory)
X = by explosive dehiscence and seeds thrown (active autochory or active ballists).
Z = animal-dispersed (zoochory)
? = a question mark after any of the symbols means that the case is uncertain.

The grass stratum comprises most of the species noted for the upland grasslands. Extensive lists are given by Macedo (1970b) for this aspect in his Complex 16.

Xerocline savanna

Open to closed canopied tree stratum attaining 10 m in height and dominated by broadleaf combretaceous species such as:

BROADLEAF COMBRETACEOUS SPECIES

Combretum fragrans (W)
C. molle (W)
C. zeyheri (W)
Terminalia mollis (W)
T. sambesiaca (W)
T. sericea (W)

KEY
W = wind (anemochory)

OTHER TREE SPECIES INCLUDE:

Afzelia quanzenis (Z)
Burkea africana (W)
Diplorynchus condylocarpon (W)
Kirkia acuminata (W)
Lonchocarpus bussei (W)
L. capassa (W)
Markhamia obtusifolia (W)
Peltophorum africanum (W)
Sterculia quinqueloba (Z)
Stereospermum kunthianum (W)
Piliostigma thonningii (Z)
Pterocarpus angolensis (W)
P. brenanii (W)
P. rotundifolia (W)
Sclerocarya caffra (Z)
Xeroderris stuhlmannii (W)

KEY
W = wind (anemochory)
Z = animal-dispersed (zoochory)

Pure woodland patches of *Millettia stuhlmannii* (X) with a closed canopy occur on sandy colluvium. This and the xerocline savanna merge into tall thicket areas, especially on the pediments and lower talus slopes of the mountain. Most species are strongly deciduous. Macedo (1970b) gives extensive lists of similar species in different combinations for the communities he recognizes on the xerocline. The grass stratum is relatively sparse compared with the mesocline slopes and is composed of:

GRASS STRATUM

Andropogon gayanus
Digitaria spp.
Heteropogon contortus
Hyparrhenia spp.
Pogonarthria squarrosa
Themeda triandra

and interspersed with tall (3 m–4 m) patches of *Beckeropsis unisetta* and *Rottboellia exaltata.*

Dispersal

On the mesocline are seven (50%) occurrences of animal dispersed fruits, six (43%) by wind and one (7%) is an active ballist. Nearly equal importance of wind and animal dispersed species pertains on the mesocline. By contrast 18 (78%) on the xerocline are wind dispersed plus four (17 %) animal dispersed and one (4%) explosively dehiscent (Fig. 8.3).

Environmental factors

The upland savannas are burnt out annually, but the intensity and reach of fire depends on the density of the grass stratum. The closed canopy patches forming woodlands are often devoid of a grass understorey and fire may burn through the leaf litter at most, otherwise they remain as unburnt patches. The upland savanna and grasslands, unlike the thicket and forest patches with which they mosaic, are relatively undisturbed by shifting cultivation as the forested soils with their high humus content are preferred by tribal cultivators.

Succession

The savanna and grass areas appear to be in quasi-equilibrium and show no active scrub encroachment or reduction of area except where local overstocking or past cultivation has disturbed the soils, resulting in the spread of low dense scrub. In the absence of such disturbance, separation of forest, savanna and grassland is determined chiefly by edaphic factors.

Scrub–thicket

The largest areas of scrub thicket occur at intervals on the lower slopes of the mountain, which have long been subjected to shifting cultivation and annual veld fires. Small patches of scrub thicket occur in the montane zone but as these usually form the field layer to trees taller than 4 m they are treated with the next physiognomic group.

On the southern and eastern slopes of the mountain the full spectrum from bracken to tall thicket occurs as a mosaic on different age cultivation fallows. Dense scrub thicket with a closed canopy at about 3 m height occurs on the lower margins of rainforest mostly on old cultivation sites. This cover is composed of a large variety of woody forest, savanna, thicket and alien species recombined from the original cover and the juxtaposed communities. Components include:

SCRUB

Acacia karroo (W? Z)
A. polyacantha (W Z)
Albizia adianthifolia (W)
Annona senegalensis (Z)
Antidesma venosum (Z)
Bauhinia petersiana (X)
Bridelia micrantha (Z)
Brachylaena rotundata (W)
Cassia petersiana (Z?)
Dombeya burgessiae (W)
Entada abyssinica (W)
Harungana madagascariensis (Z)
Heteromorpha trifoliata (W)
Lobelia johnsonii (W?)
Maesa lanceloata (Z)
Mussaenda arcuata (Z)
Securidaca longipendunculata (W)
Strychnos spinosa (Z)
Trema orientalis (Z)
Vernonia sp. (W)
Vitex payos (Z)

KEY
W = wind (anemochory)
Z = animal-dispersed (zoochory)
? = a question mark after any of the symbols means that the case is uncertain.

CLIMBERS AND SCANDENTS

Bauhinia galpinii (X)
Clematis sp. (W)
Combretum paniculatum (W)
Friesodielsia obovata (Z)
Landolphia sp. (Z)
Lantana camara (Z)
Macuna coriacea (X?)
Rhoicissus tridentata (Z)
Rubus sp. (Z)
Smilax kraussiana (Z)

KEY
W = wind (anemochory)
X = by explosive dehiscence and seeds thrown (active autochory or active ballists).
Z = animal-dispersed (zoochory)
? = a question mark after any of the symbols means that the case is uncertain.

HERBS

Afromomum sp.
Dissotis sp.
Leonotis leonurus
Pteridium aquilinum

GRASSES

Cymbopogon validus
Imperata cylindrica
Melinus sp.
Panicum maximum
Pennisetum purpureum
Setaria chevalieri

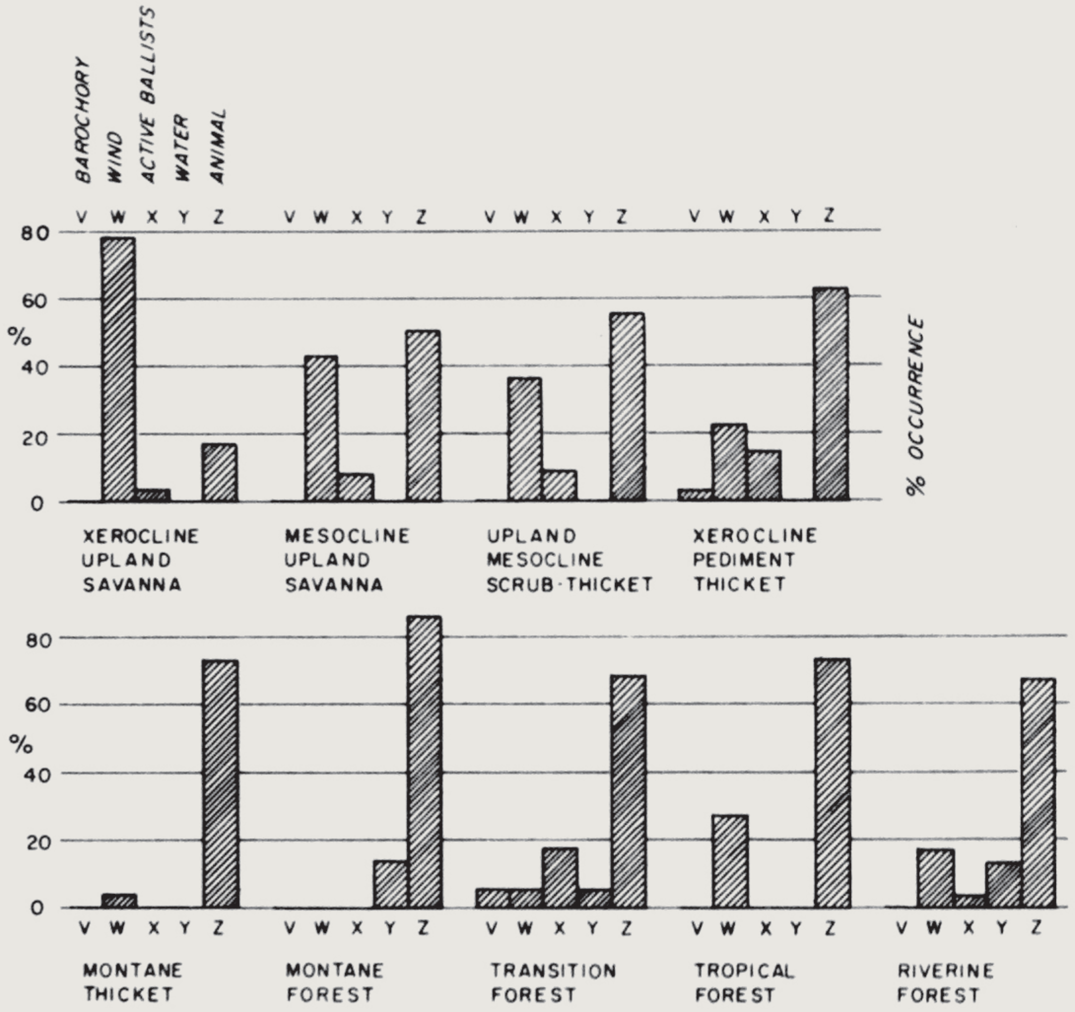


FIG 8.3 COMPARATIVE OCCURRENCE OF DISPERSAL TYPES IN WOODY COMPONENTS OF SAVANNA, THICKET AND FOREST ON GORONGOSA MOUNTAIN (PRIMA FACIE DATA)

LEFT: Figure 8.3

Comparative occurrence of dispersal types in woody components of savanna, thicket and forest on Gorongosa Mountain (prima facie data).

This thicket grades into riverine forest in the valleys where *Filicium decipiens, Halleria lucida, Oreobambos buchwaldii* (bamboo) and *Trichocladus ellipticus* are important constituents. Lone or clumped forest canopy remnants such as *Chlorophora excelsa* and *Newtonia buchananii* are left as islands in riverine and talus slope sites. Many other constituents are listed by Macedo (1970a, 1970b).

Dispersal

Of the 26 woody species listed there are 18 (55%) occurrences of animal dispersed fruits, 12 (36%) wind dispersed and three (9%) explosively dispersed (active ballists).

Environmental factors

As these scrub thickets abut on grasslands they are burnt out by veld fires during exceptionally dry periods, but otherwise largely escape annual fire.

Succession

Scrub–thicket is seral to forest through a thicket stage on the mesocline slopes of the mountain, and to thicket on the xeroclines.

Thicket

Two main kinds of thicket occur on the mountain: montane thicket in the summit areas, and tall pediment thickets adjoining riverine zones on the xerocline.

Montane thicket

The thicket areas on the summit occur in patches with a canopy varying in height from 4 m–10 m, chiefly on torfields or around the base of the domed granite outcrops. The irregular shaped patches are either interposed between the upper limits of montane forest and the summit grasslands, or occur as separate features related to the outcrop areas. The canopy spacing varies greatly from closed clumps to scattered tree specimens linked by a tangled scrub thicket field layer of shrubs and suffrutices.

Two canopy components, the cedar *Widdringtonia nodiflora* and the arborescent heath *Philippia benguelensis*, form pure even-sized stands of mature trees attaining 10 m in height.

On the numerous air traverses made by the author in a light aircraft over the mountain only one area of tall plantation-like pole-stands of *Widdringtonia* was encountered in the central area of the mountain immediately below the isolated tarn mentioned in the Aquatic Communities. This cedar woodland appears to be close to 20 m in height. The pure thickets of *Philippia,* too, are clearly discernible from forest on air photographs or from an aircraft due to their contrasting, extremely fine leaf texture. The only other woody species associated with the nearly pure thickets of *Philippia* is *Myrica pilulifera* which is similarly associated with the otherwise pure scrub–thickets of coast heath *Philippia simii* on the Cheringoma cuesta.

Montane thicket is composed of some forest species, those from forest margins, rock outcrops and its own non-forest constituents.
Components include:

TREES

Buddleia salviifolia (W)
Cassine papillosa (Z)
Curtisia dentata (Z)
Halleria lucida (Z)
Kiggelaria africana (Z)
Maesa lanceolata (Z)
Maytenus acuminata (Z)
Myrica pilulifera (Z)
Nuxia congesta (W)
Philippia benguellensis (W)
Pittosporum viridiflorum (Z)
Rhamnus prinoides (Z)
Rhus chirindensis (Z)
Strelitzia nicolai (Z)
Widdringtonia nodiflora (W)

KEY
W = wind (anemochory)
Z = animal-dispersed (zoochory)

SHRUBS AND SUFFRUTICES

Aloe arborescens
Anthospermum ammanioides
A. vallicola
Cliffortia nitidula
Hypericum revolutum
Indigofera lyallii
Myrsine africana
Philippia hexandra
Plectranthus sp. (KLT 2420)
Polygala virgata
Stoebe vulgaris
Tephrosia grandibracteata

In some areas *Indigofera lyallii* forms pure scrub–thicket patches up to 3 m in height on the margins of thicket or forest. The 7 m tall, banana-like *Strelitzia nicolai* is an important component of coast dune forest from the Eastern Cape through Natal to the Mozambique coast south of Inhaca Island. It is absent north of Inhaca but reappears again as a montane species in the Great Escarpment mountains of the Rhodesia–Mozambique frontier. Gorongosa appears to be its northernmost distribution limit.

Dispersal

Eleven (73%) of the thicket-free components have animal (mainly bird) dispersed fruits, four (27%) are wind dispersed, passive ballists (Fig. 8.3).

Environmental factors

Montane thicket is composed of mostly evergreen species but during dry months the periodic fires which occur on the summits burn into or through this cover to the edge of the forest and grassland. The dense field layer is the main fuel, but where clumped cedar occur their high resin content results in crown fires. *Philippia* patches, too, are more highly susceptible to veld fires than the other thicket cover.

Succession

Thicket can be seral to forest and grow by coalescence of patches initiated around rock outcrops. Where damaging fires occur the cover is set back to a dense scrub stage. The mature pure stands of *Philippia* and *Widdringtonia* appear to be climax on different soils to that occupied by forest. However, both these species are heliophytes and vigorous seedling, sapling and pole-stands are only found where there is an open understorey, a dense fieldlayer excludes them. It is often stated that *Widdringtonia* is a dry 'forest' but in many mountain areas, as on Gorongosa, it occurs in the highest rainfall cloud zone. The dryness or lack of understorey luxuriance is probably due to soil factors and the fallen needles. Stands of *Casuarina* on the coast, for example, are also 'dry' in comparison to the adjacent dune forest, yet they receive the same precipitation. In the sites where these two species are mixed with the components noted above, indications are that they will be overtaken by maturation of thicket and remain as canopy relics, only able to become re-established on the margins or after fire has opened up the field layer. It is the latter which may be responsible for the even-aged appearance of many *Widdringtonia* stands; simultaneous colonisation of newly opened substrates. Succession in this cover is therefore progressive, retrogressive or homeostatic depending on circumstances.

Pediment Thicket

Mostly deciduous with some evergreen species forming a closed canopy at about 20 m. Consists of a mixture from rainforest, dry forest, riverine, termitaria, and savanna systems. The tall thickets in valleys of the xerocline slopes and pediments merge with riverine and shorter thicket types of the adjoining Midlands. Components, as derived from Macedo (1970b Complex No. 16) include:

TREES (mid to upper layers)

Acacia nigrescens (W? Z)
A. sieberana (Z)
Afzelia quanzensis (Z)
Albizia glaberrima (W)
A. versicolour (W)
Burkea africana (W)
Bauhinia petersiana (X)
B. tomentosa (X)
Cassia abbreviata (Z)
Celtis sp. (Z)
Cleistanthus schlechteri (X Z?)
Combretum fragrans (W)
C. imberbe (W)
Cordyla africana (Z)
Diospyros mespiliformis (Z)
Euphorbia sp. (X Z)
Ficus 3 spp. (Z)
Flacourtia indica (Z)
Kigelia africana (V Z)
Lannea stuhlmannii (Z)
Lecaniodiscus fraxinifolius (Z)
Millettia stuhlmannii (X)
Pterocarpus rotundifolia (W)
Sclerocarya caffra (Z)
Shrebera tricoclada (W)
Sterculia appendiculata (Z)
Strychnos madagascariensis (Z)
S. potatorum (Z)
Tamarindus indica (Z)
Trichilia emetica (Z)
Ziziphus mucronata (Z)

KEY
W = wind (anemochory)
X = by explosive dehiscence and seeds thrown (active autochory or active ballists).
Z = animal-dispersed (zoochory)
? = a question mark after any of the symbols means that the case is uncertain.

Dispersal

Of 37 dispersal type occurrences, 23 (62%) are by animals, eight (22%) by wind, five (14%) by explosive dehiscence, and one (3%) by weight (barochory).

Environmental factors

Although most of the riverine and pediment thickets of the xerocline are undisturbed by man, some on the western basal slopes may have originated on old cultivation sites. Veld fires generally die out when encountering thicket, singeing the margins and extending a short way into the understorey in parts. Although the majority of components are deciduous, many are tardily or only slightly deciduous, depending on the distribution and amount of rainfall in any year. Midsummer droughts cause unseasonal leaf fall in some, followed by a new flush in February and March.

Succession

No data were personally gathered on the xerocline thickets. Macedo (1970b) only notes upper storey species, thus sapling dominance and the seral tendency is unknown. However, most of the thickets appear to be in a climo-edaphic equilibrium and are only seral to forest where moisture conditions allow, such as streambanks and valley heads.

Forest

Above the 600 m contour, which separates Gorongosa Mountain from the surrounding Midlands, 50% (300 km^2) of the mountain is covered in rainforest, 7% (40 km^2) is summit grassland and the remainder 43% (260 km^2 mostly on the flanks) is savanna. Due probably to its relatively low altitude, a clear zonation (as is apparent on the volcanic mountains of the eastern Congo for example) can only be found on Gorongosa Mountain where forest occurs as an unbroken cover from near the base to the summits. In such situations it is possible to separate the tall lowland tropical zone, a middle transitional zone with mixed species composition, and an upper montane (or Afro-temperate zone) of shorter, less luxuriant forest with an abundance of epiphytes, and summit grasslands with everlastings and the tree heaths.

Lebrun (1935) working in the eastern Congo was the first to designate what he called ‘Transition Forest’ consisting of a mixture of species from the montane and tropical formations. Chapman & White (1970) refer to this zone as submontane in Malawi, however in many sectors a greater tropical influence is apparent and it is then correctly subtropical! It is thus more realistic to maintain Lebrun’s term. The width of these zones depends on moisture conditions in different aspects and the interfingering of ravines and spurs. Tropical species occur to much higher altitudes in the ravine sites.

On Gorongosa Mountain the altitudinal limits to the three zones are similar to those given for the eastern Congo by Lebrun (1934): Tropical below c. 1,200 m, Transition 1,200–1,600 m, and Montane (Afro-temperate) above 1,600 m. Macedo (1970a, 1970b) recognized similar altitudinal limits for the montane and tropical forests on Gorongosa Mountain. On lower isolated mountains such as Morrumbala, at the junction of the Chire and Zambezi Rivers, montane and tropical species are co-dominant in the canopy at the heads of gulleys at about the 1,000 m contour. A similar situation exists on the inselbergs and fore-ranges near the frontier Great Escarpment. The greater part of the forest area of Gorongosa Mountain is probably occupied by Transition Forest as exemplified by *Podocarpus milanjianus* (Afro-temperate) and *Newtonia buchananii* (Tropical) occurring as canopy dominants side by side. Chapman and White (1970) recognize the canopy tree *Chrysophyllum gorungosanum* as the indicator for their submontane (Transition) forest. Transition Forest can thus be expected to be floristically richer than the zones above and below it.

As there is continued debate by workers on the status and affinities of these mountain forests, one fundamental factor, which becomes obvious as soon as explained, requires emphasis. Over the whole of eastern Africa, from the Cape to Ethiopia, forest is confined to three main sites: scarps, ravines and the land-sea junction.

The important point about mountain masses of any dimension is their orographic rain regime and this islanding of high rainfall zones results in an overlay of rainforest conditions with altitudinal effects. At the same time a converse situation exists where typical montane genera such as *Podocarpus*, *Philippia, Ilex*, *Rapane*a and *Myrica* occur in high rainfall lowland sites on podsalized high water table sands. On the Mozambique coast, montane components occur in swamp forest, on the margins of dambos, and in tropical evergreen forest on leached duplex sands. On the continental plateau away from montane sites, *Podocarpus* and *Philippia* are associated with dambo swamp forests (mushitu) in northern Zambia (Lawton 1963). Like river valleys and rock outcrops, termite hills are important two-way stepping stone links for forest and/or arid or desertic elements. Thus, even for an apparently conservative system such as montane forest which is essentially similar throughout Africa south of the Sahara, the interplay of geomorphic succession and biogeographic recombinations act as species filters and provide forest components a diversity of refuge sites, homeostatic habitats or initial sites for expansion, in which thickets of all kinds play a fundamental role.

Montane forest

The uppermost temperate forest zone, generally above the 1,600 m contour, is composed of mostly evergreen trees forming a closed canopy at 10 m–15 m, in some areas shorter, whilst in gullies emergents may attain 25 m. The soils are either deeply weathered, acid fersiallitics developed on fine-grained granite, or lithosols. In contrast to the lower tropical zone, the subordinate small tree layers are poorly developed as is the shrub or sapling layer, instead dense societies of acanthaceous herbs, labiates and balsams occur in patches where the tree canopy is sparse. Rocks and canopy branches are festooned with epiphytic mosses, club mosses, ferns and orchids with *Usnea* lichen hanging from exposed canopy branches. The canopy trees typically include:

CANOPY TREES

Aphloia theifomis (Z)
Curtissia dentata (Y Z)
Ilex mitis (Z)
Kiggelaria africana (Z)
Maytenus acuminata (Z)
Ocotea kenyensis (Z)
Pittosporum viridiflorum (Z?)
Podocarpus milanjianus (Z Y)
Rapanea melanophloeos (Z)
Schefflera abyssinica (Z)
Syzygium musukuense (Z)
Xymalos monospora (Z?)

KEY
Y = water (hydrochory)
Z = animal-dispersed (zoochory)
? = a question mark after any of the symbols means that the case is uncertain.

Soft-leaved herbs of the forest floor include *Impatiens cecillii*, *I. sylvicola*, *Isoglossa milanjensis, Plectranthus* sp. and *Salvia* sp. A first collection of ferns totalling 70 species was made from the southwest slope and Gogogo summit area of the mountain by Schelpe (1966).

Tropical forest

Down to about the 1,200 m contour *Chrysophyllum gorongosanum* and *Newtonia buchananii* are major canopy trees but, lower down, the forest grades into a more tropical array of species similar to those occurring on the Cheringoma Coast and the escarpments of the Midlands, including the area below the Chimanimani massif (Dutton & Dutton 1973). This lowland forest contains many equatorial rain forest species hence the phytogeographic designation of oriental, or eastern, forest domain of the Guinea–Congolian Region (Monod 1957).

The canopy is between 20 m and 30 m in height with emergents attaining 35 m, especially in gullies and ravines. The trees are a mixture of evergreen and deciduous species with plank buttresses or fluted trunks, and large leaved (mesophyll and macrophyll) physiognomy interspersed with a dominance of bipinnate, mimosa-like (nanophyll) leaflets, (e.g. *Newtonia*) or microphyll and micro-mesophyll leaflets of caesalpiniaceous (e.g. *Erythrophloeum*) canopy trees. The predominance of micro-mesophyll leaf size in the equatorial rain forest is due to the abundance of caesalpiniaceous canopy trees.

The larger areas of the lower tropical forest zone are now confined to the V-shaped patches which follow the rivers that debouch from the steep ravines of the mountain's mesocline slopes. Elsewhere this zone has been badly damaged by shifting cultivation and only single or clumped canopy relics remain on the talus slopes.

Thus species composition is now chiefly an overlay of rain forest and riverine components. The subordinate tree layers are well defined and the field or sapling layer, up to 3 m in height, is dense. Large stemmed lianes which attain the canopy are a conspicuous feature. Typical upper stratum trees include:

TYPICAL UPPER STRATUM TREES

Anthocleista grandiflora (Z?)
Blighia unijugata (Z)
Bombax rhodognaphalon (W? Z?)
Celtis gomphophylla (Z)
Chlorophora excelsa (Z)
Erythrophleum suaveolens (Z?)
Newtonia buchananii (W)
Pachystela brevipes (Z)
Pteleopsis myrtifolia (W)
Syzygium guineense (Z)

KEY
W = wind (anemochory)
Z = animal-dispersed (zoochory)
? = a question mark after any of the symbols means that the case is uncertain.

The tropical forest zone occurs, in addition to riverine zones to which it is now largely confined, on fersallitic and colluvial soils derived from gabbro or granite, or a mixture of both basic and acid talus, or on lithosols—these include Fernandes' 1968a types **Vb**, **Lb**, **Cvb**, **Cbv.**

Transition forest

Influenced by the temperate zone from above and the tropical zone from below, the bulk of the mountain is covered in transition forest which shows the full spectrum of features from both zones in height, physiognomy and understorey features including: under-canopy thickets composed of species such as *Dracaena fragrans* or *Trichocladus ellipticus*, density of climbers, epiphytes and herb societies on an altitudinal transect. Shorter and stag-headed canopy is typical on the crests of the spurs, and the tallest forest trees are usually associated with the gullies and ravines. Similar soils are occupied by transition forest as those noted for the tropical zone, and it extends in its upper limits onto ferallitic soils derived from micropegmatite granite. In the low 1 m high shrub layer, *Mostuea brunonis* is dominant in large sectors of the lower slope forest. The forest species lists, especially that of the small tree layer, has been aided in large part by the collections of Mr Tom Müller of the Salisbury Herbarium. Median to upper canopy strata trees include:

MEDIAN TO UPPER CANOPY STRATA TREES

Apodytes dimidiata (Z?)
Bersama abyssinica (Z)
Calodendrum capense (Y Z ?)
Cassipourea congoensis (Z)
Chrysophyllum gorongosanum (Z)
Cola greenwayi (Z)
Craibia brevicaudata (X)
Croton sylvaticus (Z? X?)
Cryptocarya liebertiana (Z)
Dryperes gerrardii (Z)
Ekebergia capensis (Z)
Fagara sp. (X)
Ficus kirkii (Z)
Filicium decipiens (Z?)
Garcinia milanjiensis (Z)
G. volkensii (Z)
Homalium dentatum (W? Z?)
Linociera battiscombei (Z)
Macaranga capensis (X?)
Neoboutonia africana (X Z?)
Newtonia buchananii (W)
Olea capensis (Z Y)
Phyllanthus discoideus (X Z?)
Rauvolfia caffra (Z)
Sapium ellipticum (Z?)
Schefflera umbellifera (Z)
Strombosia scheffleri (Z)
Strychnos mellodora (Z)
S. usambarensis (Z)
Tabernaemontana angolensis (V Z)
T. ventricosa (V Z)
Trichocladus ellipticus (X)
Voacanga thousarsii (Z)

KEY
V = by weight (barochory)
W = wind (anemochory)
X = by explosive dehiscence and seeds thrown (active autochory or active ballists).
Y = water (hydrochory)
Z = animal-dispersed (zoochory)
? = a question mark after any of the symbols means that the case is uncertain.

The small tree layer or field layer, generally below 5 m in height but up to 10 m on the lower slopes, includes:

SMALL TREE/FIELD LAYER

Achyrospermum laterale
Aidia micrantha
Alchornea laxiflora
Allophylus chaunostachys
Argomuellera macrophylla
Aulacalyx diervilleoides
Coffea ligustroides
Cremaspora triflora
Dovyalis macrocalyx
Dracaena fragrans
Erythrococca polyandra
Ochna oconnorii
Pauridiantha symplocoides
Phyllanthus inflatus
Psychotria zombamontana
Tannodia swynnertoni
Tarenna pavettoides

In the low 1 m high shrub layer, *Mostuea brunonis* is dominant in large sectors of the lower slope forest.

The forest species lists, especially that of the small tree layer, has been aided in large part by the collections of Mr. Tom Müller of theSalisbury Herbarium.

Ravine and riverine forest

Macedo (1970a, 1970b) lists many tree species for the ravine riverine zones throughout the mountain area. These are composed of many rainforest and thicket species as well as those more generally confined to, or typical of, stream banks. Some of the components include:

TREE SPECIES

Albizia glaberrima (W)
Adina microcephala (W)
Anthocleista grandiflora (Z?)
Bersama abyssinica (Z)
Blighia unijugata (Z?)
Bombax rhodognaphalon (W? Z?)
Bridelia micrantha (Z)
Chlorophora excelsa (Z)
Craibia brevicaudata (X)
Ekebergia capensis (Z)
Eryrthrophleum suaveolens (Z)
Filicium decipiens (Z)
Ficus capensis (Z Y)
Halleria lucida (Z Y)
Harungana madagascariensis (Z)
Khaya nyassica (W)
Millerria stuhlmannii (X)
Newtonia buchananii (W)
Pandanus sp. (Y Z)
(prob. *P. livingstonianus*)
Parkia filicoidea (Z)
Raffia sp. (Y Z)
Rauvolfia caffra (Z?)
Sapium ellipticum (Z?)
Syzygium guineense (Z)
Treculia africana (Y? Z)
Trichilia sp. (Z)
Trichocladus ellipticus (X)

KEY
W = wind (anemochory)
X = by explosive dehiscence and seeds thrown (active autochory or active ballists).
Y = water (hydrochory)
Z = animal-dispersed (zoochory)
? = a question mark after any of the symbols means that the case is uncertain.

The giant canopy liana *Entada pursaetha* with long pendant pods, 1m–1,5 m long, is abundant in riverine forest and its stems frequently attain 50 cm (dbh).

Dispersal

As the agents of dispersal of many species are uncertain only the broadest comparisons can be drawn (Fig. 8.3).

In montane forest, of 14 occurrences, 12 (86%) are animal dispersed and two (4%) are also water dispersed according to Phillips (1931). Tropical forest with 11 occurrences has eight (73%) animal dispersed species and three (27%) wind disseminated. Of 41 occurrences in transition forest 28 (68%) are animal dispersed, seven (17%) are active ballists, two (5%) by wind, two by water and two by weight (barochorous). Riverine forest trees comprise 20 (67%) animal dispersed out of 30 occurrences, five (17%) wind, at least four (13%) by water and one (3%) an explosively dispersed species. It is probable that many more, including the winged components, are disseminated by water. Despite the uncertainties the overwhelming majority of trees are animal dispersed. As no quantitative data on density or frequency of these species are available, it is unfortunately impossible to obtain an importance value from the two percentages which would probably show, for example, a high value for wind dispersal in the tropical zone due to the abundance of *Newtonia buchananii*, as well as in riverine forest where *Adina microcephala* and *Khaya nyasica* predominate. Active ballists are common in transition forest and relatively unrepresented in the zones above and below it.

Phenology

The few data noted on forest components on the mountain show a prevalence of flowering from August to December and a main fruiting period from February to June with a peak in autumn.

Environmental factors

Most of these features have been dealt with in the sections on grassland and thicket. It need only be reiterated that the montane forest margin is the only one in the entire system where progressive retreat due to fire is conspicuous (possibly associated with alteration in soil moisture balance). Elsewhere forest is badly damaged only by human activities of shifting cultivation and timber extraction.

Succession

The balance between grassland, thicket and forest in the summit areas has been dealt with above. On the xerocline lower slopes, savanna, thicket and forest appear to be in a homeostatic balance with soil moisture regimes of the different land facets, forest being confined almost exclusively to valley head and riverine sites. It is on the lower mesocline slopes where active forest extension (secondary thicket) is occurring on old cultivated areas left fallow. From the time the field is abandoned, the following progressive sequence occurs: (a) herb and suffrutex weeds with woody scrub formed by forest margin species as well as coppices of some original forest components, (b) scrub–thicket, (c) thicket (mixed savanna and forest species), (d) forest. However, where dense stands of elephant grass *Pennisetum purpureum* occur as the secondary cover, this appears to hold back (inhibit) the succession to forest, as is clearly shown in other moist areas such as the eastern Congo sector of the equatorial zone (pers. data). On the mesocline, the most important components in the scrub and thicket stages toward forest are *Bridelia micrantha*, *Harungana madagascariens* and *Trema orientalis*. *Harungana* is also important in the moist coast forests of the Cheringoma cuesta, and *Bridelia* is a canopy dominant in the secondary thickets of the Lake Kivu area of the eastern Congo (Democratic Republic of Congo).

8.4 MIDLANDS

The deeply dissected hill country of the Midlands, with rounded to flat interfluves, is covered in tall, closed miombo savanna of homogeneous appearance (the homogeneity is due primarily to the predominance of microphyll sized (15 mm x 15 mm area) leaflets which make up the canopy cover). This sea of miombo is uninterrupted except by a few inselbergs of various dimensions, and gaps where dambo remnants occur. A change in canopy texture is discernible where dendritic strips of stream bank trees and forest occur. These strips are most conspicuous at the end of the dry season when the tardily deciduous miombo canopy has dropped its leaves. The miombo upper canopy averages between 18 m and 20 m in height, contrasting with that nearer the frontier escarpment which is half this height, and its duplex structure is completed by a median to tall continuous grass stratum which is burnt annually.

As the greater part of the Midlands is formed by metamorphic, crystalline granite-gneiss, the soils are predominantly skeletal (**pg**) sandy or stony and over-drained, except on interfluve crests where they are deeper. However, where basic rocks intrude, deeply weathered latosols occur which have an improved soil moisture balance. The small dambo areas are sandy with an impervious gley subsoil (**Pgh**). Although termite hills occur in the miombo, they are seldom covered by dense thicket as their soils are generally poor in clay and are thus droughty.

Miombo occurs in the isohyet range from 900 mm to 2,000 mm in the Midlands and Gorongosa Mountain area within the ecosystem. A strongly seasonal hot, wet period occurs from November to April and a six month dry season from May to October. Mid-summer droughts occur periodically and interrupt the phenophase cycles.

The hill miombo of the Midlands is related to that in Rhodesia, Malawi and parts of Zambia and has a different appearance and successional status, although they are floristically similar, to dambo miombo as exemplified by the Cheringoma cuesta and the Zambezi–Congo watershed.

The most striking seasonal feature of miombo in Mozambique is the contrast between the lush midsummer situation, when the sounds of massed cicadas and the liquid whistles of the migrant European oriole predominate, and the bleak, silent, grey sea of trunks and blackened ground after fire in the dry season.

Visual experience in the miombo savanna woodlands is wholly introvert due to the tall closed canopy, which excludes the sky and long vistas. Except when hot fires have singed the canopy, the spectacular synchronous flush of red leaves in the pre-rain spring, noted on the interior continental plateau in Rhodesia, is not a feature of the coastal or lowland miombo.

Of the 15 communities mentioned below, only the inselberg communities assume local prominence; the remainder are small and patchy, or narrow and linear in the case of riverine sites. Closed tree savanna covers more than 90% of the Midlands.

Aquatic Herb Communities

Except for the waters which rise on Gorongosa Mountain, most of the stream and river network in the Midlands is seasonal. In rocky perennial streams the submerged aquatic *Hydrostachys* sp. is common, and on the banks and islands emergents include tall reeds *Phragmites mauritianus* fronted by floating mats of *Echinochloa pyramidalis* along the water's edge.

No data are available on the vegetation of the seasonal pans and vleis which occur on the relic dambo floors of the Midlands.

Rockfaces

The herb constituents of rock faces in the Midlands are related to those on Gorongosa Mountain but with the absence of the dominant sedge *Coleochloa setifera*. Components include:

HERBS

Aloe chabaudii
Aloe cryptopoda
Crassula spp.
Euphorbia spp.
Myrothamnus flabellifolia
Orchidaceae
Vallozia sp.

Root mats are formed on gently sloping faces in which scattered small trees take root. The rock fig, *Ficus soldanella,* is characteristic of even the smallest outcrops of rock in the miombo.

Scrub Savanna

In the Midlands, scrub savanna is confined to areas of secondary growth on old cultivation sites, subject to annual fires, and is essentially a developmental stage to tree savanna, as opposed to thicket, due to the established grass stratum. Thus the woody scandents and climbers typical of scrub–thicket are absent and the scrub is comprised of components from all strata of tree savanna.

Tree Savanna

Tall closed canopied tree savanna or savanna woodland covers the greater part of the Midlands. The height of miombo canopy trees changes at the two ends of the moisture–altitudinal gradient, becoming shorter in the drier zones and in the wetter uplands. Although a large number of upper storey tree species occur, it is the predominance of the genera *Brachystegia* and *Julbernardia* which give the miombo its characteristic small-leaved uniformity. The canopy trees are mostly compound leaved, bipinnate, deciduous species. The benign hydrothermal regime of central Mozambique, from combined maritime and orographic influences, appears to be responsible for individual rather than synchronous leaf phases exhibited by miombo canopy trees and the facultative deciduousness in some species such as *Brachystegia spiciformis,* which varies with site and the amount of precipitation in a season.

The number of distinguishable layers in savanna, in addition to the basic duplex combination of woody plants and grass strata, depends on various permutations of life-form height classes and the degree of suppression or competition imposed by the upper canopy layer. Other contributory factors include the frequency and intensity of environmental factors such as frost, fire, utilization by herbivores and edaphic influences.

In the miombo of the study area, four strata are defined by height classes and characterised by species usually confined to them. These are: (A) canopy and emergent trees, (B) medium tree layer, (C) small tree layer, and (D) grass or herbaceous stratum. In some areas stratum (A) is in the height interval 16 m to 28 m and in others 13 m to 23 m. However, in upland areas, best exemplified in Rhodesia, the miombo is much shorter and the A and B strata are merged so that a species such as *Diplorhynchus condylocarpon* has equal status to the *Brachystegi*a species in size and abundance. At the other end of the profile the grass stratum is clearly separated from the small tree layer when it is of median height up to 2 m. In many areas however, where *Hyparrhenia* species predominate, the grass stratum is between 3 m and 4 m in height and effectively submerges the small tree layer.

In scarp and hilltop areas subject to orographic fog the emergent canopy trees, in particular *Brachystegia spiciformis*, have their canopy branches and upper bole festooned with an abundance of epiphytic orchids and ferns comprising some six species of each. Herbaceous scandents and climbers are common in the grass stratum and lianes are relatively rare, but are responsible for initiating thicket clumps where deeper soils occur. Thorny components are rare except in secondary growth on old cultivation sites where *Acacia polyacantha* may assume local temporary dominance. A special woody life form associated with miombo is the bamboo *Oxytenanthera abyssinica* which occurs in clumps and forms societies in the median tree layer (Fig. 8 14). Succulence is totally absent in the tree strata and is exhibited solely by some herbs of the grass stratum.

Physiognomy and structure are illustrated by a profile diagram drawn in the field, which shows the crown and growth form characteristics (Fig. 8.14). Most upper tree strata species exhibit the savanna ‘sun’ growth form with umbrella-shaped crowns and crown branches diverging midway up the bole. An exception is *Xylopia* *parviflora* which has a more typical forest or 'shade' growth form with a straight, clean bole and small rounded crown. The small tree and shrub layer typically have deformed shapes due to damage by fire and wild ungulates.

Three quantitative examples of tall, closed miombo savanna are given from the Midlands area west of the Rift Valley (Table 8.4 /Fig. 8.14). These show the variable dominance of several species in all strata depending on the selective influences such as substrate, dispersal, fire and human activities. The species occurrence in the several woody layers also shows the presence of stratal indicators, or characteristic species, and the major contribution of canopy species at different stages of growth.

In the canopy or upper tree layer one of the following species is dominant or co-dominant in the three highest densities: *Brachystegia boehmii, B. spiciformis, Erythrophloeum africanum, Julbernardia globiflora* and *Pterocarpus angolensis*. In the northwest of the ecosystem *Brachystegia glaucescens* is the sole dominant, patchily, over large areas. *Brachystegia glaucescens, Julbernardia globiflora* and *Ricinodendron rautananii* tend to form pure species societies within the miombo system. Locally *Burkea africana, Monotes* spp., and *Pericopsis angolensis* can assume high density. In the subordinate tree layers *Diplorhynchus condylocarpon* is by far the most abundant and characteristic species throughout the central Mozambique Midlands. Local mid-stratum dominance is also shown by combretaceous, *Combretum* and *Terminalia* species, *Pterocarpus* species or *Pseudolachnostylis maprouneafolia*. No quantitative data are available for the grass stratum, but mosaic dominance occurs of tall *Hyparrhenia* spp., *Heteropogon melanoleuca, Andropogon gayanus* and *Bekeropsis uniseta* with median height swards of *Loudetia. superba, Digitaria milanjiana, Panicum maximum, Schizachyrium sanguinem* and *Themeda triandra*. The miombo grass stratum contains a rich herbaceous, suffrutex and dwarf shrub flora, examples of which are listed in Table 8.4. Geophytes and other annuals, especially ginger plants *Zingiberaceae*, are conspicuous in post-fire flush and flowering in spring.

Aspects of the Miombo Ecosystem

TOP FAR LEFT:

Closed-canopied miombo woodland on white duplex sands with a dense field-layer of thicket and forest saplings interspersed with a sparse grass cover. The epiphvte is a staghorn fern *Platycerium peltatum*.

TOP CENTRE:

Closed-canopied miombo savanna woodland on sandy latosols with a continuous but light grass stratum. Other areas have a dense grass layer 2 m in height. Typical of Midlands and red sands of the coast plateau.

TOP LEFT:

Dambo and miombo margin after a veld fire. Note widely spaced grass tufts typical on sand substrates.

BOTTOM:

Dambo miombo, sandy, high water table drainage line grasslands and termitaria thicket islands fringed by miombo woodland and forest mosaic (dry season aspect).

TABLE 8.4
Analysis of woody strata in 1 ha of woodland on the Midlands

	A. CANOPY AND EMERGENTS >13 M–23 M	NO. OF TREES	TOTAL BASAL AREA CM^2
	Julbernardia globiflora	29	545,199
	Erythrophleum africanum	26	579,764
	Brachystegia boehmii	19	321,826
	Burkea africana	15	344,335
	Brachystegia spiciformis	9	191,742
	Sterculia quinqueloba	5	15,843
	Ricinodendron rautanenii	2	34,650
	Pseudolachnostylis maprouneifolia	2	3,218
	Combretum zeyheri	2	2,044
	Shrebera tricoclada	2	1,521
	Xeroderris stuhlmanii	1	707
	Pericopsis angolensis	1	1,018
	Sclerocarya caffra	1	2,828
	Amblygonocarpus andongensis	1	314
14 spp.		115	2,045,009
	B. MEDIUM TREE LAYER > 7 M–13 M	NO. OF TREES	TOTAL BASAL AREA CM^2
	Diplorhynchus condylocarpon	19	155,591
	Pseudolachnostylis maprouneifolia	11	23,245
●	*Erythrophleum africanum*	10	38,375
●	*Brachystegia boehmii*	6	8,015
●	*Julbernardia globiflora*	5	5,413
●	*Sclerocarya caffra*	5	7,701
	Xylopia parviflora	3	5,677
●	*Amblygonocarpus andongensis*	2	1,964
	Strychnos madagascariensis	2	856
●	*Ricinodendron rautanenii*	1	1,591
●	*Xeroderris stuhlmanii*	1	491
	Hymenocardia acida	1	201
●	*Burkea africana*	1	133
●	*Brachystegia spiciformis*	1	314
●	*Sterculia quinqueloba*	1	707
	Crossopterix febrifuga	1	177
	Swartzia madagascariensis	1	133
17 spp.		71	250,584
	C. SMALL TREE LAYER 2 M–7 M	NO. OF TREES	TOTAL BASAL AREA CM^2
	Diplorhynchus condylocarpon	34	106,984
●	*Erythrophleum africanum*	12	12,276
	Xeromphis obovata	11	8,828
	Byrsocarpus orientalis	6	3,423
●	*Pseudolachnostylis maprouneifolia*	4	1,521
●	*Julbernardia globiflora*	3	531
●	*Brachystegia boehmii*	3	1,135
●	*Sclerocarya caffra*	3	755
	Holarrhena pubescens	3	616
●	*Brachystegia spiciformis*	2	177
●	*Millettia stuhlmannii*	2	416
●	*Xeroderris stuhlmannii*	2	707
	Flacourtia indica	2	314
	Hymenocardia acida	1	50
	Ziziphus mauritiana	1	79
●	*Amblygonocarpus andongensis*	1	79
	Combretum zeyheri	1	177
	Lannea discolour	1	177
	Piliostigma thonningii	1	20
	Kigelia africana	1	20
	Strychnos spinosa	1	20
	Crossopterix febrifuga	1	79
	Commiphera serrata	1	50
	Ximenia caffra	1	20
	Eugenia spp.	1	20
25 spp.		99	138,474
Grand Total in 1 ha: 35 spp.		285	2,434,067

Cont.

KEY
● = potential canopy components

In sites where deeper soil pockets occur, small thicket patches may be initiated around the boles of canopy trees by woody climbers, particularly *Artabotrys brachypetalus* and *Friesodielsia obovata* which are animal dispersed species.

Dispersal

The three main woody strata of tall miombo savanna are clearly characterised by the predominance of particular modes of seed dispersal. Wind and animal dispersed types have the highest occurrence in all strata, but the addition of density data for each type immediately gives their real importance in each strata (Fig. 8.4).

Although wind and animal dispersed types considerably exceed those with exploding legume pods which throw their seeds (active ballists) this group contains the *Brachystegia* and *Julbernardia* dominants which have the highest density. By contrast animal dispersed components of the canopy have a low density.

In the median tree layer wind dispersal has the highest importance value due to the abundance of *Diplorhynchus condylocarpon* and *Combretaceae* in occurence and density. Active ballists are rare apart from the abundance of canopy species present in this stratum. Animal dispersed types have the highest occurrence and density in the small tree and shrub layer (Fig. 8.4).

Scrub thicket

Primary scrub thicket occurs in discontinuous patches, related to deeper pockets of soil in the miombo chiefly on the crests of interfluves, occasional patches around the base of tree boles, and amongst rock outcrops. The interstage growth of bamboo *Oxytenanthera abyssinica* thicket also forms a low impenetrable scrub. These will be dealt with in the following section.

By far the greatest extent of continuous scrub–thicket with a canopy at 3 m–4 m is secondary regrowth on fallow areas left by the rotation of shifting cultivation. The largest areas occur in the Midland sector of latosols immediately south of Gorongosa Mountain. Scrub thicket is only continuous as a mosaic alternating with scrub savanna.

Scrub thicket components include:

SCRUB

Acacia polyacantha

Acacia seyal
Annona senegalensis
Antidesma venosum
Combretum fragrans
C. molle
C. zeyheri
Dalbergia melanoxylon
Entada abyssinica
Harrisonia abyssinica
Julbernardia globiflora
Lippia javanica
Markhamia obtusifolia
Piliostigma thonningii
Securidaca longipendunculata
Strychnos madagascariensis
S. spinosa
Vangueria infausta
Vernonia spp.
Vitex payos

SCANDENTS CLIMBERS

Asparagus spp.
Bauhinia galpinii

Dalbergia arbutifolia
Dalbergia lactea
Lantana camara
Macuna coriacea
Smilax kraussiana

GRASSES

Pennisetum purpureum

Rottboelia exaltata

Scrub thicket rarely grows beyond 5 m before being cleared again for cultivation, or is opened up by annual fires, thus forming a savanna with scrub patches.

Thicket

Four main types of thicket occur as island patches within miombo savanna. These are: (a) thicket on deep sand pockets, (b) termitaria thickets, (c) bamboo thickets on rock outcrops. That which occurs on termitaria in sandy lithosols is the most poorly developed due to the excessive drainage, and only a few trees typical of bottomland clays occur together with miombo tree species on the termite hills. In the heavier latosols, termitaria thickets are better developed and in many areas are covered by a pure stand of bamboo *Oxytenanthera abyssinica*. Only on the margins of the relic dambos are there well developed termitaria thickets similar to those in the Rift Valley and on the Cheringoma cuesta.

Thicket on deep sand pockets

These thickets are composed of a mixed assemblage of woody plants derived from moist forest, dry forest, termitaria, rock outcrops, and bottomland savanna as well as from

RIGHT: Figure 8.4

Comparative importance of dispersal types (occurrence plus density) in three woody strata of closed *Brachystegia* (miombo) savanna on the Midlands section of the Gorongosa ecosystem.

FAR RIGHT: Figure 8.5

Predominance of animal-dispersed woody species in various kinds of thicket occurring in miombo.

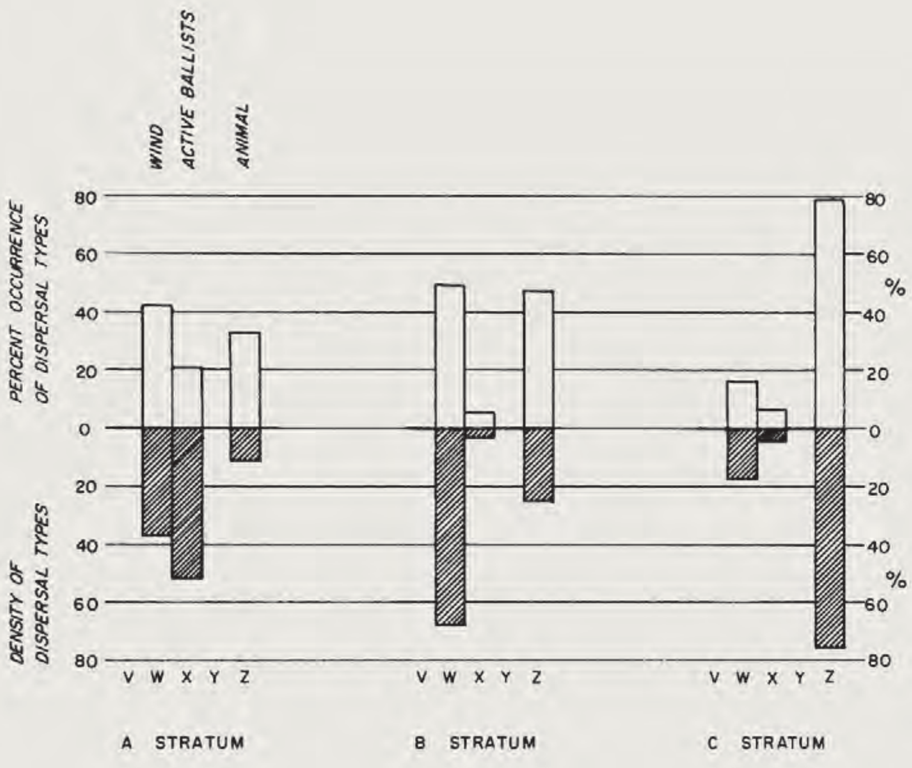


FIG. 8.4 COMPARATIVE IMPORTANCE OF DISPERSAL TYPES (OCCURRENCE PLUS DENSITY) IN THREE WOODY STRATA OF CLOSED BRACHYSTEGIA (MIOMBO) SAVANNA ON THE MIDLANDS SECTION OF THE GORONGOSA ECOSYSTEM

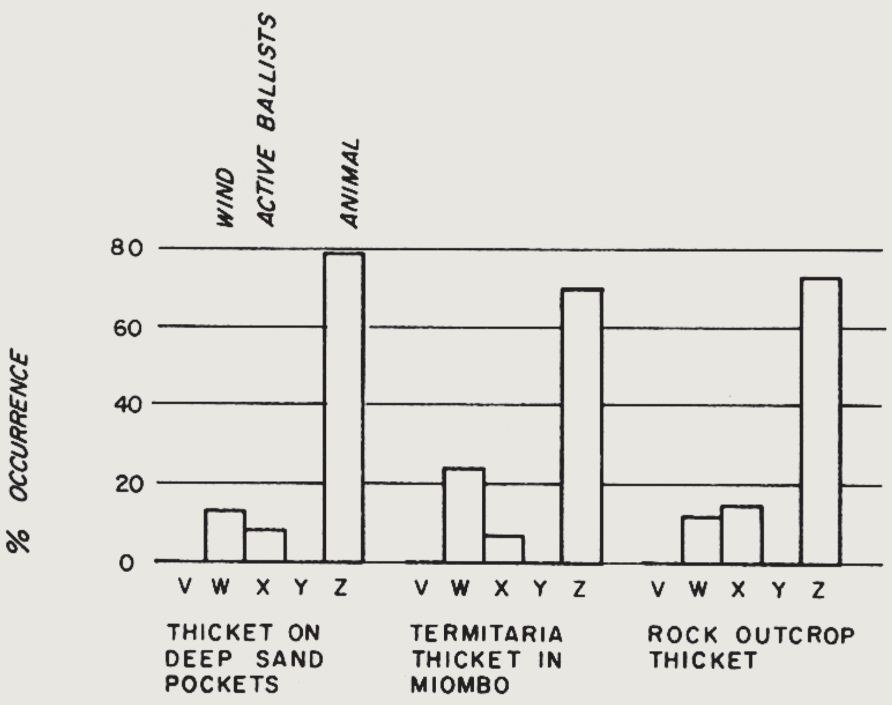


FIG. 8.5 PREDOMINANCE OF ANIMAL-DISPERSED WOODY SPECIES IN VARIOUS KINDS OF THICKET OCCURRING IN MIOMBO

the miombo field layer itself. Climbers and scandents are abundant and these roof in a closed canopy between 6 m and 8 m. Above this rise emergents such as *Pteleopsis myrtifolia* and *Erythrophleum suaveolens* to 15 m or 20 m. The density of climbers in the canopy at 6 m to 8 m is such that a dense tangle is formed which replicates the under-canopy thickets formed in some forests, and enables forest understorey birds such as the terrestrial bulbul *Phyllastrephus terrestris*, to use the canopy as a 'dislocated' feeding zone. An example of this thicket type is illustrated by a profile bisect in which the components are listed (Fig. 8.14). The thicket field layer is dominated by small Rubiaceous trees such as *Polysphaeria lanceolata* and *Canthium crassum* which occur in riverine and other moist forests, and patches of *Oplismenus, Olyra* and *Panicum* shade grasses.

Termitaria thickets

Though the termitaria thickets are poorly developed in the hill miombo a large variety of woody species occur on them. These are derived from five sources: riverine, moist forest, bottomland clay savannas, the surrounding miombo, and species typical of termite hills throughout the ecosystem. Of these, 60% are termite hill and clay savanna species typical of the Rift Valley and arid savannas elsewhere. Components include the following:

WOODY SPECIES

Acacia nigrescens (W Z)
A. nilotica (Z)
Annonaceae sp. indet. (Z)
* *Allophylus alnifolia* (Z)
* *Asparagus* sp. (Z)
Azanza garckeana (Z)
Bauhinia galpinii (X)
Brachystegia boehmii (X)
Capparis erythrocarpos (Z)
Combretum hereroense (W)
C. molle (W)
Commiphora schimperi (Z)
Cordia pilosissima (Z)
Dalbergia boehmii (W)
Dalbergia melanoxylon (WZ)
Dichrostachys cinerea (Z)
* *Diospyros mespiliformis* (Z)
* *Diplorhynchus condylocarpon* (W)
* *Ehretia amoena* (Z)
* *Flacourtia indica* (Z)
* *Friesodielsia obovata* (Z)
Grewia lepidopetala (Z)
* *Julbernardia globiflora* (X)
Lecaniodiscus fraxinifolius (Z)
Markhamia acuminata (W)
Maytenus senegalensis (Z)
Ormocarpum trichocarpum (W?)
Oxytenanthera abyssinica (W? Z?)
Piliostigma thonningii (Z)

KEY
W = wind (anemochory)
X = by explosive dehiscence and seeds thrown (active autochory or active ballists).
Y = water (hydrochory)
Z = animal-dispersed (zoochory)
? = a question mark after any of the symbols means that the case is uncertain.
* = asterisk denoting those with the highest frequency from 10 termitaria

Bamboo thicket

Dense pure societies of solid-stemmed bamboo *Oxytenanthera abyssinica* thicket occur on the heavier soils in the Midlands, including sandy loams and latosols usually on valley slopes of higher rainfall (> 1,200 mm) miombo. In the high water table sands of the Cheringoma Coast, bamboo is confined almost entirely to the heavier soils of termite hills, and extends into lower rainfall miombo on termite hills, deep soil pockets and streambank sites. An example of bamboo clumps forming the mid and lower strata of miombo is shown in Fig. 8.14. *Oxytenanthera* is deciduous and has a periodic gregarious flowering and seeding after which it dies. New growth is from seed, and the vigorous vegetative shoots put out every rainy season result in the formation of large clumps.

Thickets on rock outcrops

These are composed of a mixture of species derived from seven sources—riverine, moist forest, dry forest, thicket, rock surfaces, arid, and moist savanna. The larger thickets, which form an apron of various dimensions around the base of inselbergs, grade into a mesic evergreen forest, composed of a mixture of rain forest and dry forest elements. Inselberg forests and thickets were not sampled.

Woody components of small rock outcrops in the Midlands sector of the ecosystem south of Gorongosa Mountain include:

WOODY SPECIES

Allophylus alinifolius (Z)
Bauhinia galpinii (X)
Berchemia discolour (Z)
Bersama abyssinica (Z)
Cleistochlamys kirkii (X Z)
Cleistanthus schlechteri (X Z)
Combretum apiculatum (W)
Diospyros senensis (Z)
Erythoxylon emarginatum (Z)
Euphorbia sp. (X Z)
Ficus ingens (Z)
Ficus soldanella (Z)
Flacourtia indica (Z)
Friesodielsia obovata (Z)
Garcinia livingstonei (Z)
Kirkia acuminata (W)
Lannea stuhlmannii (Z)
Oncoba spinosa (Z)
Pseudocassine transvaalensis (Z)
Strychnos potatorum (Z)
Terminalia sansibarica (W)
Xylotheca tettensis (Z)
Zizyphus mucronata (Z)

KEY
W = wind (anemochory)
X = by explosive dehiscence and seeds thrown (active autochory or active ballists).
Z = animal-dispersed (zoochory)

Dispersal

Dispersal in all thicket types in the miombo system is predominantly zoochorous (Fig. 8.5). An exhaustive listing of species may change the relative importance of those dispersed by wind and explosive dehiscence (active ballists), but would likely only reinforce the predominance of animal dispersed types especially in the higher rainfall zones where forest elements are commoner constituents.

An important element in the composition of almost every type of thicket community is the presence of widespread thicket forming species. The majority are animal dispersed (particularly by birds and primates) and are related to two basic features in an environment:

(1) perches, and (2) water-based sites. In the first group are any prominences including trees, termite hills, rock outcrops, stumps and human artifacts such as fence posts, walls, gates, buildings etc. The second includes stream banks, the periphery of open waters, ravines and dongas, springs and fountains. The implications of these in landscape evolution and the interrelations of communities will be dealt within a later section (9.9).

Forest

Forest in the hill miombo system is confined to sites with high soil moisture, including stream banks, alluvial fans, escarpments, ravines, and the basal pediments of inselbergs. The forests are thus patchy and isolated or linear, linked by the narrow line of riverine trees in miombo which widen on meander and talus deposits on incised streams, or by a stepping stone archipelago-like series of small thicket islands, described above, which occur to a greater or lesser degree in different situations.

Immediately to the west of Gorongosa Mountain, on the interfluve between the Nhandue and Vunduzi Rivers, are dry forest remnants on relic duplex sands, and below them on sands of alluviated valleys, now incised, is dry forest in riverine situations. The evolution of this landscape and ecosystem cycle is reconstructed in Chapter 6.2 (Fig. 6.2).

The riverine strips traversing miombo are narrow lines of tall trees which widen in areas with islanded or marginal alluvial deposits. Where the deposits are predominantly sandy, dry forest or its elements form the more extensive cover and the true riverine tree species form a single line confined to the actual riverbanks.

The two most abundant riverine trees in the Midlands are *Adina microcephala* and *Khaya nyasica* which are wind (and water?) dispersed. For extensive lists of riverine components reference should be made to Macedo (1970b: 8.12, 11.4). Commoner components include the following:

CANOPY TREES

Adina microcephala (W)
Albizia glaberrima (W)
Blighia unijugata (Z)
Bombax rhodognaphalon (W)
Diospyros mespiliformis (Z)
Ekebergia capensis (Z)
Erythrophleum suaveolens (Z)
Ficus capensis (Z)

Garcinia livingstonei (Z)
Khaya nyasica (W)
Millettia stuhlmannii (X)
Newtonia buchananii (W)
Parkia filicoidea (Z)
Sterculia appendiculata (Z)
Syzygium guineense (Z)

KEY
W = wind (anemochory)
X = by explosive dehiscence and seeds thrown (active autochory or active ballists).
Z = animal-dispersed (zoochory)

SMALL TREES

Antidesma venosum (Z)
Bersama abyssinica (Z)
Bridelia micrantha (Z)
Draecaena reflexa (Z)
Mimusops fruticosa (Z)

Nuxia oppositifolia (W)
Phoenix reclinata (Z)
Rothmannia manganjae (Z)
Tricalysia nyassae (Z)
Turraea nilotica (Z)

KEY
W = wind (anemochory)
X = by explosive dehiscence and seeds thrown (active autochory or active ballists).
Z = animal-dispersed (zoochory)

HERBS

Brilliantaisia pubescens

CLIMBERS

Entada pursaetha
Rhoicissus spp.

In drier valleys in the miombo, trees such as *Acacia robusta, Diospyros fruticosa, Diospyros mespiliformis, Cordyla africana, Lonchocarpus capassa, Tamarindus indica,* and *Xanthocercis zambesiaca* are typical of the riverine strips.

Dispersal

As little is known about the composition of escarpment and inselberg forests, the following remarks are confined to the riverine cover. Although *Adina* and *Khaya* are wind (and water?) dispersed trees, , the most abundant riverine species, more than 60% of the total woody species listed by Macedo (1970b), have animal dispersed diaspores, which is similar to the prima facie analysis given for the riverine forest on the mountain (Fig. 8.3). In drier valleys the relative importance of animal dispersal types remains predominant, as proven by the data from the Rift Valley.

Environmental Factors

The Midland miombo savanna and its subordinate inclusions of thicket and forest patches experience: a bimodal radiation regime with peaks in November and March due to the screening effect of heavy cloud during the rains; a unimodal five month summer rains period from November to March followed by a seven month dry period from April to October; and no frost in the winter dry season. The two major climatic phases can be divided into four seasons by hydrothermal indices (Fig. 4.13):

(1) spring torrid period (August to October)
(2) summer sweltering period (November to February)
(3) autumn hot-drying period (March and April)
(4) winter cool dry/humid period (May to July).

Due to orographic, or nocturnal katabatic, fog and heavy guttation and dew formation in the autumn and midwinter period, the cool season is dry by day and humid at night. Of the 93 rain days per year, 68 (73%) occur between November and April. Five months receive more than 100 mm (perhumid) rainfall in the long term. Variability of rainfall is only 26% as compared to the adjacent Rift Valley which has a regime nearly three times more variable. A feature of the regional climate expressed most drastically in areas of lower rainfall, is midsummer drought in January, or February and March. A rapid means of determining drought periods, apart from the conspicuous leaf discolouration of the vegetation, is by the use of De Martonne's index of Aridity ($I = {}^{P}/_{T} + 10$) described under Climate (Ch. 4). Midsummer droughts are defined by indices between 1 and 2.5 or by a period of more than two weeks with less than 15 mm rainfall. The greatest temperature range occurs in the pre-rain spring (August to October) and the least in autumn.

Closely related to these wetting and drying phases and intervention of midsummer droughts, is the occurrence of annual fire in the miombo savanna. Today, mostly due to human agency, annual fires sweep through the miombo savanna, burning for weeks or months according to the density of grass fuel, wind and its ability to cross the riverine strips. Fire intensity is greatest late in the dry season, singeing the upper canopy trees to nearly 15 m where a tall 3 m to 4 m *Hyparrhenia* grass stratum occurs. Fires occurring earlier in the dry season, including those which may be initiated as early as March or April following midsummer droughts, typically burn in a mosaic and are of low intensity, many dying out at night when heavy guttation occurs. Such areas can be burnt again in the late dry season. The predominance of fire scars on trees, on the leeward side (northwest) of the prevailing trade winds is due to the longer duration of fire out of the wind, and the differential susceptibility of trees more than 3 m in height to fire. *Erythrophleum africanum* was by far the most scarred, and 20% (57/284) of all trees in 1 ha were fire scarred.

The densest settlement of tribal cultivators in the Midlands sector within the ecosystem is in the area south and east of the Gorongosa Mountain. Shifting cultivation of two to three years on one site followed by a fallow period of up to 15 or 20 years is practised on the poor sandy lithosols (**Pg**), and semi-permanent cultivation of about 10 years with a short fallow period on the red latosols (**Vb**). This introduces a mosaic pattern into the landscape: many sites at different stages of regressive or progressive succession.

No domestic stock are kept, due to the presence of tsetse fly and nagana, and the wild, large herbivore populations in the miombo are extremely low with periodic short influxes from the Rift Valley related to post-fire flush of grasses, maturation of indigenous fruits such as marula *Sclerocarya caffra*, or tribal food crops of maize and sorghum (Ch. 9)

Phenology

Foliage phenophases

Except where late season fires have destroyed the leaves of the median and upper canopy, the spring aspect to the miombo in the maritime continental margin shows a mosaic of phases. A species, such as *Brachystegia spiciformis*, can be in full mature leaf and pod in one site, and nearby, the same species is bare or in new scarlet leaf flush. The mosaic pattern in spring, autumn and winter is clearly conspicuous from a low flying aircraft.

Where tall grasses have enabled the flames to reach into the middle or upper canopy, singeing if not burning tree leaves, an earlier and more synchronised new leaf flush and flowering occurs at the end of July and early August. However, in the Midlands this synchronism, which is typical of the miombo on the continental interior plateau subjected to frost, is lost in the autumn and winter dry season when, as there is no frost to trigger leaf fall, there is a differential leaf fall of species and individuals in response to soil moisture depletion. In Salisbury the first frost month is June and a month earlier in the centre of the subcontinent in northern Botswana and the Caprivi.

The phenogram for miombo savanna trees in the Midland physiographic unit shows a gradation of leaf phenophases into four seasons, and a bimodal flowering regime in the equinoxes (Fig. 8.6). The first new leaves on trees appear in early August or July if triggered by fire, and the most leafless period is over September when the lowest Aridity Index (0.8) occurs. However, trees bare of leaves occur as early as April when *Pterocarpus angolensis* and *Ricinodendron rautanenii* are the first to show leaf discolouration and leaf fall. The same two species were the first to react to low night temperatures in northeast South West Africa in May 1966, despite late main rains (pers. obs.). These species are also the first indicators of midsummer drought conditions, when their leaves turn yellow and fall if rainless conditions persist, resulting in a new flush of leaves and flowering if wet conditions return in March or April.

Superimposed on these climo-edaphic controls are the effects of leaf defoliating caterpillars on *Burkea africana*, *Erythrophleum africanum*, or *Sclerocarya caffra* in November causing a new leaf flush (and flowering in some) in January. Certain of the caterpillars, like the mopane 'worm', are highly prized as food by tribal people.

Reproductive phenophases

Lack of experimental or quantitative correlations between climatic and edaphic factors allows for only an interpretation for the flowering peaks by way of the coincident relationships between climo-edaphic parameters and reproductive peaks. For example, quantitative correlations from the northern tropics in West Africa showed that flowering was closely related not only to the incidence of rain in two woody species studied, but also to the temperature drop associated with rainfall (Rees 1964a, 1964b). Rees (1964b, p.16) concludes that if these relationships are true 'flowering would occur in response to either a low minimum temperature (in the absence of rain) or a rapid temperature-drop, almost invariably associated with heavy rain in the wet season or a rainstorm in the dry season'.

Reproduction in the tree layers

The most striking feature of reproduction in miombo trees in the Midlands are bimodal phenophases coincident with the bimodal radiation and insolation peaks about the time of the equinoxes (Fig. 8.6). The radiation and heat peaks just before and after the summer rains are due to the screening effect of a dense cloud cover blanket during the rains (see Ch. 4 Climate). However, the equinoctial peaks may also result from solsticial triggers, particularly as midwinter fires simulate the ground warming which begins about a month after the winter solstice (mid July) (also the time when many passerines in the area begin their reproductive period). Judging by Bonsma's (1940) monthly chemical analysis of browse foods, this bimodality may, however, be in response to endogenous mobilization of nutrients in spring and again in autumn when fruits are being formed.

A subtle phenomenon, first noted commonly in the Rift Valley savannas and emphasized by the discovery of marula fruit in elephant dung at the 'wrong' time of the year, is the bimodal flowering exhibited by individual trees of certain species.

Individual bimodal flowering is very often, but not always, coincident with the equinoctial periods. Tree species in the miombo which exhibit this phenomenon are *Milletia stuhlmannii* (Aug.–Nov./Feb.–Mar.), *Sclerocarya caffra* (Sept./Apr.), *Piliostigma thonningii* (Dec./Apr.–May) and *Heteropyxis natalensis* (Nov./Mar.). All except the last species occur outside the miombo system as well, on the Rift Valley plains and in riverine sites. Trees suspected of flowering twice include *Brachystegia spiciformis*, *Albizia versicolour* and *Xeroderris stuhlmannii.*

This bimodal flowering is not to be confused with the dropping of opened flowers (due to their failing to set, insect damage or other reasons) and renewed flowering in close sequence within consecutive months. This sequence is shown by individual trees of conspicuous flowering genera such as *Acacia, Cassia* and *Pterocarpus* and noted during extremely dry summer periods interspersed with short heavy falls of rain.

The importance of sap rise and bark characteristics in different seasons determines the resource use of certain miombo canopy trees by man and elephant. *Brachystegia boehmii, B. spiciformis* and *Julbernardia globiflora* trunk bark is stripped off by tribal bee-keepers to construct hives, and elephant strip and eat the bark of *B. boehmii*, in the dry season and leave other miombo species relatively unscathed. Of these species, the bark of only the first strips cleanly off the bole throughout the year; the bark of the other two species adheres to the wood and can only be stripped cleanly in midsummer. There is thus a strong selective preference for *Brachystegia boehmii* by man and beast.

Herb layer

No quantitative phenological data on the herbaceous layer in miombo was recorded. Generally the herbaceous layer comes into full flush soon after the first rains in November, and the flowering of grasses, particularly, occurs in November and December. However, in many areas fire induces a pre-rain vegetative flush from August to October and it is at this time that suffrutices and geophytes are conspicuous, such as members of the *Zingiberaceae* with large brightly coloured flowers. However, other geophytes such as a purple-flowered *Afromomum* sp. and *Haemanthus multiflorus* are only abundant in November. Many of the forbs flower mainly in the late summer and autumn, examples include: *Aerva leucura*, *Agathis anthemum bojori*, *Borreria scabra*, *Cassia mimosoides*, *Celosia trigyna, Cissus bathyrhakodes, Cleome monophylla, Crotalaria virgulata, Desmodium gangeticum, D. velutimun, Melochia corchorifolia, Vernonia cinerea, Vigna unguiculata* and *Wormskoldia longipendunculata*. lt is likely, however, that the flush and flowering of herb layer components is most closely tied to the annual variations in rain occurrence, particularly the differential effect of July rains on burnt and unburnt areas.

Maximum growth of the grasses appears to be reached in February, but taller components such as *Hyparrhenia* spp. attain their maximum in the autumn. It is significant that only two tall grass feeders, Lichtenstein's hartebeest and sable, remain in the miombo throughout the annual cycle; most of the other large wild herbivores are visitors from the Rift Valley, mainly in the pre-rain spring when the miombo herb layer has flushed due to fire or unseasonal rain. In the autumn the herbivores visit the few dambo areas of the miombo. Otherwise the mature coarse grass stratum of miombo remains relatively untouched by wild ungulates. Hopkins (1968) notes that in the herb stratum of Nigerian miombo, maximum dry weight is reached and growth ceases two months before cessation of the rains.

In summary, Midland miombo phenophases divide the annual cycle into five seasons similar to those recognised by Boaler (1966) and Malaisse (1976). These are:

(1) pre-rain woody spring, leafless–flowering period (mid-Aug. to Oct.)
(2) first rains herbaceous spring (November)
(3) main summer rains, mature foliage period (Dec. to mid-March)
(4) autumnal drying and fruit maturation period (mid-March to mid-May)
(5) mild winter dry season leaf fall and fruit dispersal period (mid-May to mid-Aug.).

Succession

Geo-ecological succession and landscape evolution in the Midlands is dealt with in Chapter 6 and Fig. 6.2, in which the role of the miombo savanna system is traced from the relic Plio-Pleistocene surfaces that survive on flat interfluves, to the present deeply dissected hill miombo predominant over the greater part of the Midlands in central Mozambique, and indeed over most of northern Mozambique as well.

As shown by the moist savanna symbols in the block diagram sequences (Fig. 6.2), miombo forms an interzone between forest and the dry clay savannas of bottomlands. Eroding back of the plains and interfluve areas, as well as the bottomland dambo surfaces, allowed the extension of miombo in both directions. On the Midlands in the north of the ecosystem, where duplex sands are being actively eroded, the leached clays exhumed from beneath the sand is invaded by nearly pure scrub or pole stands of *Julbernardia globiflora*, The evidence from this marginal area of the Midlands indicates that the floristically poorer and drier climo-edaphlc end of the miombo spectrum undergoes little, or very slow, further development from its *Julbernardia* dominance unless further sands are added to the soil profile, either from above by colluvial sheetwash processes, or possibly in the longer term by eluviation of the exposed sandy clays, which would alter the soil moisture balance to the mesic.

In hill miombo, the island thickets, which occur either on deep soil pockets, on termitaria, or around tree bases, are not actively invading the surrounding greater extent of miombo savanna. The differential leaf fall of the same miombo canopy trees under the same rainfall regime, but on different substrates and land facets of the same hillslope, indicate, not only that many of the species are facultatively deciduous but also that soil moisture balance underlies both deciduousness and the role of forest/thicket extension.

Fire is naturally a major factor in suppressing the extension and establishment of forest/thicket precursors, particularly if there are fierce burns in the late dry season. However, evidence from the Midland and Cheringoma evolutionary sequences (Figs 6.2 and 6.5), which will be referred to more fully below, indicates that the efficacy of fire is not only dependent on which part of dry season it occurs in, or the abundance of grass fuel, but also on the fundamental factor of soil moisture balance. If forest/thicket occurs on the mesic to xeric (droughty) side, their extension appears to be more easily destroyed by fire as their components would be in disequilibrium with the substrate. But if the soil moisture balance is above the mesic, then a dense grass sward of 3 m to 4 m height producing extremely fierce fires in the late dry season is insufficient to eliminate even the small tree-base thickets. Examples of this occur in the Rift Valley savannas where a permanent water table exists at 7 m to 10 m in depth. West (1965, pp.10–11, 23–24) reports on the quite different responses to fire of *Acacia* savanna on compact skeletal latosols and adjacent *Burkea–Terminalia* savanna on deep sands under an identical rainfall regime, due apparently to the contrasting soil moisture status of the two soils. Trapnell (1959, p.165) admits that 'a good deal (of forest invasion of miombo) probably depends on local soil moisture conditions'.

Burning experiments laid down in the miombo of northern Zambia in 1934 were studied and described by Trapnell (1959) who distinguished three main categories according to their response to fire: (a) fire tender or semi-tolerant, (b) semi-tolerant to tolerant, and (c) tolerant. The Ndola area is dambo miombo plainsland which has quite a different soil moisture balance to hill miombo, and is therefore closely equivalent to that on the Cheringoma cuesta in Gorongosa.

The *Brachystegia* and *Julbenardia* dominants became extinct in the plots burnt annually in the late dry season in Zambia (Trapnell 1959) but under Rhodesian conditions, where fires were apparently less fierce, these dominants were highly fire tolerant (West 1965, pp. 14–15). In the *Pterocarpus–Dialium–Baikiaea* 'filtered out miombo' in northern South West Africa and the Caprivi, no changes could be discerned after 10 years of burning experiments due to the wide spacing of the tufted grass stratum on Kalahari sands resulting in light fires during any part of the dry season.

A feature of miombo savanna is the mosaic formed by the grassland understorey, changing in height and density in different areas and sites. The experimental evidence sited above indicates, therefore, that the changes in relative dominance of tree species in different areas may be selected by different intensity of fires as well as by substrate characteristics. The quantitative data from the Midlands show clearly mosaic dominance and recruitment of canopy trees in different areas, but these data are unfortunately not correlated with characteristics of the grass stratum.

In one quantitative sample from the Midland miombo in Gorongosa, 20% (57 out of 284 trees > 3 m in height) of the trees in 1 ha were scarred by fire. Although *Julbernardia* and *Erythrophleum* were nearly equally predominant in the sample, *Erythrophleum* trees were scarred by fire more than double than the next species (*Julbernardia*, *Brachystegia boehmii* and *Diplorhynchus*) although it is classified as fire tolerant by the Ndola experiments. The Ndola experiments showed clearly that the fire-tender to semi-tolerant species, in particular the *Brachystegia* and *Julbernardia* canopy dominants, increased under an early burning regime (late autum – early winter) and in the protected plots.

Miombo trees are heliophytes and, where all stages of forest invasion of miombo are found on the Cheringoma Plateau, the miombo is shaded out and becomes extinct except for relic emergent canopy trees such as *Brachystegia spiciformis*. Within the dispersal radius of these relics, rare straggling saplings of the same species can be found where openings occur in the forest/thicket understory.

The great miombo system has been regarded as a fire-subclimax but Trapnell (1959, p. 167) concludes from the evidence of the burning experiments, 'that there is no present justification for regarding the ordinary woodland as fire induced type except in respect of its understorey and small tree and shrub components'. Fanshawe (1971), forest ecologist in Zambia, maintains that miombo is secondary, occurring after the destruction of dry evergreen forest by fire. This conclusion appears to be accepted by Malaisse (1977) working in the southern Congo. Aubreville (1947, 1949b) and Walter (1971, 1973) look upon most, if not all, of the miombo system as moist anthropogenic savannas.

In the absence of human influences miombo would have been burnt periodically by lightning–induced fires in the late dry season – first rains period, resulting in extremely fierce fires which however would have been extinguished in a mosaic pattern by the occurrence of thunderstorm rain. With the advent of cultivator man, these late dry season fires would have become an annual event as fields are prepared from September onward (vide Chap. 7). Both these sources of fire, and shading, militate against the evolution of fire-tender heliophytic *Brachystegia* and *Julbernardia* as canopy dominants across vast expanses of the African continent, and against the evolution of its unique faunal associates. Thus the only fire regime which would play a fundamental part in the evolution and maintenance of miombo would be those which occurred early in the dry season.

The only possible source of fire early in the dry season over the millennia is from man; honey hunters who rob hives in the main miombo honey season between April and June, and from fires made by game hunters to attract wild ungulates to unseasonal new grass flush. It is no accident that most of the bee-keeping tribal people in Africa are those associated with the miombo whose canopy dominants are renowned honey trees. The main honey flow is related to the gregarious flowering of either or both *Julbernardia globiflora* and *J. paniculata*. Another honey flow occurs in midsummer after flowering of the several *Brachystegia* tree species, but honey gathering at this time does not result in extensive fires. In the equatorial rain forest there is a definite honey season from June to July which is the highlight of the annual cycle for the hunter-gatherer Mbuti pygmies in the Ituri Forest (10^0N) (Turnbull 1961, pp. 46–51).

It is worth speculating that the co-relations of man, honey and fire may extend to one million or more years ago, and from this, early dry season fires would have favourably selected for *Brachystegia* and *Julbernardia* predominance and thus the enhancement of a prolific honey tree resource, a co-active evolutionary relationshlp.

Interpretation of the evidence depicted by the contrasting hill and dambo type miombo systems and their soil characteristics indicate that over vast areas, miombo is climax, or in dynamic equilibrium with climo-edaphic determinants and the fire factor, the damaging effect of which is modified by the soil moisture balance of different soils and land facets.

8.5 RIFT VALLEY

The central feature of the Urema Trough is the lake surrounded by extensive open floodplain grasslands which extend 30 km northwards. On calm, clear days Gorongosa Mountain is reflected in the Urema Lake, and below it the three Bunga Inselbergs and the sides of the Rift are conspicuous. The floodplains disappear into mirages to the north and terminate abruptly against tree lines of savanna, thicket or forest on alluvial fans entering from the valley sides. The wooded cover occurs in a distinct mosaic of clumped and linear patterns related to the alternation of alluvio-catena soils.

This heterogeneity is enhanced by the abundance of large island thickets on termite hills which, archipelago-like, overlay all communities — distinct from, but part of the larger ecosystems. These dark-foliaged thickets, like those in discontinuous patches and strips along water-courses, are particularly conspicuous in the dry season.

The seasonal extremes experienced in the Rift Valley are even more striking than in the miombo. The steaming summer is oppressively hot, with vast flooded shallows under floating pastures and flowering waterlilies, lushly foliaged trees, bird and frog choruses, barbel and turtles in the rain-flooded savannas far from permanent water. The impression is one of overwhelming verdant growth set off against a sky dominated by giant cumulo -nimbus thunderstorms releasing heavy curtains of rain over the plains and Gorongosa Mountain.

In contrast the dry season has brown grasslands, leafless savanna trees, a total absence of surface water, except in the main rivers and lake, and hard-baked ground. Grasslands on base saturated soils turn a golden-brown, reminiscent of the margins of the Etosha and Makgadikgadi salt lakes. The dry season tones are often transformed to a blackened landscape by fire, leaving the island thickets on termitaria and forest patches singed but otherwise unscathed. In the dry season a dense haze of smoke closes off the far vistas, and valley fog is a feature of the early mornings. The essence of the Rift Valley ambiance is superbly captured in the writings of Vaughan-Kirby and Vasse, quoted in the frontis.

Aquatic Herb Communities

Two distinct aquatic systems occur on the Rift floor. One system consists of the seasonal rain-filled pans that are linked temporarily, if at all, during heavy downpours of rain. The deeper of these pans retain water until about June. The second is made up of both a seasonal flood and ebb regime, typified by the floodplains, and perennial waters of streams, the lake and oxbow lagoons. The hygrophilous communities of the seasonal pans most closely resemble those of the floodplains. A full gradation of overlapping aquatic community types occurs from briefly inundated habitats to permanent waters. The herbaceous constituents include:

(A) SUBMERGED AQUATICS

Ceratophyllum demersum
Lagarosiphon spp.
Ottelia exserta
Potamogeton spp.
Najas interrupta

(B) FLOATING AQUATICS

Azolla nilotica
Eichhornia crassipes
Lemna spp.
Pistia stratiotes
Wolffia spp.
Trapa natans

(C) ROOTED AQUATICS WITH FLOATING AERIAL PART HERBS

Alternanthera sessilis
Ipomoea aquatica
Ludwigia stolonifera
Marsilia minuta
Neptunia oleracea
Nymphaea capensis
N. caerulea
Nymphoides indica
Utricularia stellaris

GRASSES

Echinochloa pyramidalis
Echinochloa stagnina
Oryza longistaminata
Paspillidium obtusifolium
Vossis cuspidata

(D) EMERGENT AQUATICS

Aeschynomene indica
Cyperus digiratus
Cyperus papyrus
Sesbania mossambicensis
Sesbania sesban
Phragmites mauritianus
Typhus sp.

The reedbeds occur in stream bank sites and in the more permanent backwaters. Only one area of papyrus occurs within the ecosystem sector of the Rift floor, in the southeast at the foot of the Cheringoma slopes between the Mutsambire and Musapasso streams.

Mudflat communities

These are dense ephemeral herb societies that germinate on the mudflats left by the receding floodwaters. Attaining between 20 cm and 50 cm in height, these plants are at the height of their reproductive phases between June and September. Some constituents of this species-rich community are heavily grazed by wild ungulates whilst others are ignored.

Fire Patterns, Meander Scrolls, Savanna Pans and Clump Thickets on the Rift Floor

RIGHT:

Edaphic control of the passage of fire by short grasslands on saline clays and on overdrained ecotones (between convex and low surfaces) which act as firebreaks, depicted by the linear fire-limit in the middle distance.

FAR RIGHT:

Alternating stacks and ridges of a meander scroll sequence on the Pungue River east of Chitengo Camp. Accentuated by the contrasting physiognomies of grassland in the slacks and savanna and thicket clumps on the rises.

Typical components include:

GRASSES

Crypsis schoenoides
Diandrochloa pusilla (on sand)

SEDGES

Cyperus alopecuroides
Cyperus esculenta
Cyperus digitata
Mariscus hemisphaericus

HERBS

Altenanthera sessilis
Amaranthes graecizans
Ambrosia maritima
Basilicum polystachyon
Bergia mossambicensis
Caperonia serrata
Chrozophora plicata
Coldenia procumbens
Euphorbia minutiflora
Glinus lotoides
Glinus oppositifolius
Gnaphalium hispida
Gomphrena celosiodes
Gyrodoma hispida
Heliotropium indicum
H. ovalifolium
Ludwigia stolonifera
Melochia corchorifolia
Phyllanthus niruri
Polygonum plebium
Rorippa micrantha
Sphaeranthus gazensis
Sphenoclea zeylaniea

SUFRUTICES

Aeschynomene indica
Sesbania mossambicensis
Sesbania sesban

WOODY SHRUB

Mimosa pigra

Fire Patterns, Meander Scrolls, Savanna Pans and Clump Thickets on the Rift Floor cont.

TOP LEFT:

Knobthorn *Acacia nigrescens* savanna and clump thickets with an abundance of rain-filled pans (3/ha) developed mostly on eroded termite hill sites. Clump thickets on termite hills and around tree-bases.

BOTTOM LEFT:

Thicket of baobab *Adansonia digitata. Acacia welwitschii, Albizia brevifolia* and *Euphorbia halipedicola,* on convex sandy clay.

TABLE 8.5
Composition of Sporobolus kentrophyllus saline grassland from 30 m^2 quadrats

SALINE GRASSLAND	NO. OF QUADS	REL FREQ. %
Sporobolus kentrophyllus	29	41
Mariscus hemisphaericus	22	31
Sporobolus ioclados	11	16
Eriochloa fatmensis	3	4
Chloris mossambicensis	1	1
Crotalaria sp.	1	1
Echinochloa sp. nr. *haploclada*	1	1
Tephrosia pumila	1	1
Trianthema salsoloides	1	1
9 spp. (5 grasses, 1 sedge, 3 forbs)	70	

SOIL PROFILE

Depth cm.	Texture	pH	Salinity (ohms)	CaCO$_3$	Colour (Munsell)
0-4	SdLm	6.4	1 480	—	Black (10YR 2/1)
4-25	SdCl	7.3	70	5%10%	Brownish-black (2.5 Y 3/1)
25-100	Cl(G)	7.6	70	10%	Greyish-olive (5 Y 4/2)

The mimosa is a favoured browse food and only attains shrub growth form during inundations; the remainder of the time it assumes a prostrate growth form in response to heavy utilization by herbivores.

Floodplain Grasslands

Typically, these perennial hygrophilous grasslands exhibit a mosaic of dominance made conspicuous by their different heights and stratification. Basically there are short, medium, and tall grasslands. In the first category are the *Sporobolus* communities on saline soils, and the micro-perennial lawns of *Cynodon dactylon* and *Digitaria swazilandensis*, whose leaves are generally below 15 cm in height with inflorescences reaching to 30 cm. The second is characterized by *Panicum coloratum, Eriochloa stapfiana* and *Setaria* species which attain 100 cm in height. Tall grasslands are those formed by dense, nearly pure swards of *Vetiveria nigritana* which have an average height of 220 cm. In some areas associations of elephant grass *Pennisetum purpureum, Hyparrhenia* species and a giant form of *Panicum maximum* attain 3 m to 4 m in height.

Structurally the median to tall grasslands are quite different to the short swards. The latter comprise only a single layer of grasses, sedges and forbs. Many of these constituents, including the *Cynodon* and *Digitaria* dominants, form a subordinate stratum within and between the tufts of the median to tall grasses. Due to the low gradient, floodplain grasslands merge almost imperceptibly into savanna grasslands characterized by their overlay of woody tree and shrub strata. All depressions in the savannas are merely remnants of former floodplain grassland extensions.

Short grassland

Saline grassland

The simplest grass community is that dominated almost exclusively by *Sporobolus kentrophyllus* on highly saline clays capped by 3 cm to 5 cm of sand. Where a surface sandy loam soil of 15 cm to 20 cm depth overlies sodic clays, the above grass community merges into another, which is dominated by the halophyte *Sporobolus ioclados* and which has a richer mixture of savanna and floodplain species. Analysis in a one hectare area showed the following relationships (Table 8.6).

Micro-perennial lawn grassland

The greater part of the flood plains surrounding the Urema Lake on the South and northwest sides are covered by short 10 cm high stoloniferous grassland of *Cynodon* and *Digitaria swazilandensis*. Similar grasslands occur again on the Macoreia Plains north of the lake. These grasslands, which are a major pasture for medium and short grass grazers, are inundated shallowly to a greater or lesser extent every year. In years of low floods they are dependent on direct rainfall and show rapid changes in flush or drying out (see section 9.4).

Table 8.6
Composition of *Sporobolus ioclados* saline grassland from 30 m^2 quadrats.

SALINE GRASSLAND	NO. OF QUADS	REL FREQ. %
Sporobolus ioclados[1]	30	15
Tephrosia pumila	27	14
Fimbristylis hispidula	23	12
Digitaria milanjiana[1]	19	10
Urochloa mosambicensis[1]	14	7
Mariscus hemisphaericus	14	7
Echinochloa sp. nr. *haploclada*	12	6
Cassia mimosoides	12	6
Cienfugosia hildebrandtii	11	6
Pankum coloratum[1]	8	4
Setaria eylesii[1]	8	4
Barleria spinulosa	7	4
Duosperma quadrangulare	4	2
Dichrostachys cinerea	3	2
Digitaria swazilandensis[1]	1	1
Eriochloa fatmensis[1]	1	1
E. stapfiana[1]	1	1
Panicum sp. (K LT 2573)[1]	1	1
Sporobolus kentrophyllus[1]	1	1
Stylochiton sp.	1	1
20 spp. (11 grasses[1], 2 sedges, 4 forbs, 2 suffrutices, 1 woody)	197	

SOIL PROFILE

Depth cm.	Texture	pH	Salinity (R)	$CaCO_3$	Colour (Munsell)
0-6	**CILm**	7.4	780	—	Brownish-black (10YR 2/2)
6-25	**CI**	7.6	140	—	Brownish-black (10YR 3/1)
25-100	**CI(G)**	7.5	70	—	Greyish-olive (YR 5/2)

KEY
*<250 = saline

Analyses of a 20 km^2 area of these grasslands south of the Urema Lake and its Sungue arm showed the followingrelationships. (Table 8.7).

Table 8.7
Composition of micro-perennial Cynodon–Digitaria lawn grasslands of the southern Urema Plains derived from 30 m^2 quadrats in 18 one hectare sites (total of 540 m^2 quadrats).

HERB LAYER	NO. OF QUADS	REL. FREQ. %
Cynodon dactylon[1]	474	20
Euphorbia minutiflora[1]	270	11
Digitaria swazilandensis	244	10
Echinochloa stagnina[1]	241	10
Mariscus hemisphaericus[2]	179	7
Vossia cuspidata[1]	124	5
Alternanthera sessilis	99	4
Paspalidium obtusifolium[1]	84	3
Eriochloa fatmensis[1]	80	3
Echinochloa sp. nr. *haploclada*[1]	66	3
Panicum sp. (KLT. 1873)	57	2
Gomphrena celosioides	49	2
Rorippa micrantha	49	2
Tephrosia pumila	48	2
Corchorus olitorius	40	2
Coldenia procumbens	35	1
Eichhornia crassipes	33	1
Ambrosia maritima	33	1
Sida alba	28	1
Phyllanthus niruri	25	1
Heliotropium ovalifolium	21	1
Neptunia oleracea	19	1
Eragrostis atrovirens[1]	16	1
Mimosa pigra (prostrate)	16	1
Euphorbiaceous weed (indt.)	15	1
Ludwigia stolonifera	14	1
Ipomea aquatica	12	1
Marsilia minuta	10	< 1
Melochia corchorifolia	10	< 1
Ammania auriculata	7	1
Cyperus michelianus	5	1
Chrozophora plicata	4	1
Amaranthus graecizens	3	< 1
Gyrodoma hispida	3	< 1
Euphorbia sp.	2	< 1
Heliotropium indicum	2	< 1
Sesbania mossambicensis	2	< 1
Solanum panduriforme	2	< 1
Abutilon guineense	1	< 1
Dactyloctenium aegyptium[1]	1	< 1
Eragrostis aethiopica	1	< 1
Indigofera spicata	1	< 1
Sesbania sesban	1	< 1
Talinum portulacifolium	1	< 1
Urochloa mosambicensis	1	< 1
45 spp (12 grasses[1], 2 sedges[2], 30 forbs and suffrutices, 1 woody)	2428	

Cont.

WOODY PLANTS*	TOTAL NO.	REL. DENSITY % (180,000 M^2)
Mimosa pigra	1 016	95
Acacia xanthophloea	28	3
Hyphaene benguellensis	25	2
Acacia albida	3	0.3
4 spp. (* = only sapling stages represented)	1072	

SOIL PROFILE

Depth cm.	Texture	pH	Salinity (R)*	$CaCO_3$	Colour (Munsell)
0-12	ClLm	5.8	470	—	Black (10 YR 2/1)
12-18	Cl	5.9	220	—	Brownish-black (10 YR 2/2)
18-50	ClLm	6.4	120	—	Brownish-black (2.5 YR 3/2)
60	ClLm (G)	7.0	70	—	Olive-brown (2.5 YR 4/3)

These short grasslands merge into medium to tall grass communities which are waterlogged for longer periods, and which thus occur either in the lower parts and depressions on the plains or in maldrained areas of perched floodplains at a higher contour.

Medium height grasslands

The two examples of saline grasslands noted above (Tables 8.5 and 8.6) are the xeric end of a microrelief catena on base saturated alluvium. These and the *Cynodon–Digitaria* (Table 8.7) grasslands merge gradually or abruptly with the two following grass communities which occur on a mosaic of waterlogged, black vertisol clays of quite different texture and consistence. In the less moist parts and on sandy clays are *Setaria eylesii* (or *S. holstii* or *S. woodii*) swards, alternating with *Echinochloa stagnina* on granular clay loams. The *Setaria* grassland type has a mean height of 100 cm and contains a subordinate short grass and forb layer below. An example showed the following composition:

TABLE 8.8
Setaria floodplain grassland analysed from 30 m^2 quadrats across one hectare (Road 5 area).

FLOODPLAIN GRASSLAND	NO. QUAD.	REL. FREQ.%
Setaria eylesii[1]	28	22
Mariscus hemisphaericus	28	22
Echinochloa sp. nr. *haploclada*[1]	23	18
Chloris mossambicensis[1]	9	7
Vernonia kirkii	9	7
Sporobolus kentrophyllus[1]	7	5
Cienfugosia hildebrandtii	6	5
Panicum coloratum[1]	5	4
Sesbania sesban	4	3
Eriochloa stapfiana[1]	2	2
Barleria spinulosa	2	2
Phyllanthus niruri	2	1
Enicostema hyssopifolium	1	1
Commelina sp.	1	1
Echinochloa stagnina[1]	1	1
Asparagus sp.	1	1
16 spp. (7 grasses[1], 1 sedge, 8 forbs and suffrutices)	129	

SOIL PROFILE

Depth cm.	Texture	pH	Salinity (R)	CaCO$_3$	Colour (Munsell)
0-4	SdCl	5.9	420	—	Black (10 YR 2/1)
4-30	Cl	7.2	180	—	Olive-black (5 Y 3/1)
30-50	Cl(G)	7.3	70	5%	Olive-black (5 Y 3/2)

The shorter 40 cm tall *Echinochloa stagnina* grassland either occurs as a mosaic with *Setaria* or forms extensive areas where it is singly dominant. An example is given in Table 8.9.

TABLE 8.9
Echinochloa stagnina marsh grassland analysed from 30 m^2 quadrats across 1 hectare (Road 5 area).

MARSH GRASSLAND	NO. QUAD.	REL. FREQ. %
Echinochloa stagnina[1]	29	31
Panicum coloratum[1]	27	28
Mariscus hemisphaericus	19	20
Vernonia kirkii	5	5
Cienfugosia hildebrandtii[1]	4	4
Enicostema hyssopifolium	3	3
Barleria spinulosa	2	2
Setaria eylesii[1]	2	2
Eriochloa stapfiana[1]	1	1
Ischaemum afrum[1]	1	1
Sesbania sesban	1	1
11 spp. (5 grasses[1], 1 sedge, 5 forbs and suffrutices)	94	

SOIL PROFILE

Depth cm.	Texture	pH	Salinity (R)	CaCO$_3$	Colour (Munsell)
0-4	ClLm	5.6	810	—	Brownish-black (5 Y R 2/1)
4-25	Cl	6.4	320	—	Brownish-black (2.5 Y 3/1)
35-50	Cl(G)	6.8	100	—	Brownish-black (2.5 Y 3/2)

In all the above tables the presence of *Cienfugosia hildebrandtii* or *Duosperme quadrangulare*, which are vigorous suffrutices with large basal parts, are indicative of the drying-out trend in the hygrophilous grasslands. In areas of gilgai microrelief, these species occur on the higher rims separating each microbasin; sites which are later invaded by mopane *Colophospermum mopane*, or acacias such as *A. borleae* and *A. polyacantha*. In the microperennial grassland, fever trees and palm are the most vigorous invaders of the savanna front. Sandy patches are colonised by winter thorn *Acacia albida* or dry forest precursors.

Tall grassland

Tall floodplain grassland is characterised by the *Vetiveria nigritana* community which attains an average height of 225 cm. This community occurs on similar soils to those on which *Echinochloa stagnina* is found, but under a more seasonally waterlogged condition. An example from half a hectare area is given in Table 8.10. The double layered structure in *Vetiveria* grassland is well developed and the lower storey grasses are grazed the most by ungulates, whilst the rank *Vetiveria* and *Ischaemum* are largely ignored until they produce a new regrowth flush after fire. The lower grass layer is of soft-leaved species: *Digitaria swazilandensis, Panicum coloratum, Eriochloa stapfiana*, and *Echinochloa stagnina*.

These various floodplain grasslands merge with those of the savannas and are repeated throughout the savannas wherever appropriate substrates occur. On the Rift floor alluvia, tall grass habitats are not confined to riverine sites but occur as a mosaic with medium and short grass habitats through the savannas, hence animals usually associated with the tall grass zone of riverbanks are widespread.

Environmental factors

The lawn grasslands, *Setaria* and *Echinochloa* communities, are all inundated to a greater or lesser extent every year. In wet years they are flooded by rising river and lake waters as well as from direct rainfall and local runoff. Under these circumstances waterlogged conditions endure for about 3 to 4 months between December and March. In dry years flooding is temporary and fluctuates with the incidence of rain.

The highly saline *Sporobolus* grass communities occur on the upper parts of microrelief and are waterlogged for shorter periods than the hygrophilous grasslands.

Annual fires burn all the floodplain grasslands except the *Cynodon–Digitaria* lawn community. This grassland and the *Echinochloa–Vossia* community bear the brunt of year-round heavy grazing pressure by the wild ungulates.

TABLE 8.10

Vetiveria nigritana grassland analysed from 30 m^2 quadrats in a 0.5 ha sample (Road 5 area).

PLANTS	NO. OF QUADS	REL. FREQ. %
Vetiveria nigritana[1]	30	28
Ischaemum afrum[1]	29	27
Bothriochloa glabra[1]	14	13
Mariscus hemisphaericus	14	13
Digitaria swazilandensis[1]	3	3
Panicum coloratum[1]	3	3
Cassia mimosoides	2	2
Echinochloa stagnina[1]	2	2
Eriochloa stapfiana[1]	2	2
Phyllanthus niruri	2	2
Vernonia kirkii	2	2
Heteropogon contortus[1]	1	1
Hyparrhenia rufa[1]	1	1
Panicum maximum[1]	1	1
Paspalum scrobiculatum[1]	1	1
Rhynchosia sublobata	1	1
Tephrosia pumila	1	1
17 spp. (11 grasses [1], 1 sedge, 5 forbs)	109	

SOIL PROFILE

Depth cm.	Texture	pH	R(Ohms)	$CaCO_3$	Colour (Munsell)
0-10	CILm	6.3	1 100	—	Black (7.5 YR1, 7/1)
10-60	CI	6.2	580	—	Brownish-black (10 Y R 2/2)
70	CI(G)	7.1	150	5%	Brownish-black (2.5 Y 3/1)

Succession

A grassland and grazing succession occurs on the floodplains which is sensitive to fluctuations in environmental factors such as flooding, drying, drought and fire. These aspects are dealt with in the following chapter (Section 9.4). Successional replacement of grasslands by woody communities is described at the end of the Rift Valley section.

Scrub Savanna

The largest continuous area of scrub savanna is formed by pure stands of *Acacia borleae* on gilgai vertisols of the Nhamisangu floodplain in the north, and by palm *Hyphaene benguellensis* in the south. The *Acacia borleae* cover is between 1 m and 2 m in height with variable density. In parts of the Macoreia Plains this species is mixed with short *Acacia polyacanth*a. The scrub growth form of the palm *Hyphaene benguellensis*, which otherwise attains up to 20 m in height, is maintained by heavy elephant browsing. The spacing in this community varies from widely separated clumps to dense continuous areas of scrub thicket 3 m to 4 m in height. These species, in common with *Acacia xanthophloea*, are actively invading floodplain areas that are drying out, and characteristically form pure species communities, but also occur in close mosaic where soils alternate on alluvia–catenas.

Below Bunga Inselberg, on either side of the Vundudzi River, and in the Chitengo area near the Pungue River, large patches of scrub savanna occur on old cultivation sites of some 20 years standing. Areas cultivated in the past on the Rift floor are shown in Fig. 7.2. The chief scrub constituents here are *Combretum fragrans, Lonchocarpus capassa*, and to a lesser extent *Piliostigma thonningii*. Heavy browsing by elephant and annual fire have contributed to maintaining their scrub growth form.

In the north, adjacent to the Lunga drainage, is an isolated area of pure *Acacia nilotica* scrub savanna on sheet-eroded sandy clays with a short sparse grass stratum.

Tree Savanna

The tree savannas of the Rift are physiogomically and floristically diverse due to the association of fine leaved (nanophyll) thorn trees, with broad-leaved (mesophyll) species, and large-leaved (megaphyll) palms. Diversity is multiplied by the mosaic occurrence of mixed species associations alternating with communities dominated by only one or two species.

The grass stratum of the savannas is equally diverse in physiognomy and species associations. The grasses occur in a mosaic pattern and also form communities dominated over large areas by a few species. Clumped dispersal is thus exhibited by all layers in the savannas.

The appearance of the Rift savannas is characterized by tall trees up to 20 m in height with

RIGHT:

Clay savanna of *Hyphaene petersiana (benguellensis)* on saline vertisols with 1 m to 2 m high *Setaria eylesii* grass stratum (3 m measuring rod in middle distance). Typical two-aged structure with adult palms (first slack invaders) and palm shrub stratum kept short by elephant browsing. Dark trees are *Trichilia emetica* on a termite hill.

FAR TOP RIGHT:

Sand savanna of *Burkea africana, Terminalia sericea* and *Hyperthelia dissoluta* grass stratum.

FAR BOTTOM RIGHT:

Fever tree *Acacia xanthophloea* marginal floodplain woodland. Note quasi-even-aged structure of canopy trees, treeless median layer and mixed weed and grass groundlayer with a few palms (autumn aspect).

Rift Valley Savanna Communities (cont.)

LEFT:

Tall mopane woodland. Lay figure Signet for scale (dry season).

umbrella-shaped canopies, interspersed with the distinctive growth forms of baobabs and islands of large termitaria thicket clumps.

The spacing of the wooded grasslands varies between an open tree savanna and closed-canopied savanna woodlands. Six major tree savanna communities occur on the Rift floor in changing species associations related to soil and moisture gradient changes. The main communities are:

(1) mixed savanna (*Acacia*, *Albizia*, *Lonchocarpus*, *Piliostigma, Sclerocarya*)
(2) marginal floodplain woodland (*Acacia albida, Acacia xanthophloea)*
(3) knob thorn savanna (*Acacia nigrescens*)
(4) sand savanna (*Burkea africana, Terminalia sericea*)
(5) mopane savanna (*Colophospermum mopane*)
(6) palm savanna (*Hyphaene benguellensis, Borassus aethiopica*)

As many of these communities occur in closely juxtaposed mosaics due to the close alternation of different soils and their ecotones, it has been possible to sample two or three different kinds within a one hectare sample area. Analysis of three examples includes: (1) a fever tree, winter thorn and palm mosaic association, (2) mopane savanna woodland, (3) an *Acacia nigrescens* – *Burkea africana* mosaic association.

Marginal floodplain woodland

The fever tree and winter thorn woodlands grow typically in quasi-even-aged stands of various heights, the youngest occurring on the leading edge invading the floodplain grasslands. The sequence is illustrated by a profile diagram with the fever tree as an example (Fig. 8.15). Sandy alluvium in the lower parts of the Urema slackbasin occur in relatively small patches, hence winter thorn will probably decrease relative to the fever tree and palm invasion (increase) of the floodplain. An example of the floristic and dominance relationships in marginal floodplain woodland is given in Table 8.11.

Mopane Savanna Woodland

Like the above species, mopane tends to form pure species stands of various ages. In the centre of the park sector of the Rift Valley two isolated areas of mopane occur on sodic calcareous clays. The larger patch measuring 2 km x 7 km (14 km^2) occurs in the converging delta area at the head of the Urema Lake, and the other a small area of about 1.5 km^2 west of the Urema Lake (Road 5 area).

In the north between the Nhandue and Nhamapaza Rivers more extensive areas of mopane occur, mixed with other tree species, on fossil interdistributary slack soils. Even when mixed with other species such as *Dalbergia melanoxylon* and *Spirostachys africana*, all three species tend to form their own clumps. In Gorongosa, mopane are tall, averaging 15 m, and have a deltoid crown shape. The physiognomy and structure of mopane savanna

RIGHT: Figure 8.6

Comparative importance of dispersal types in three woody strata of mopane savanna woodland on the Rift Valley floor.

FAR RIGHT: Figure 8.7

Comparative importance of dispersal types in three woody strata of *Acacia-Burkea* savanna mosaic.

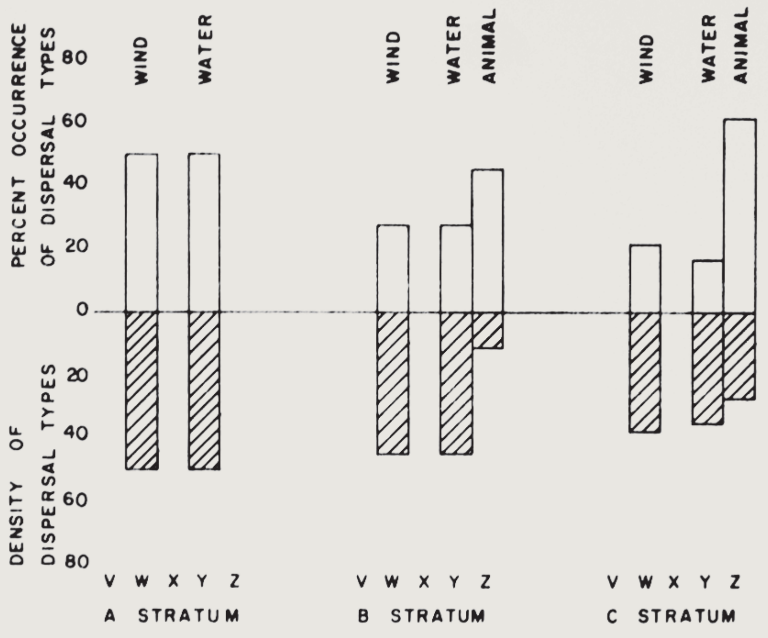


FIG. 8.6 COMPARATIVE IMPORTANCE OF DISPERSAL TYPES IN THREE WOODY STRATA OF MOPANE SAVANNA WOODLAND ON THE RIFT VALLEY FLOOR

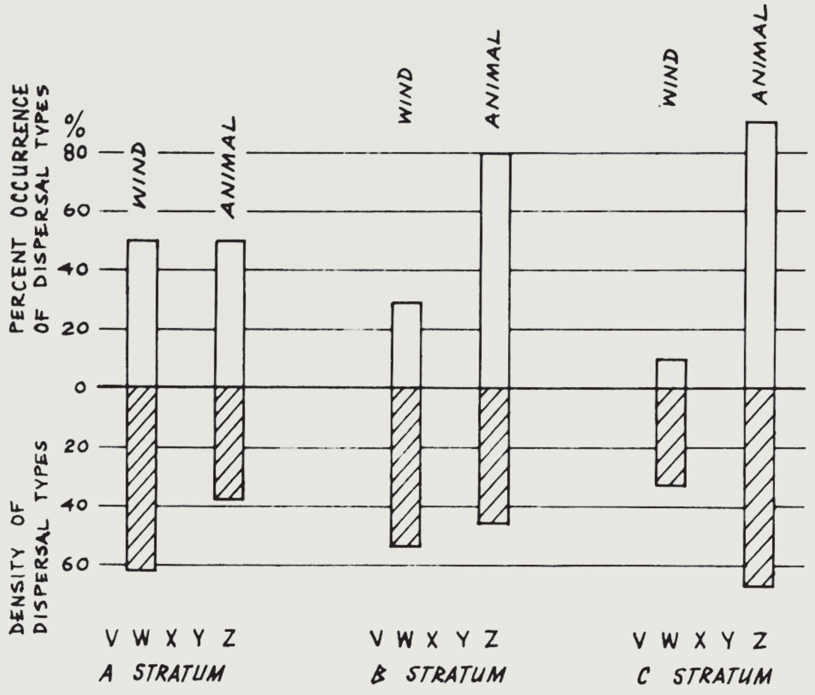


FIG 8.7 COMPARATIVE IMPORTANCE OF DISPERSAL TYPES IN THREE WOODY STRATA OF ACACIA - BURKEA SAVANNA MOSAIC.

is shown in a profile diagram where the community alternates with dry forest and vlei grassland on alluvio-catena sequences (Fig. 8.18).

An example of the composition and dominance relationships in the several layers of mopane savanna woodland is given from the smaller patch west of the Urema Lake (Table 8. 12). The exceptionally high density of mopane per unit area compared to fever tree woodlands, which have a similar canopy spacing, is indicative of the very different crown diameters and inter-tree distances in the two species.

The large spinescent shrub *Dichrostachys cinerea*, occurs in mopane communities wherever sand overlies the clays as depicted in the sample and associated soil profile. The field layer in the larger mopane area, which has a dense canopy cover, is sparse and poorly developed with few species and large patches of bare ground where standing water occurs in the rains. The mature mopane trees in the same area are clumped in related patterns to the micro-ridges of gilgai vertisols.

Dispersal

Mopane is chiefly dispersed by wind and water. Proof of the latter is shown by seedlings germinating along swashlines left after a downpour of rain. The single species dominance in the canopy gives equal importance to these dispersal methods. In the median (B) tree layer and shrub (C) stratum the same importance is maintained due to the predominance of *Dalbergia, Aloe* and pole stands of mopane. However, the diversity of zoochorous species increases progressively in the lower woody layers (Fig. 8.6).The whole system is thus over-whelmingly either wind and/or water dispersed. It is possible that anemochory is more important where there is a continuous groundcover, and hydrochory where sheet wash is operative under sparsely covered or bare ground conditions. The importance of zoochory in the lowest layer is compounded by the development of tree-base thicket initials around many trees.

Phenology

The phenophases recorded in mopane savannas will be dealt with in conjunction with other Rift Valley communities. The behaviour of the mopane tree, however, deserves special mention as it is semi-evergreen rather than deciduous in habit.

Leaf-fall occurs synchronously in the month of October, the height of the dry season, and the subordinate layers receive maximal direct insolation at this time for one month. At this period many of the sapling mopane come into new leaf and also have a leaf flush response to fire. Flowering occurs typically in January and February (in 1969 it occurred in May as well) but is more conspicuous in some years than others. Fruit dispersal occurs from June onwards.

Environmental factors and succession will be dealt with at the end of the section on the Rift Valley.

Acacia nigrescens – Burkea africana mosaic

Alternating on sandy clays and sands are two tall tree–tall grass savannas dominated by knob thorn on clays and *Burkea* on sands (Table 8.13). The most abundant species in median and shrub layers is *Combretum fragrans*. This species is an indicator of old cultivation areas where it occurs in pure stands.

Although *Urochloa mosambicensis* is predominant in the example analysed, it forms a mosaic with tall *Hyparrhenia rufa* (on clays) and *H. dissoluta* (with *Burkea* on sand) which occur as dominants over large areas.

Some of the sectors where *Combretum fragrans* and *Urochloa mosambicensis* predominate were cultivated in the past (20 to 30 years ago), but other areas were unmodified according to local tribesmen. There is a general association between *Urochloa* grassland and the **Chd** and **Cd** soils which are characterised by favourable texture (SdLm and SdCILm) and the highest phosphorus values in the Rift Valley (Appendix 1).

A notable feature of the example analysed is the complete absence of young stages of the two canopy dominants, *Acacia nigrescens* and *Burkea africana*. Elephant are responsible for ring-barking the adults of these two species, resulting in the death of many 20 m high specimens, but their selective influence on the young stages is unrecorded as saplings were not represented in the area.

TABLE 8.11
Analysis of marginal floodplain woodland in 1 hectare. Mixed fever tree, winter thorn and palm community on an alluvio-catena.

A. CANOPY AND MIDSTRATUM > 3 m-20 m	NO. TREES IN 1 ha	TOTAL BASAL AREA cm^2
Acacia xanthophloea	20	643,221
Acacia albida	13	476,804
Hyphaene benguellensis	4	
3 spp.	61	1,120.025
B. SHRUB LAYER 0.5 m–3 m	TOTAL IN 500 m^2	REL. FREQ. %
Hyphaene benguellensis	14	78
Acacia xanthophloea	3	17
Capparis erythrocarpos	1	
3 spp.	18	
C. GRASS STRATUM	NO.	FREQ. % IN 30 QUAD.
Sida alba	24	80
Digitaria swazilandensis	22	73
Gomphrena celosioides	17	57
Tephrosia pumila	16	53
Eriochloa fatmensis	13	43
Solanum panduriforme	13	43
Panicum maximum	12	40
Tephrosia astragalina	9	30
Panicum infestum	8	27
Weed indet.	7	23
Amaranthus graecizans	6	20
Phyllanthus niruri	5	17
Abutilon angulatum	4	13
Vernonia cinerea	4	4
32 spp. (less than 4 occurrences omitted)		

TABLE 8.12

Analysis of mopane savanna woodland in 1 hectare on sodic calcareous clays (Road 5 area).

A. + B. CANOPY AND MIDSTRATUM >3 m–17 m	NO. TREES IN 1 ha.	TOTAL BASAL AREA cm^2
Colophospermum mopane (WY)	410	3214,240
Dalbergia melanoxylon (WY)	82	409,580
Aloe marlothii (WY)	18	33,342
Ziziphus mucronata (Z)	18	16,748
Trichilia capitata (Z)	1	154
Sterculia africana (Z)	1	16,520
Commiphora pyracanthoides (Z)	1	314
Maerua angolensis (Z)	1	113
Acacia welwitschii (WY)	1	616
9 spp	533	3691,627

C. SHRUB STRATUM 0.5 m-3 m	TOTAL IN 500 m^2	REL. FREQ. %
Aloe marlothii (WY)	42	37
Dichrostachys cinerea (Z)	24	21
Colophospermum mopane (WY)	18	16
Ehretia amoena (Z)	5	4
Capparis erythrocarpos (Z)	4	4
Zygoon graveolens (Z)	4	4
Combretum mossambicense (W)	4	4
Thilachium africanum (Z)	3	3
Ziziphus mucronata (Z)	2	2
Manilkara mochisia (Z)	2	2
Dalbergia melanoxylon (WY)	2	2
Vepris zambesiaca (Z)	1	1
Kigelia africana (Z)	1	1
Canthium setiflorum (Z)	1	1
Maerua kirkii (Z)	1	1
15 spp.	114	

D. GRASS STRATUM (30 X 1 m^2)	NO. QUAD	REL. FREQ %
Urochloa mosambicensis	13	8
Tephrosia pumila	11	7
Barleria spinulosa	10	6
Coelorhachis/Rytachne (KLT 2586)	9	6
Setaria sp. nr. *holstii*	9	6
Mariscus hemisphaericus	8	5
Panicum coloratum	8	5
Jasminum sp.	7	5
Ruellia patula	7	5
Enteropogon macrostachyus	6	4
Panicum sp. (KLT 2572)	6	4
Sporobolus ioclados	6	4
Dichrostachys cinerea	5	3
Digitaria milanjiana	5	3
Heteropogon contortus	5	3
42 spp. (less than 5 occurrences omitted.)		

KEY

W = wind (anemochory)

Y = water (hydrochory)

Z = animal-dispersed (zoochory)

SOIL PROFILE

Depth cm.	Texture	pH	Salinity (R)	$CaCO_3$	Colour (Munsell)
0-20	Sd	6.4	2650	—	Black (7.5 YR 2/1)
20-30	Sd	6.4	3350	—	Brownish-black (10 YR 3/2)
30-35	ScCILm	6.2	1120	—	Brownish-black (10 YR 3/2)
35-50	SdCI	6.2	270	—	Olive-brown (2.5 YR 4/3)
50-70	SeDI	8,1	130	10%	Olive-brown (2.5 YR 4/3)

TABLE 8.13

Analysis of *Acacia nigrescens* - *Burkea africana* savanna mosaic in 1 ha. on clay-sand alluvio-catena.

A. CANOPY TREES 10 m–21 m	NO. OF TREES IN 1 ha.	TOTAL BASAL AREA cm^2
Burkea africana (W)	17	491,607
Acacia nigrescens (WZ)	14	355,873
Piliostigma thonningii (Z)	8	111,673
Combretum fragrans (W)	7	44,881
Lonchocarpus capassa (W)	7	64,268
Xeroderris stuhlmannii (W)	6	56,433
Sclerocarya caffra (Z)	5	102,963

Cont.

A. CANOPY TREES 10 m–21 m	NO. OF TREES IN 1 ha.	TOTAL BASAL AREA cm^2
Crossopterix febrifuga (Z)	3	12,474
Kigelia africana (Z)	1	1,591
Strychnos madagascariensis (Z)	1	1,257
Terminalia sericea (W)	1	1,257
11 spp.	70	1244,277
B. MID-STRATUM TREES 3 m–10 m		
Combretum fragrans (W)	45	385,000
Cleistochlamys kirkii (Z)	18	21,651
Crossopterix febrifuga (Z)	3	270
Kigelia africana (Z)	3	1,521
Cordia goetzei (Z)	2	255
Lonchocarpus capassa (W)	2	707
Antidesma venosum (Z)	1	113
Cassia abbreviata (Z)	1	79
Diospyros usambarensis (Z)	1	79
Piliostigma thonningii (Z)	1	80
Trichilia capitata (Z)	1	176
Xeroderris stuhlmannii (W)	1	177
Ziziphus mucronata (Z)	1	20
14 spp.		410,207

C. SHRUB LAYER 0.5 m–3 m	TOTAL IN 500 m^2 (5 X 20) 5
Combretum fragrans (W)	21
Securinega virosa (Z)	11
Dalbergia boehmii (W)	6
Combretum mossambicense (W)	5
Grewia lepidopetala (Z)	5
Harrisonia abyssinica (Z)	5
Tricalysia jasminiflora (Z)	4
Cleistochlamys kirkii (Z)	3
Diospyros usambarensis (Z)	3
Lonchocarpus capassa (W)	3
Phyllanthus reticulatus (Z)	3
Allophylus alnifolius (Z)	2
Annona senegalensis (Z)	2
Antidesma venosum (Z)	2
Crossopterix febrifuga (Z)	2
Deinbollia xanthocarpa (Z)	2
Ehretia amoena (Z)	2
Markhamia obtusifolia (W)	2
Piliostigma thonningii (Z)	2
Stereospermum kunthianum (W)	2
Ziziphus mucronata (Z)	2
Commiphora schimperi (Z)	1
Kigelia africana (Z)	1
Lecaniodiscus fraxinifolius (Z)	1
Maytenus senegalensis (Z)	1
Rubiaceae indet. (Z)	1
Strychnos madagascariensis (Z)	1
Vangueria infausta (Z)	1
28 spp.	96

D. GRASS STRATUM	OCC. IN 30 QUAD.	REL. FREQ. %
Urochloa mosambicensis	27	22
Panicum maximum	23	19
Heteropogon contortus	16	13
Setaria sp.	7	6
Acalypha senensis	6	5
Digitaria milanjiana	5	4
Hyparrhenia rufa	5	4
Combretum fragrans	4	3
Urtica urens	3	2
Asystasia gangetica	2	2
Hyperthelia dissoluta	2	2
Pogonarthria squarrosa	2	2
31 spp. (7 grasses, 11 forbs, 11 woody. Less than 2 occurrences omitted)		

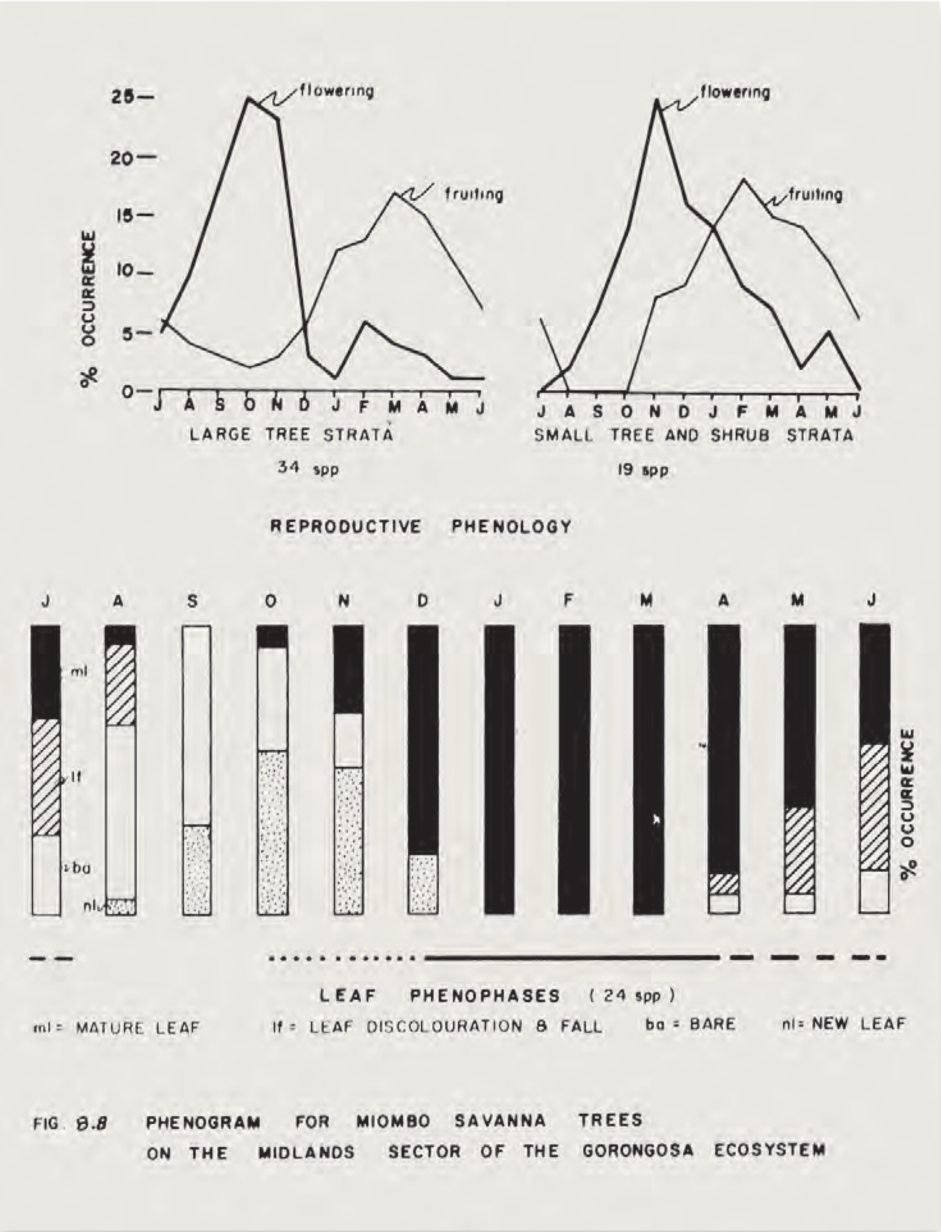
KEY
W = wind (anemochory)
Z = animal-dispersed (zoochory)

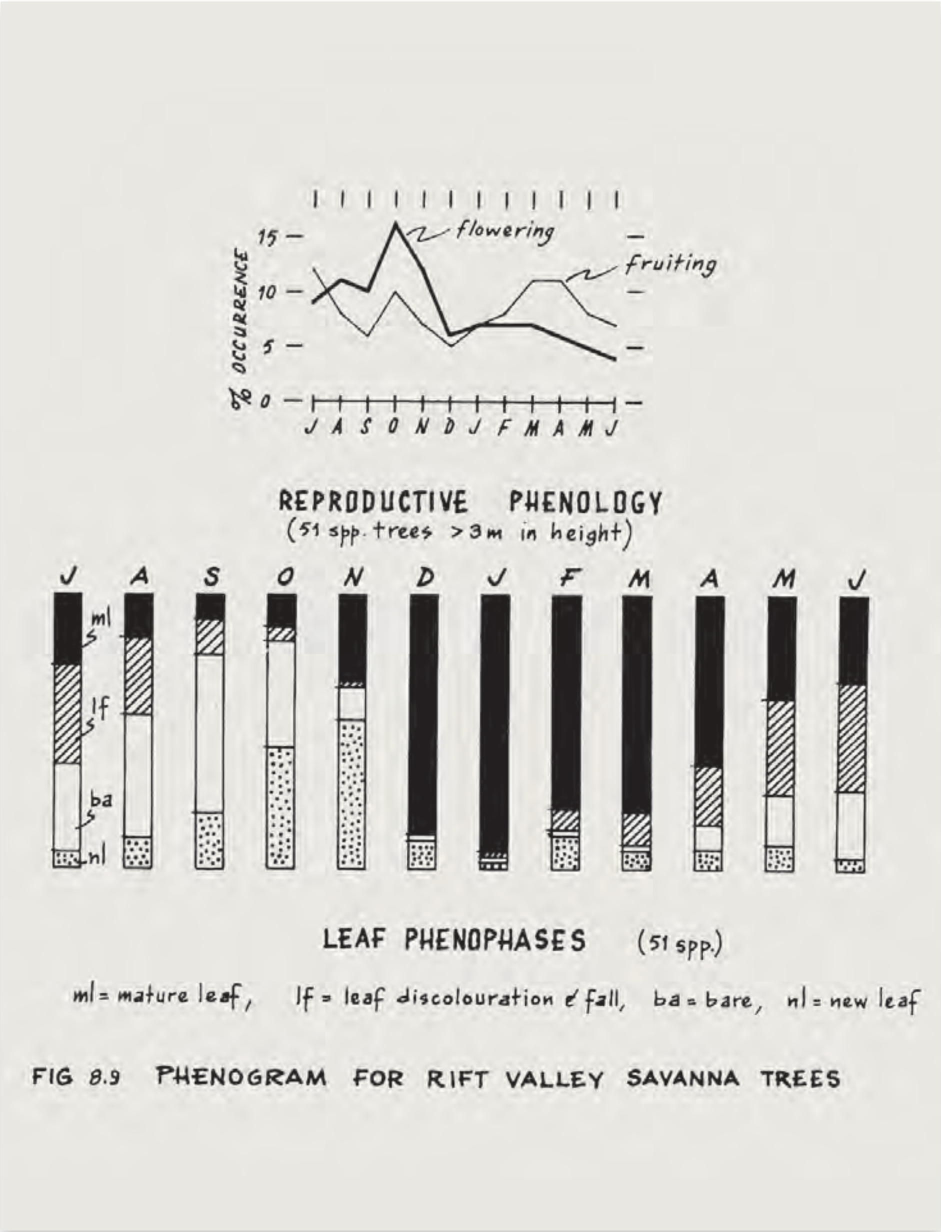
RIGHT: Figure 8.8

Phenogram for miombo savanna trees in the Midlands of the Gorongosa ecosystem.

FAR RIGHT: Figure 8.9

Phenogram for Rift Valley savanna trees.





Dispersal

The parallel predominance of anemochorous and zoochorous species in all strata is due mostly to the abundance of *Combretum fragrans* which reproduces at all three levels (Fig. 8.7). Otherwise wind dispersal is the main characteristic of the canopy components, with zoochory increasingly important down to the shrub layer. The increase in density and number of animal dispersed species in the lowest woody layer is due mainly to the frequency of tree-base thicket elements in this savanna type. The sectors with tall, dense *Hyparrhenia* grassland are poor in shrub layer constituents, and the reverse occurs adjacent to trees (perch sites) and in shorter, or sparsely, grassed areas.

Scrub thicket

The only mature scrub thicket habitat on the Rift floor is that formed by pure stands of *Antidesma venosum* along the Mucombezi riverbanks, and on some of the old Pungue channels in the Dingedinge area. Otherwise, the dense woody cover less than 4 m in height, which occurs around tree bases and on new termite hills marginal to the floodplains, is young stages of the thicket described next.

Thicket

Four main kinds of thicket occur on the Rift floor, all of which contain canopy trees attaining just over 20 m in height. One species, *Sterculia appendiculata*, a forest tree from East Africa, occurs as an emergent to nearly 30 m in riverine and termitaria thickets. The thicket types include: (1) riverine, (2) alluvial fan, (3) tree-base, (4) termitaria.

All of these thickets have a similar floristic make-up which varies kaleidoscopically from site to site. The majority are animal dispersed species with drupaceous or baccate fruits (Fig. 8.10). The major difference between the first and second pair of thickets is the abundance of savanna and floodplain margin trees in canopy constituents of the former. The latter pair are dominated by true thicket-forming species and contain relatively few savanna or forest components.

Those termitaria in dry forest on duplex sands and adjacent to forest naturally have a much higher content of forest species of the Urema Trough. These are interspersed with true forest on the duplex sands of splays or aggraded distributaries and linked by disconnected patches of riverine thicket along functional watercourses.

A typical example of the mixed character of alluvial fan thicket is shown by the following partial list from near the Muaredzi–Urema confluence:

Acacia robusta (W? Z?)
Acacia welwitschii (W)
Adansonia digitata (Z)
Afzelia quanzensis (Z)
Albizia brevifolia (W)
Berchemia discolour (Z)
Boscia salicifolia (Z)
Cassia abbreviata (Z)
Cleistanthus schlechteri (Z)
Cleistochlamys kirkii (Z)
Commiphora schimperi (Z)
Cordyla africana (Z)
Diospyros senensis (Z)
D. usambarensis (Z)

KEY
W = wind (anemochory)
Z = animal-dispersed (zoochory)
? = a question mark after any of the symbols means that the case is uncertain.

Riverine thicket contains a similar assortment but with a greater preponderance of species such as *Ficus sycamorus, Diospyros mespiliformi, Mimusops fruticosa*, *Trichilia emetica, Ekebergia capensis,* and *Khaya nyasica*. In a few parts these and other species form a closed, stratified forest community noted in the following section.

Tree-base thicket

This thicket type is abundant, and a vigorous invader of most of the Rift Valley wooded savannas. The full sequence from animal dispersed seeds in dung around the bases of trees, seedlings, scrub stage to mature coalesced patches are particularly common in the area between the Urema Plains and the Pungue River.

Like termitaria thicket, the tree-base type is composed chiefly of animal dispersed seeds which are centrifugally dispersed to perch sites in a habitat. Melton (in press) shows that baboons preferentially defaecate on termite hills in his Uganda study area.

Related to both these perch-based thickets are those which develop on civet dung middens in open ground. The three thicket types are similar in composition as similar fruits are taken by primates, civet, and birds such as the green pigeon (cf. fruits eaten by baboon and civet). Further details on this subject are concluded in Chapter 9. The composition of tree-base thickets is indicated in the following tables: 8.14, 8.15, 8.16, 8.17.

The change in composition and predominance of tree-base thicket constituents in different systems is well exemplified by the following examples from marginal floodplain woodland, knob thorn and mopane communities.

The presence of wind-dispersed species such as *Combretum mossambicense, Dalbergia melanoxylon* and *Lonchocarpus cappasa* in tree-base thickets indicates either that their seeds are also zoochorous or they are caught up against obstacles such as tree trunks or thickets when blown.

TABLE 8.14
Occurrence of animal dispersed thicket initials recorded from the base of 112 savanna canopy trees.

ANIMAL DISPERSED THICKET PLANTS	PRESENCE	REL. FREQ.
Capparis erythrocarpos	46	10
Ziziphus mucronata	37	8
Deinbollia xanthocarpa	33	7
Jasminum sp.	30	7
Trichilia capitata	29	6
Tamarindus indica	24	5
Cleistochlamys kirkii	22	5
Tricalysia jasminiflora	19	4
Lecaniodiscus fraxinifolius	17	4
Ximenia americana	16	3
Thilachium africanum	14	3
Combretum mossambicense	12	3
Dalbergia melanoxylon	12	3
Grewia microcarpa	11	2
Landolphia kirkii	11	2
Phyllanthus reticulatus	10	2
Allophylus alnifolius	9	2
Commiphora schimperi	9	2
Ehretia amoena	9	2
Securinega virosa	9	2
Diospyros mespiliformis	7	2
Maclura africana	7	2
Diospyros usambarensis	6	1
Harrisonia abyssinica	6	1
Boscia salicifolia	5	1
Diospyros senensis	5	1
Drypetes mossambicensis	5	1
Grewia sulcata	5	1
Lonchocarpus capassa	5	1
66 spp. (less than 1% frequency omitted)		

TABLE 8.15
Variation in the predominant constituents of tree-base thicket initials in different savannas.

FEVER TREE SAVANNA WOODLAND	OCCURRENCE FROM 34 TREES
Capparis erythrocarpos	30
Ziziphus mucronata	25
Deinbollia xanthocarpa	21
Tamarindus indica	20
Ximenia americana	16
MOPANE SAVANNA WOODLAND	OCCURRENCE FROM 52 TREES
Jasminum sp.	29
Asparagus africanus	22
Dalbergia melanoxylon	11
Grewia macrocarpa	10
Trichilia capitata	10
KNOB THORN TREE SAVANNA	OCCURRENCE FROM 18 TREES
Lecaniodiscus fraxinifolius	12
Cleistochlamys kirkii	9
Phyllanthus reticulatus	9
Capparis erythrocarpos	8
Securinega virosa	8

TABLE 8.16
Examples of tree-base thicket frequency in one hectare samples from various Rift Valley savanna woodlands.

SAVANNA	NO. TREE-BASE THICKETS	NO. CANOPY TREES	%
Acacia xanthophloea	34	43	79
Mixed *Acacia albida – Hyphaene benguellensis – Acacia xanthophloea*	28	61	46
Mixed *Acacia nigrescens – Burkea africana*	28	69	41
Colophospermum mopane	55	417	13

TABLE 8.17

Termitaria thicket woody constituents. Presence of species on 42 termitaria from various habitats on the Rift floor.

TERMITARIA THICKET	OCCUR.
Salvadora persica (Z)	24
Capparis erythrocarpos (Z)	23
Thilachium africanum (Z)	23
Trichilia capitata (Z)	23
Cleistochlamys kirkii (Z)	22
Ziziphus mucronata (Z)	16
Allophylus alnifolius (Z)	15
Dalbergia arbutifolia (W, Z)	15
Tamarindus indica (Z)	15
Ehretia amoena (Z)	14
Tricalysia jasminiflora (Z)	14
Afzelia quanzensis (Z)	13
Deinbollia xanthocarpa (Z)	13
Lecaniodiscus fraxinifolius (Z)	13
Combretum mossambicense (W)	13
Mimusops fruticosa (Z)	12
Cassine schlechterana (Z)	11
Combretum microphyllum (W)	11
Xanthocercis zambesiaca (Z)	11
Ximenia americana (Z)	11
Boscia salicifolia (Z)	10
Phoenix reclinata (Z)	10
Drypetes mossambicensis (Z)	10
Harrisonia abyssinica (Z)	9
Hyphaene benguellensis (Z)	9
Lannea stuhlmannlii (Z)	9
Maclura africana (Z)	9
Cadaba termitaria (Z)	3
Saba floribunda (Z)	9
Securinega virosa (Z)	9
Sterculia appendiculata (Z)	9
Xylotheca tettensis (Z)	9
Commiphora schimperi (Z)	8
Cordyla africana (Z)	8
Diospyros mespiliformis (Z)	8
D. senensis (Z)	8
D. usambarensis (Z)	8
Berchemia discolour (Z)	7
Maerua angolensis (Z)	7
Pavetta catophylla (Z)	7
Strychnos potatarum (Z)	7
Alima tetracantha (Z)	6
Capparis tomentosa (Z)	6
Cassia abbreviata (Z)	6
Diospyros quiloensis (Z)	6
Maytenus senegalensis (Z)	6
Phyllanthus reticulatus (Z)	6
Spirostachys africana (X, Z)	6
Cordia pilosissima (Z)	5
Euclea schimperi (Z)	5
Euphorbia ingens (X, Z)	5
Kigelia africana (Z)	5
Lonchocarpus capassa (W)	5
Manilkara mochisia (Z)	5
Sterculia africana (Z)	5
55 spp. (182 total woody spp. recorded)	

KEY

W = wind (anemochory)

Z = animal-dispersed (zoochory)

X = by explosive dehiscence and seeds thrown (active autochory or active ballists).

TABLE 8.18

Analysis of strata in a termitaria thicket (Road 3 area). Total area 314 m^2 (3%/ha)

A. CANOPY AND EMERGENTS >10 m–20 m	NO. IN 314 m^2	RD %
Mimusops fruticosa	5	36
Lannea stuhlmannii	4	29
Sterculia appendiculata	3	21
Lonchocarpus capassa	1	7
Dalbergia arbutifolia	1	7
5 spp.	14	

Cont.

B. MEDIUM TREE LAYER >3 m–10 m		
Cleistochlamys kirkii	8	25
Trichilia capitata	8	25
Diospyros senensis	7	22
Cordia goetzei	3	9
Strychnos potatarum	2	6
Berchemia discolour	1	3
Cassia abbreviata	1	3
Drypetes mossambicensis	1	3
Tabernaemontana elegans	1	3
9spp.	32	

C. FIELDLAYER 50 cm–300 cm	NO. IN 100 m^2	RD %
Capparis erythrocarpos	33	18
Diospyros mespiliformis	20	11
Deinbollia xanthocarpa	19	10
Tricalysia jasminiflora	16	9
Allophylus alnifolius	10	5
Cleistochlamys kirkii	10	5
Cassine schlechterana	8	4
Pavetta catophylla	7	4
Securinega virosa	7	4
Lecaniodiscus fraxinifolius	7	4
Trichilia capitata	7	4
Diospyros sinensis	6	3
Dalbergia arbutifolia	6	3
Phyllanthus reticulatus	5	3
Cordia goetzei	4	2
Lonchocarpus capassa	3	2
Berchemia discolour	2	1
Xylotheca tetenis	1	1
Sterculia appendiculata	1	1
Tamarindus indica	1	1
Premna senensis	1	1
Grewia sulcata	1	1
Thilachium africanum	1	1

Cont.

C. FIELDLAYER 50 cm–300 cm	NO. IN 100 m^2	RD %
Trichilia emetica	1	1
Ehretia amoena	1	1
Boscia salicifolia	1	1
Strychnos sp. ‘warty fruit’	1	1
Dalbergia boehmii	1	1
28 spp.	182	

D. GROUND LAYER (20 X 1 m^2 = 20 m^2) 10 cm–50 cm	NO. QUADS	REL. FREQ. %
Asystasia gangetica	18	14
Achyranthes aspera	14	11
Cleistochlamys kirkii	7	5
Saba floribunda	9	7
Jasminum sp.	8	6
Cleistochlamys kirkii	7	5
Pavetta catophylla	7	5
Anisocycla blepharosepula	6	5
Capparis erythrocarpos	6	5
Diospyros mespiliformis	6	5
Dalbergia arbutifolia	5	4
Lecaniodiscus fraxinifolius	5	4
Commelina sp.	5	4
Pupalia lappacea	4	3
Flaggelaria guineensis	4	3

D. GROUND LAYER (20 X 1 m^2 = 20 m^2) 10 cm–50 cm	NO. QUADS	REL. FREQ. %
Glycine wightii	4	3
Deinbollia xanthocarpa	4	3
Combretum microphyllum	4	3
Panicum heterostachyum	3	2
Abutilon sp.	3	2
Securinega virosa	3	2
Diospyros senensis	3	2
Cordia goetzei	2	1

Cont.

D. GROUND LAYER (20 X 1 m^2 = 20 m^2) 10 cm–50 cm	NO. QUADS	REL. FREQ. %
Phyllanthus reticulatus	2	1
Tricalysia jasminiflora	2	1
Bussea wolfhorstii	1	1
Capparis sepiaria	1	1
Sterculia appendiculata	1	1
Diospyros usambarensis	1	1
Tamarindus indica	1	1
Cassine schlechterana	1	1
Ceropegia sp.	1	1
Ipomoea albivenia	1	1
Oplismenus burmannii	1	1
Basilicum polystachyon	1	1
Aerva leucura	1	1
35 spp.	131	

Termitaria thicket

A major component of the Rift Valley savannas and the 'dambo miombo' of the Cheringoma Plateau are the large island-clumps of thicket on termite hills. In some areas termitaria thickets occur at a density of three per hectare. Termitaria thickets are physiognomically important in savanna and 'tando' areas, and in the dry season their tardier leaf fall makes them particularly conspicuous.

All stages of woody plant community development on termite hills are evident in Rift Valley examples—from bare hills with seeds deposited on them, to trees 25 m in height, and clumps of 20 m in diameter. Most of the woody species are animal dispersed.

The occurrence of woody constituents on 42 termitaria in the Rift Valley is noted in Table 8.17. No species show a high frequency predominance due to the kaleidoscopically changing composition from one termite hill to another, and the influences of the communities with which they are juxtaposed.

Dispersal

The outstanding feature of all thicket types in the Rift Valley, as elsewhere in the transect, is the predominance of animal dispersed plant species (Fig. 8.10). Thickets are initiated from seeds dispersed by animals, which are perch orientated (e.g. primates and birds), or those which preferentially use dung middens (e.g. civet), and bare areas (see Section 9.8, 9.9).

Due to their base saturated soils, termite hills show highest frequency of certain species, *Capparaceae* in particular (Wild 1952). The same species are predominant as tree-base (or other perch site) thicket components, on base-rich substrates. Thus the underlying climo-edaphic control of their distribution is overlain by their preferential use and dispersal by animals.

A single example of the analysis of all strata in one termitaria thicket is given in Table 8.18. Environmental factors, phenology and successional aspects are dealt with at the end of the Rift Valley section.

Forest

On the Rift floor only two kinds of forest occur: riverine forest, and dry forest on duplex sands. The former is rare and confined to isolated occurrences, mostly on cut-off meanders. Dry forest also occurs in disjunct patches related to the fan pattern of aggraded fossil distributaries.

Riverine forest

The largest patch occurs on the north bank of the Nhandue River one kilometre downstream from Cangantole camp. Here a high canopy and emergent stratum of trees between 22 m and 30 m in height occurs with a sparse median tree layer and a dense patchwork of under-canopy thickets formed by shrubs and scandent *Acacia*. Tall island patches of riverine forest occur on old courses of the Pungue River east of Chitengo camp. The most important large riverine trees include:

LARGE RIVERINE TREES

Albizia glaberrima (W)
Blighia unijugata (Z)
Bombax rhodognaphalon (W)
Cordyla africana (Z)
Diospyros mespiliformis (Z)
Ekebergia capensis (Z)
Ficus sycamorus (Z)
Khaya nyasica (W)
Sterculia appendiculata (Z)
Syzygium guineense (Z)
Trichelia emetica (Z)

KEY
W = wind (anemochory)
Z = animal-dispersed (zoochory)

Riverine forest is evergreen to deciduous, depending on the species dominance in each area. *Sterculia appendiculata* forms nearly pure species stands in some areas and is deciduous early in the dry season. *Diospyros* and *Trichilia* are mostly evergreen and these stand out as dark clumps where they predominate.

Animal dispersed species predominate in all strata, but due to the numerical abundance of *Khaya*, wind dispersal is a feature of the canopy. This is similar to the swamp forests of the Cheringoma Coast which are dominated in some areas by the anemochorous (and hydrochorous?) *Adina microcephala*.

Dry forest

Dry forest is a unique forest formation of the coast sands and Kalahari Sands of south central Africa. Extending from the west coast (Angola and lower Congo) across the centre of the subcontinent (S. Congo, Zambia, Rhodesia) to the Mozambique Plain, and the Tanzania and Kenya coasts. Typically, dry forest occurs in a rainfall range between 500

RIGHT: Figure 8.10

Comparative importance of dispersal types among woody constituents of clump thickets.

FAR RIGHT: Figure 8.11

Comparative importance of dispersal types in three woody strata of dry forest.

LOWER STOREY COMPONENTS

Cordia goetzii (Z)
Diospyros senensis (Z)
Erythroxylum emarginatum (Z)
Garcinia livingstonei (Z)
Lecaniodiscus fraxinifolius (Z)
Oncoba spinosa (Z)
Tabernaemontana elegans (Z)

KEY
Z = animal-dispersed (zoochory)

FIELD LAYER COMPONENTS

Acacia schweinnfurthii (Z?)
Capparis erythrocarpus (Z)
Cleistochlamys kirkii (Z)
Dalbergia boehmii (W?)
Tricalysia jasminiflora (Z)

KEY
W = wind (anemochory)
Z = animal-dispersed (zoochory)

? = a question mark after any of the symbols means that the case is uncertain.

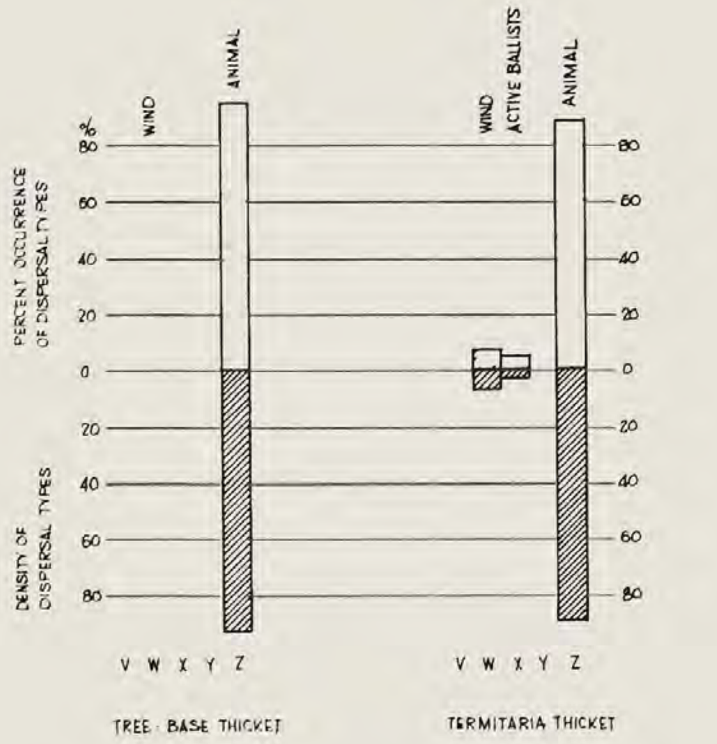


FIG 8.10 COMPARATIVE IMPORTANCE OF DISPERSAL TYPES AMONG WOODY CONSTITUENTS OF CLUMP THICKETS ON THE RIFT FLOOR (UREMA TROUGH)

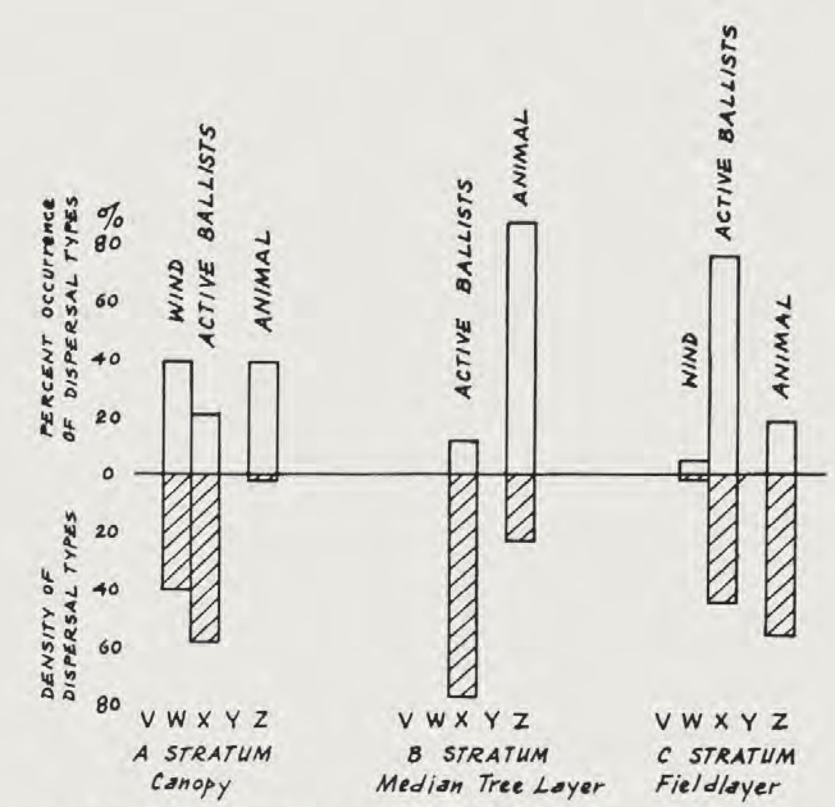


FIG 8.11 COMPARATIVE IMPORTANCE OF DISPERSAL TYPES IN THREE WOODY STRATA OF DRY FOREST.

mm p.a. and 1,000 mm p.a. either on duplex sands or on fine-grained compact sands. The species dominance between the two coasts varies kaleidoscopically with endemic centres in the west (defined by *Tessmannia camoneana* for example), in the centre (defined by *Cryptosepalum* and *Baikiaea*) and on the east coast (defined by *Newtonia hildebrandtii, Cynometra* spp., *Guiboutia schliebenii, Xylia torreana,* et al.).

This forest type has up to the present been erroneously included as part of the Eastern Forest Domain of the Guineo–Congolian phytogeographic region (White 1965, 1971). White (op.cit.) refers to this as the Usambara–Zululand domain. In fact both these terms correctly refer only to the Guineo-Congolian elements and forests confined to the orographic or coastal moist areas of the east coast. The dry forest components are not equatorial rainforest species, though related to them, and should rather be designated as a Southern Tropical Sand Forest domain. Within its range on the Mozambique plain alone, several centres of endemism can be defined by woody components in one or other stratum.

At the end of the dry forest ecocline, and where this formation meets thickets on base saturated duplex sands, it overlaps with thicket species. At the moist end on leached duplex sands or fine compact sands, it overlaps with rainforest tree species.

In the southern Rift Valley sector dry forest occurs only to the Chire Trough (Hall-Martin 1972). On the east coast it occurs sporadically through to the Kenya–Somalia

TOP LEFT:

View across the clay-sand alluvio-catena sequence. From mopane and aloe savanna on a convex clay surface in the foreground, across a seasonally waterlogged lower dambo surface to the forested duplex sands of the convex surface of an aggraded distributary bed.

BOTTOM:

Oblique air view of dry forest confined to aggraded distributary bed of a fossil alluvial fan. The relatively sharp margins and narrow ecotone is due to rapid lateral change of duplex forest sands to grassland vertisol clays (slack fines).

Rift Valley Dry Forest and Tree-Base Thicket Communities *(cont.)*

TOP:

Tree-base thicket of zoochorous species around a baobab tree, and a dry forest strip in the background. Dimensions of the thicket indicated by the lay figures and 3 m measuring rod (mid-dry season aspect).

frontier. A characteristic dry forest species, such as *Hymenocardia ulmoides* occurs intermittently across the whole range of the Sand Forest Domain.

Dry forest is structured similarly to other forest types, but in some sites the upper canopy trees are sufficiently widely spaced so that the mid-stratum is the effective canopy. The upper canopy trees in such situations are thus emergents. Dry forest is deciduous to semi-deciduous depending on the species predominant in the canopy of each patch, and the severity of dry season drought conditions.

In the Urema Trough, dry forests occur in abrupt changes from the surrounding grassland and savanna, due to the generally sharp change between the duplex sand substrate on old distributary courses of fossil alluvial fans, and the other soil types of alluvial-catenas. The composition of one dry forest example from the Urema Trough is shown in Table 8.19.

In common with other disjunct communities, each dry forest patch appears to have different species combinations and canopy dominants. This feature is related to the

RIGHT:

Tree-base thickets of zoochorous species around palms and fever trees in *Urochloa mosambicensis* grassland on phosphorous-rich sandy loams.

clumped dispersion shown by many species within the more extensive dry forest areas. A canopy dominant in one patch can be quite absent from others and so on. Some of the canopy and high mid-stratum trees not recorded in the hectare sample of the Sangarassa Forest include:

CANOPY AND HIGH MID-STRATUM TREES NOT RECORDED

Albizia brevifolia (W)
Aloe bainesii (W)
Balanites maughamii (Z)
Cladostemon kirkii (Z)
Euphorbia hallipedicola (X, Z)
E. lividiflora (X, Z)
Erythrina livingstoniana (Z)
Exoecaria bussei (W)
Fernandoa magnifica (W)
Ficus sansibarica (Z)
Guibourtia conjugata (Z)
Gyrocarpus americanus (W)
Hymenocardia ulmoides (W)
Inhambanella henriquesii (Z)
Paropsia schliebeniana (Z)
Ptelepsis myrtifolia (W)
Strychnos decussata (Z)

KEY
W = wind (anemochory)
X = by explosive dehiscence and seeds thrown (active autochory or active ballists).
Z = animal-dispersed (zoochory)

Dispersal

Though an equal number of wind and animal dispersed canopy species occur in dry forest, when density data (from 1 ha sample) are added, those with physically thrown (active ballists) and wind dispersed seeds predominate by far (Fig. 8.11). The high density of *Xylia torreana* and *Millettia mossambicensis* are responsible for active ballist dominance in this sample.

In the median tree layer, the dominance by two active ballist species, *Craibia* and *Millettia*, over large areas is responsible for the low percentage of this dispersal type but with the highest density. This contrasts with the much lower variety of zoochorous species which occur in a relatively small number.

In the field layer the reverse situation occurs where a large diversity of active ballists (mainly large woody Acanthaceae) are surpassed in density by relatively few zoochorous species (Fig. 8.11).

When compared with other communities the importance of dispersal types in the canopy shows the same pattern as miombo. It shows a slight, though greater than its relationships with most other forest or thickets, resemblance to the *Acacia–Burkea* and mopane savannas. However, a closer relationship exists with the tropical rain forest zone on Gorongosa Mountain where anemochory is a feature of the canopy dominant *Newtonia buchananii.* Wind dispersal is also a feature of hygrophilous forest canopy trees such as *Khaya nyasica* and *Adina microcephala.*

The predominance of active ballists in all three woody strata of dry forest appears to be a unique feature in the transect. Where dry forest contains the euphorbiaceous *Androstachys johnsonii* as a single canopy dominant, explosive dehiscence remains the most important means of dispersal. However, subsequent zoochory, mainly by ground feeding doves, may be equally important, giving equal weight to the two methods.

Some of the lianes which reach the canopy in dry forest are also wind dispersed species, including *Combretum schumannii*, *Hippocratea africana*, *H. crenata* and *Strophanthus kombe.*

Environmental features

The most important features in the Rift Valley are the seasonal wet and dry extremes, the wet exaggerated by flooding or waterlogging to greater or lesser extent annually, and the dry exaggerated by widespread occurrence of veld fires.

As shown by Fig. 4.11 the highest rains and most extensive floods recorded in the decade of readings from Chitengo Camp occurred in December 1969 (530 mm total), followed by three consecutive dry years with up to 163 mm less than mean annual rainfall. The year prior to the 1969/70 floods was the driest year recorded. Precipitation thus shows wide variation (> 60%) every year above and below the mean.

These extremes are aggravated by late summer droughts in January, February or March in six out of the 10 years. These droughts are caused by the passage of hurricanes (tropical cyclones) in the Mozambique Channel (see Ch. 4). In 1972 two consecutive months were arid (February and March) resulting in widespread leaf discolouration and fall in certain deciduous trees, e.g. *Sterculia spp., Lannea stuhlmannii, Commiphora schimperi*. With the recurrence of adequate rain a new leaf flush and flowering was initiated. At this time the short grasslands on base saturated clays also become brown and dry out rapidly. Clear nights during these arid spells result in valley fog development in summer. As shown by Fig. 4.13, the Urema Trough experiences a two month mild period in mid-winter, followed by rapid heating up from the last week of July, becoming increasingly hot over the torrid dry season peak, prior to the rains.

TABLE 8.19
Analysis of Dry Forest 2 km northwest of Chitengo Camp on the Rift floor (Sangarassa Forest).

A. CANOPY AND EMERGENTS >12 m–22 m	TOTAL TREES IN 1 ha	REL. FREQ. %
Xylia torreana (X)	29	29
Pterocarpus antunessii (W)	28	28
Millettia mossambicensis (X)	22	22
Newtonia hildebrandtii (W)	14	14
Acacia welwitschii (W)	4	4
Millettia stuhlmannii (X)	2	2
Hymenodictyon parvilolium (W)	1	1
Lecaniodiscus fraxinilolius (Z)	1	1
Ziziphus pubescens (Z)	1	1
9 spp.	101	

B. MIDSTRATUM >3 m–12 m	TOTAL TREES IN 2,500 m^2	REL. FREQ. %
Craibia zimmermannii (X)	80	51
Millettia mossambicensis (X)	32	20
Strychnos mitis (Z)	19	12
Hunteria zeylanica (Z)	11	7
Thilachium africanum (Z)	6	4
Cola greenwayi (Z)	2	1
Coffea racemosa (Z)	1	1
Cordia pilosissima (Z)	1	1
Diospyros senesis (Z)	1	1
Strychnos (spinosa) 'warty fruit' (Z)	1	1
Tarenna neurophylla (Z)	1	1
Xylia torreana (X)	1	1
Indet.	1	1
13 spp.	157	

Cont.

C. FIELD LAYER 0.5 m–3 m	OCCUR. IN 20 (25 m X 1 m) BELTS 500 m^2	REL. FREQ. % (333 OCCUR.)
Alchornea laxiflora	73	22
Craibia zimmermannii	66	20
Thilachium africanum	44	13
Phyllanthus kirkianus	28	8
Adhatoda bagshawei	24	7
Ancylanthus sessiliflorus	23	7
Pavetta catophylla	14	4
Millettia mossambicensis	10	3
Capparis erythrocarpos	6	2
Hunteria zeylanica	6	2
Canthium crassum	5	2
Vepris reflexa	5	2
Xeromphis obovata	5	2
Strychnos mitis	3	1
Xylia torreana	3	1
Xylotheca tettensis	3	1
Combretum mossambicensis	2	1
Rubiaceae indet.	2	1
Tarenna neurophylla	2	1
Indet.	2	1
27 spp. (less than 1% omitted)		

D. GROUND LAYER <50 cm	OCCUR. IN 55 m^2 QUAD.	REL. FREQ. % (309)
Craibia zimmermannii	28	9
Acacia kraussiana	23	7
Leptochloa uniflora (g)	22	7
Justicia stachytarphetoides	21	7
Justicia sp. (KLT 2591)	20	7
Ilysanthes sp. ?	20	7
Acacia welwitschii	13	4
Oplismenus burmanii (g)	13	4
Barleria spinulosa	10	3
Dicliptera mossambicensis	10	3

Cont.

D. GROUND LAYER <50 cm	OCCUR. IN 55 m² QUAD.	REL. FREQ. % (309)
Psilotrichum scleranthum	10	3
Alchornea laxiflora	9	3
Lepturus radicans (g)	9	3
Commelina sp.	8	3
Hippocratea africana	8	3
Strychnos mitis	7	2
Abutilon lauraster	6	2
Phyllanthus kirkianus	6	2
Stylochiton sp.	5	2
Cyperus mapanioides	5	2
Justicia flava	5	2
Hibiscus migeodii	5	2
45 spp. (less than 2% omitted)		

KEY
W = wind (anemochory)
X = by explosive dehiscence and seeds thrown (active autochory or active ballists).
Z = animal-dispersed (zoochory)
? = a question mark after any of the symbols means that the case is uncertain.
(g) = shade grasses

In dry years, veld fires begin early in the autumn and occur through until October, or as long as grass fuel is available. In wet years they occur from May or June onward. Fortunately the incidence of midwinter rain showers is often sufficient to douse the fires. Their resurgence is often from honey and game hunters.

Few months in the decade of records received no rain. In the long term there are six wet months (four perhumid) and six dry months (Fig. 4.1).

The flood and ebb features of the Urema Trough are dealt with in Chapter 9. It is sufficient to emphasize that the moisture factor is the major environmental feature, particularly as extensive areas are saline clays.

Phenology

Leaf phenophases

The march of the seasons as shown by leaf phenophases in the Rift Valley (Fig. 8.9), although similar to that in the adjacent miombo, has some marked differences (Fig. 8.8). The Rift Valley savannas have more species in leaf in the torrid period and certain trees are more rapidly deciduous in the late summer. The small percent occurrence of bare trees in midsummer is due to the winter thorn *Acacia albida* which is active during the dry season. As I lived among the Rift savannas, a much more detailed record was kept of phenological events, which showed new leaf production in every month of the year.

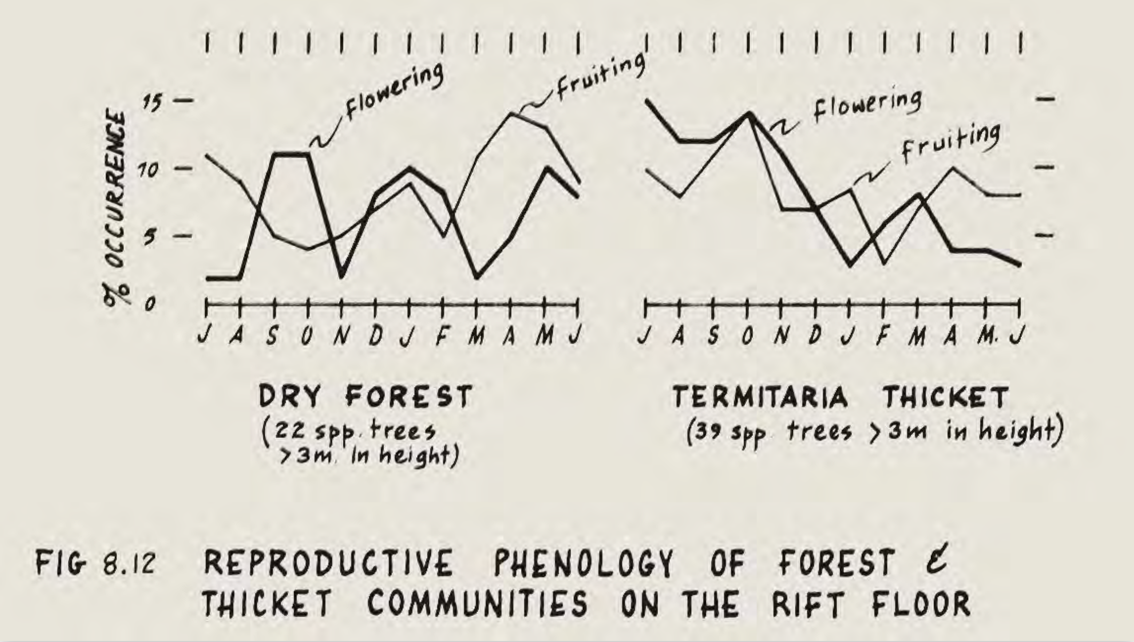


FIG 8.12 REPRODUCTIVE PHENOLOGY OF FOREST & THICKET COMMUNITIES ON THE RIFT FLOOR

LEFT: Figure 8.12

Reproductive phenology of forest and thicket communities on the Rift floor.

Reproductive phenology

Again the Rift savanna trees show a parallel with the miombo, their main flowering peak occurring in October with a second lesser peak in late summer and autumn (Fig.8.9). A much larger number of Rift savanna trees, however, flower throughout the year and three fruiting peaks are evident in July, October, and over the autumnal equinox. Both savanna types show low flower and fruiting occurrence over the summer solstice.

Bimodal peaks in nutrient levels over the equinox periods are intimated by the spring flowering peak and the fruiting peak in autumn.

Termitaria thicket tree components generally show a similar pattern to the Rift savannas but have the highest flowering peaks in July and October, coincident with, or following, the winter solstice and spring equinox. A third smaller flowering peak occurs in March (Fig. 8.12).

Contrasting with these patterns is that of dry forest on the Rift floor which exhibits boldly defined bimodal flowering peaks over the equinoxes and the summer solstice

(Fig. 8.12), parallel to the flowering of the mountain summit grassland components. The flowering peaks are followed three to four months later by three fruiting peaks in July, January and April (Fig. 8.12).

Succession

Savanna and thicket components are actively invading floodplain grasslands on all fronts, depending on the soil type exposed by inadequate flooding or waterlogging.

Base saturated clays are invaded by *Hyphaene benguellensis* and *Colophospermum mopane* but these never occur together in the Urema Trough. Where floodplain gilgai microrelief is invaded by mopane and *Acacia borleae* the seeds appear to survive best on the micro-ridges where they form a clumped pattern. Mature mopane woodlands clearly show the original microrelief patterning although the irregularities are, in many sites, flattened out by erosion.

Fever tree, *Acacia xanthophloea,* is the most vigorous invader of hydromorphic clays, and *Acacia albida* invades on sandy alluvium. In some areas an aggressive invasion of floodplain grassland by suffrutices with large basal root plates is preceding the above tree succession. *Duospermum quadrangulare* and *Cienfugosia hildebrandtii* are the most common suffrutex invaders, with *Maerua brunnescens* to a lesser extent.

Sandy clays, duplex sands and sandy loams are invaded directly by savanna and thicket species including *Acacia sieberana, Piliostigma thonningii, Dalbergia melanoxylon, Combretum fragrans, Crossopterix febrifuga, Borassus aethiopum* and others. All of these suffrutex and tree invaders of floodplains characteristically occur in pure species stands.

Once tree saplings grow above the canopy of the grass stratum, they are conspicuous perch sites in otherwise treeless grasslands, and their use by frugivores results in a saltatory succession of thicket as the second invading phase. Termite hills in grassland cause a similar direct invasion of woody thicket species to occur as they are also used as perch sites by frugivores.

Where dongas have cut into the floodplain clays, *Ziziphus mucronata* and *Antidesma venosum* (both zoochorous species) are the most common invaders along these seasonal watercourses.

Various thicket types are extending in some areas by coalescence of clumps, whilst in other areas they are in a homeostatic state, neither expanding or contracting. Active extension of thicket clumps occurs chiefly on the sandier soils, whilst a more static situation exists where the thicket clumps occur on termite hills or around tree bases in saline clay areas. In saline clay areas, tree-base thickets appear to be confined by the higher water input from stem-flow runoff of rain from the 'mother-tree' around which they were initiated. The importance of this phenomenon in dry areas has been measured by Glover et al. (1962) in East Africa.

The preferential use of termitaria and tree-base thickets results in a trampled out perimeter which protects the clumps from fire. In many termite hill sites, however, a natural firebreak is afforded by the change from tall to medium height grasslands to short, or lawn-like, grasses on the saline micropediment around the base of the termitaria.

As shown in Section 6.3 however, termite hills undergo a process of landscape reversal to form pans in areas of high browsing ungulate density.

Only on the microscale on the Rift floor are new grasslands being formed. These sites are on the aggraded floors of the donga incisions of the plains. Everywhere else (excluding slack areas), the young stages of savanna trees and shrubs are encountered in floodplain grasslands. Within a decade many of the areas designated as grasslands by this study will have been converted to the duplex savanna structure with growth of the saplings above the

Swamp Forest and Fynbos on the Cheringoma Coast

BOTTOM RIGHT:

External aspect of tall (25 m) swamp forest down the centre of a dambo viewed from the fringing miombo forest mosaic. Predominant upper canopy trees are *Adina microcephala* and *Barringtonia racemosa.*

BOTTOM CENTRE:

Internal view of the same swamp forest shown in bottom left with the tree trunks festooned by the climbing fern *Stenochlaena tenuifolia*. The primitive epiphytic quillwort *Psilotum nudum* hangs from rot-holes and clefts in the tree trunks.

BOTTOM FAR RIGHT:

Oblique aerial view of pure stands of *Phillipi simii* fynbos scrub thicket patches on white podsolized sands, surrounding a forest patch formed by coalescence of termitaria thickets. 'Blackwater' catchment areas.

grass canopy. If the active erosion process continues unabated on the Rift floor, within two or three decades savanna will have taken over large sectors of the floodplains. The southern margin of the Urema Plains is where fast invasive sequences are taking place.

8.6 CHERINGOMA PLATEAU AND COAST

As the miombo of the coastal cuesta is generally similar to that of the Midlands, the diversity of plant communities in this area will be described solely by means of profile and photographic examples.

8.7 PLANT COMMUNITY RELATIONSHIPS

A preliminary analysis of the relationships of grass and woody communities in the montane to mangrove transect was made using Sorenson's Coefficient of Similarity (vide Curtis 1959, p. 83). The formula used is 2w/a+ b, where 'a' is the total number of species in one community and 'b' the total of another, and 'w' is the number of species common to both. The resulting index of similarity is expressed as a percent.

The major relationships are presented in diagrammatic forms (Fig. 8.13) which show several interesting patterns.

Grassland Communities

The closest affinity (52%) is shown between the miombo grass stratum and those of the Rift Valley savannas. Montane grasslands and the coastal high water table dambo grasslands show a relatively high affinity of 25%. Shade grass communities are most similar between the mountain rainforest and coast moist evergreen forests.

Suprisingly, the grass communities of heavy floodplain alluvia show relatively low affinities when comparing those of the Urema Trough with the Zambezi Delta (Fig. 8.13). This may be explained by the mosaic dominance of a few species over large areas.

Woody Communities

Gorongosa Mountain

The three communities show little affinity with each other despite their being closely juxtaposed.

Midlands

Likewise, relatively little relationship is exhibited by the communities contained in the Midland miombo. The highest (< 20%) is between miombo and the termitaria inclusions.

Rift Valley

The conspicuous feature of the Rift Valley communities is the large number of closed canopy systems which are related to one another clinally; from mopane to dry forest and riverine thicket (Fig. 8.13). For example, mopane and dry forest related directly have few species in common, but they are strongly related via a series of three thicket types. The mixed savannas have a relatively low affinity with any of the closed communities.

Cheringoma Plateau and Coast

Only riverine and swamp forests show a high number of species in common (51%), and the remainder, only a median to low affinity despite their close juxtaposition in the field. This feature appears to be characteristic of communities on leached, acid soils.

Summary of Community Relationships Between Each Physiographic Unit

The miombo of the Midlands and coast plateau have the highest number of species in common (67%) yet this is a low figure for an ecosystem which is essentially homogenous in its species array over extensive areas. A high affinity is probably not attained because of the many forest margin and median layer species which invade miombo on the white duplex sands. If the miombo on the red latosols alone are compared with the Midlands, the number of species in common is very much higher.

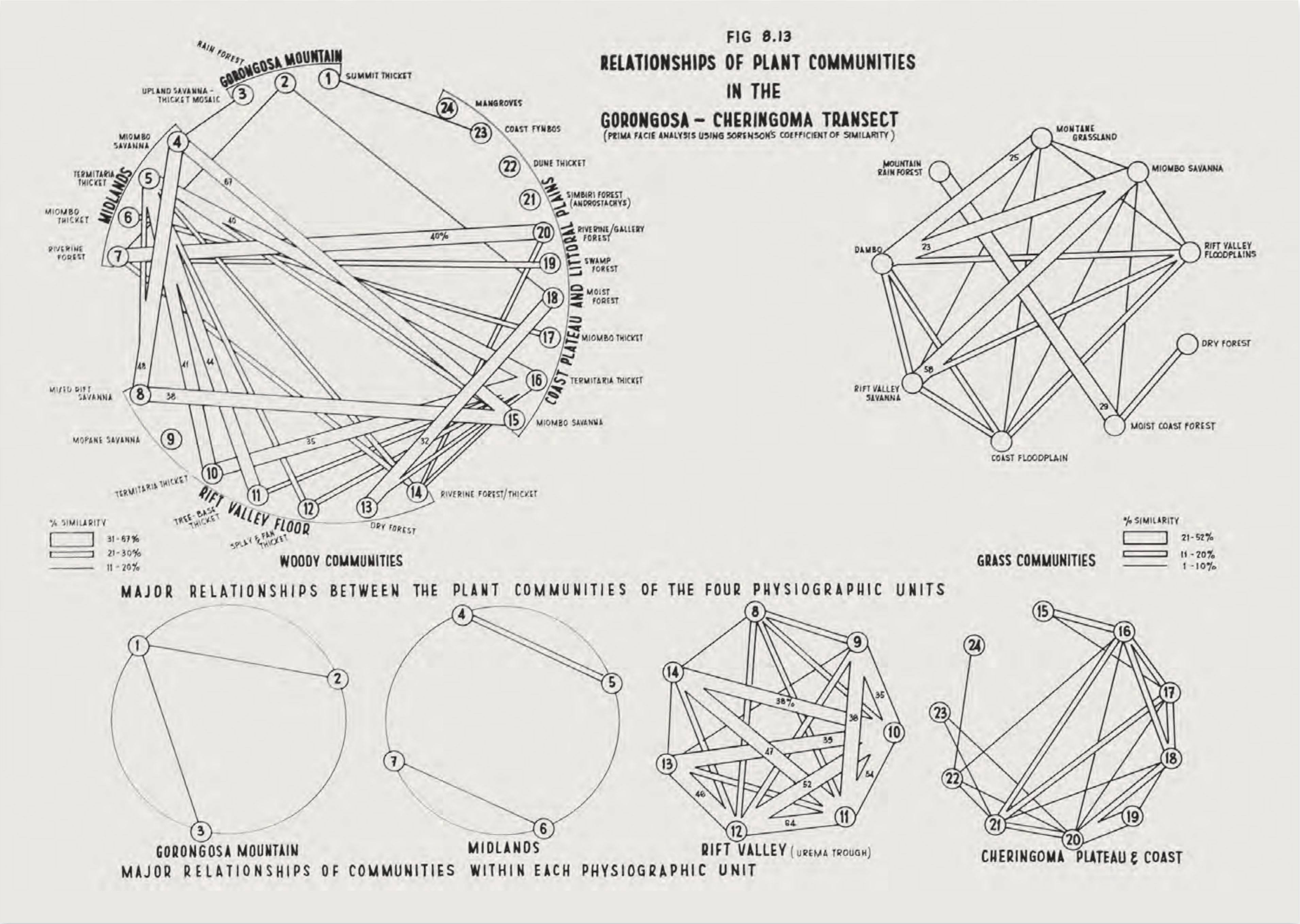
The mixed Rift savannas have an index of 48% with the Midland miombo, and 38% with the coast miombo due to the species common to sand savannas wherever they occur in the transect.

The next highest number of species in common is shared by termitaria thickets of each unit excluding the mountain.

Overall, therefore, the closest relationships are shown by the Rift Valley communities due primarily to the widespread occurrence of the same zoochorous species in all perch, water-based and bare soil sites.

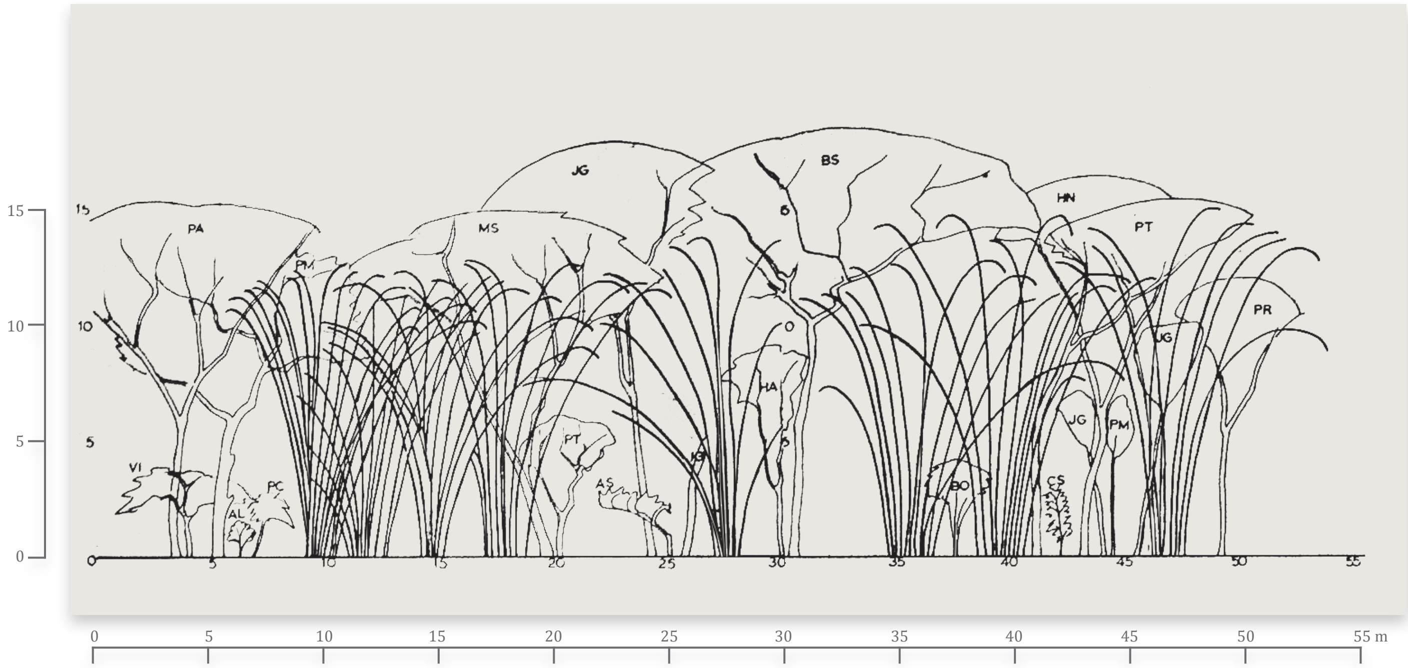
RIGHT: Figure 8.13

Relationships of plant communities in the Gorongosa-Cheringoma transect.



LEFT: Figure 8.14

Profiles of Midland plant communities.



MIOMOBO
Belt 10 m wide

AL	*Allophyllus alnifolia*
AS	*Anona senegalensis*
BO	*Byrsocarpus orientalis*
BS	*Brachystegia spiciformis*
CS	*Commiphora serrata*
JG	*Julbernardia globiflora*
HA	*Hymenocardia acida*
HN	*Heteropyxis natalensis*
MS	*Millettia stuhlmanii*
OA	*Oxytenanthera absyssinica*
PA	*Pterocarpus angolensis*
PC	*Psychotria capensis*
PM	*Pseudolachnostylis maprounifolia*
PR	*Pterocarpus rotundifolia*
PS	*Piliostigma thonningii*
VI	*Vangueria infausta*

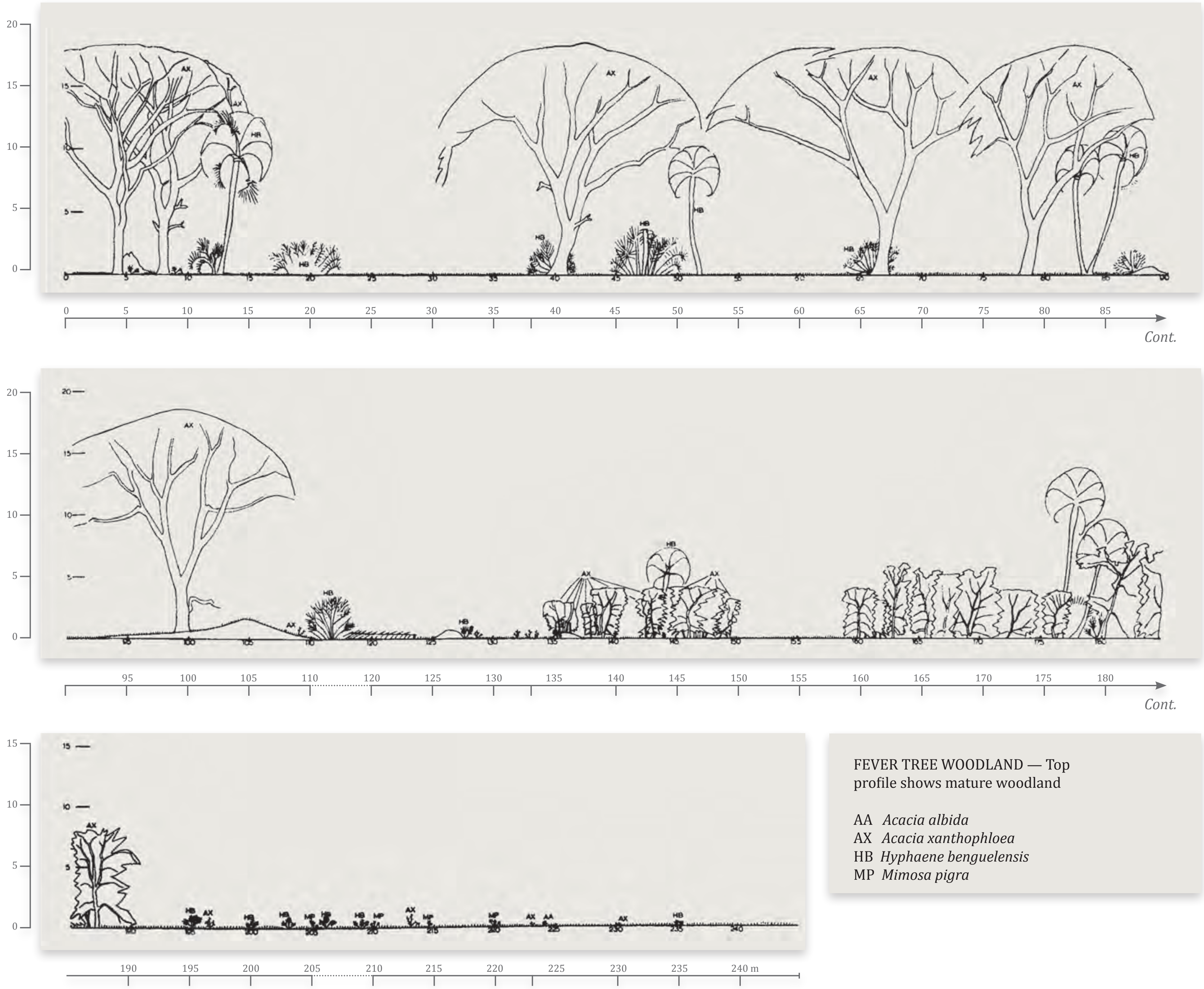
MIOMBO THICKET
Belt 2 m wide

AL	*Allophylus alnifolia*
BA	*Burkea africana*
BE	*Bersama abyssinica*
BG	*Bauhinia galpinii*
BO	*Byrsocarpus orientalis*
CA	*Cassia abbreviata*
CB	*Carissa bispinosa*
CC	*Canthium crassum*
DC	*Diplorhynchus condylocarpon*
DU	*Diospyros usambarensis*
EN	*Euclea natalansis*
FO	*Friesodielsia obovata*
GL	*Grewia lepidopetala*
HA	*Harrisonia abyssinica*
JG	*Julbernardia globiflora*
KA	*Kigelia africana*
MA	*Markhamia acuminata*
OA	*Oxytenanthera abyssinica*
OO	*Ozoroa obovata*
PL	*Polysphaeria lenceolata*
PM	*Pteleopsis myrtifolia*
PR	*Pavetta revoluta*
R	*Rhoicissus sp.*

RIGHT: Figure 8.14
cont.
Profile of miombo woodland.

MIOMBO SAVANNA WOODLAND
Belt 10 m wide

AA *Amblygonocarpus andongensis*
BA *Burkea africana*
BB *Brachystegia boehmii*
BO *Byrsocarpus orientalis*
BP *Bauhinia petersiana*
BR *Brackenridgea arenaria*
BS *Brachystegia spiciformis*
DC *Diplorhynchus condylocarpon*
CZ *Combretum zeyheri*
EA *Erythrophyllum africanum*
JG *Julbernardia globiflora*
HA *Hymenocardia acida*
LD *Lannea discolor*
MS *Millettia stuhlmanii*
PM *Pseudolachnostylis maprouneafolia*
RR *Ricinodendron rautenenii*
SC *Sclerocarya caffra*
SQ *Sterculia quinqueloba*
XO *Xeromphis obovata*
XP *Xylopia parvifolia*
XA *Xeroderris stuhlmanii*

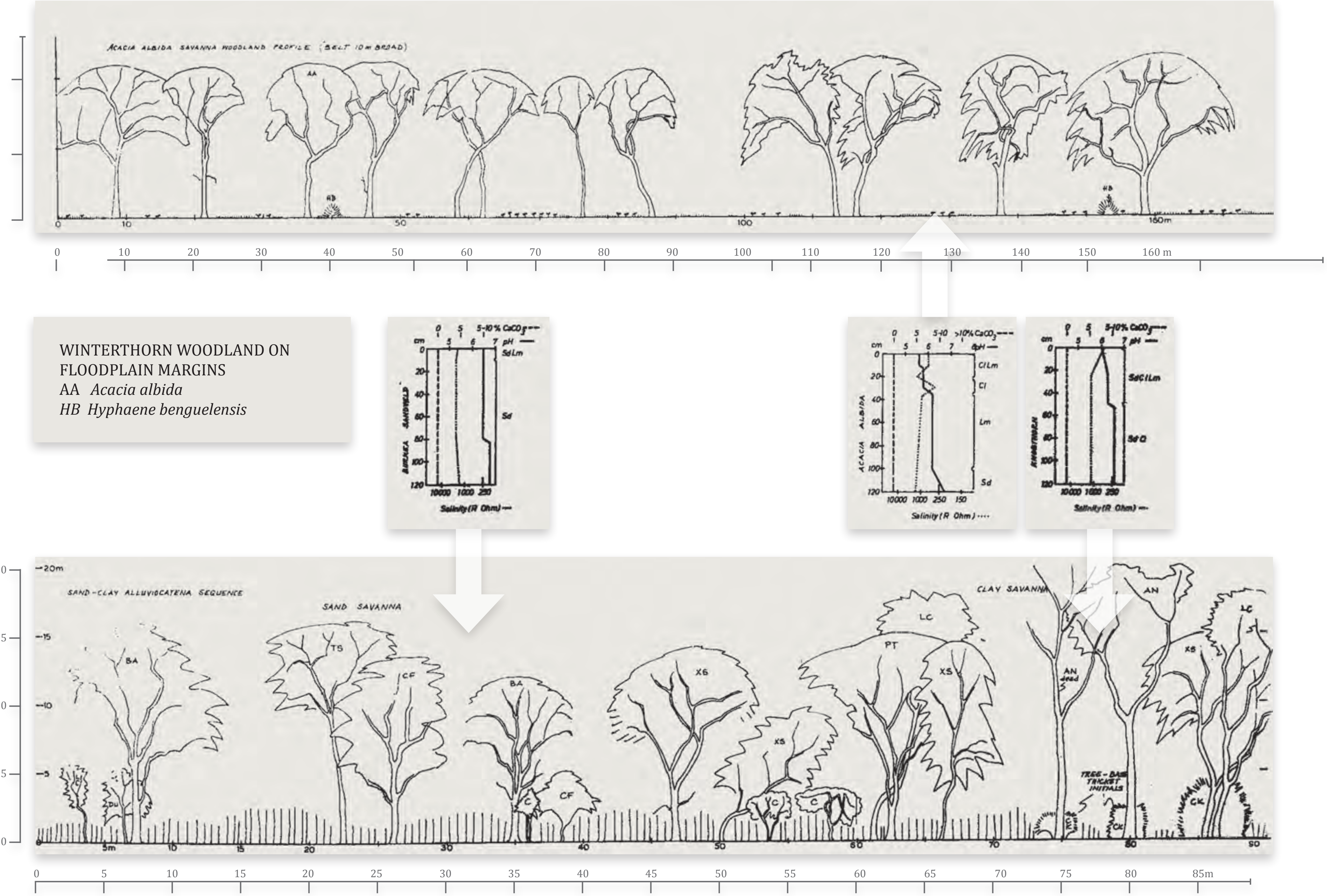


LEFT: Figure 8.15

Profile of three-stage invasion of floodplains by fever tree woodland. Top profile shows mature woodland.

RIGHT: Figure 8.16

Profiles of marginal winterthorn woodland and a sand-clay savanna mosaic on the Rift floor.



WINTERTHORN WOODLAND ON FLOODPLAIN MARGINS

AA *Acacia albida*
HB *Hyphaene benguelensis*

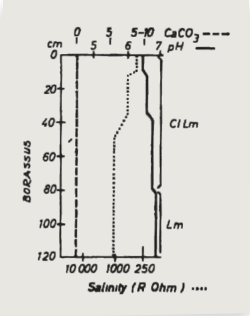
SAND-CLAY ALLUVIOCATENA SAVANNA SEQUENCE

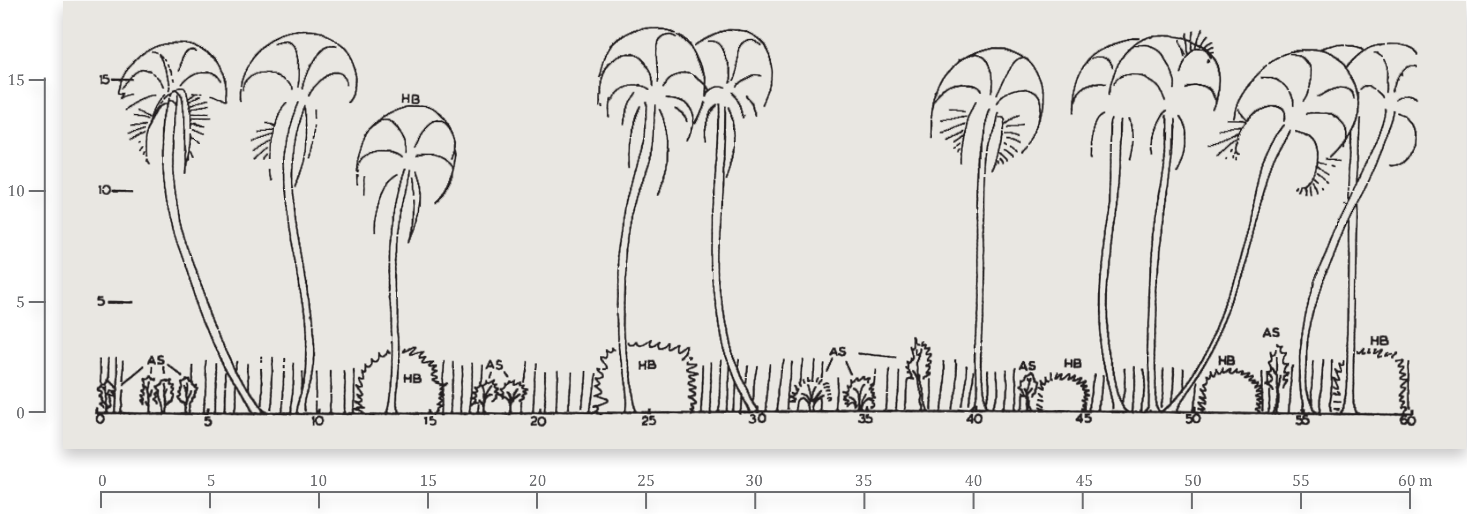
AN *Acacia nigrescens*	CF *Crossopterix febrifuga*	LC *Lonchocarpus capassa*
BA *Burkea africana*	CK *Cleistochlamys kirkii*	TS *Terminalia sericea*
C *Combretum fragrans*	DU *Diospyros umbarensis*	XS *Xeroderris stuhlmanii*

LEFT: Figure 8.17

Profiles of palm savannas and thickets on the Rift floor.

BORASSUS PALM SAVANNA
BO *Borassus aethiopium*
LC *Lonchocarpus capassa*
PT *Piliostigma thonningii*



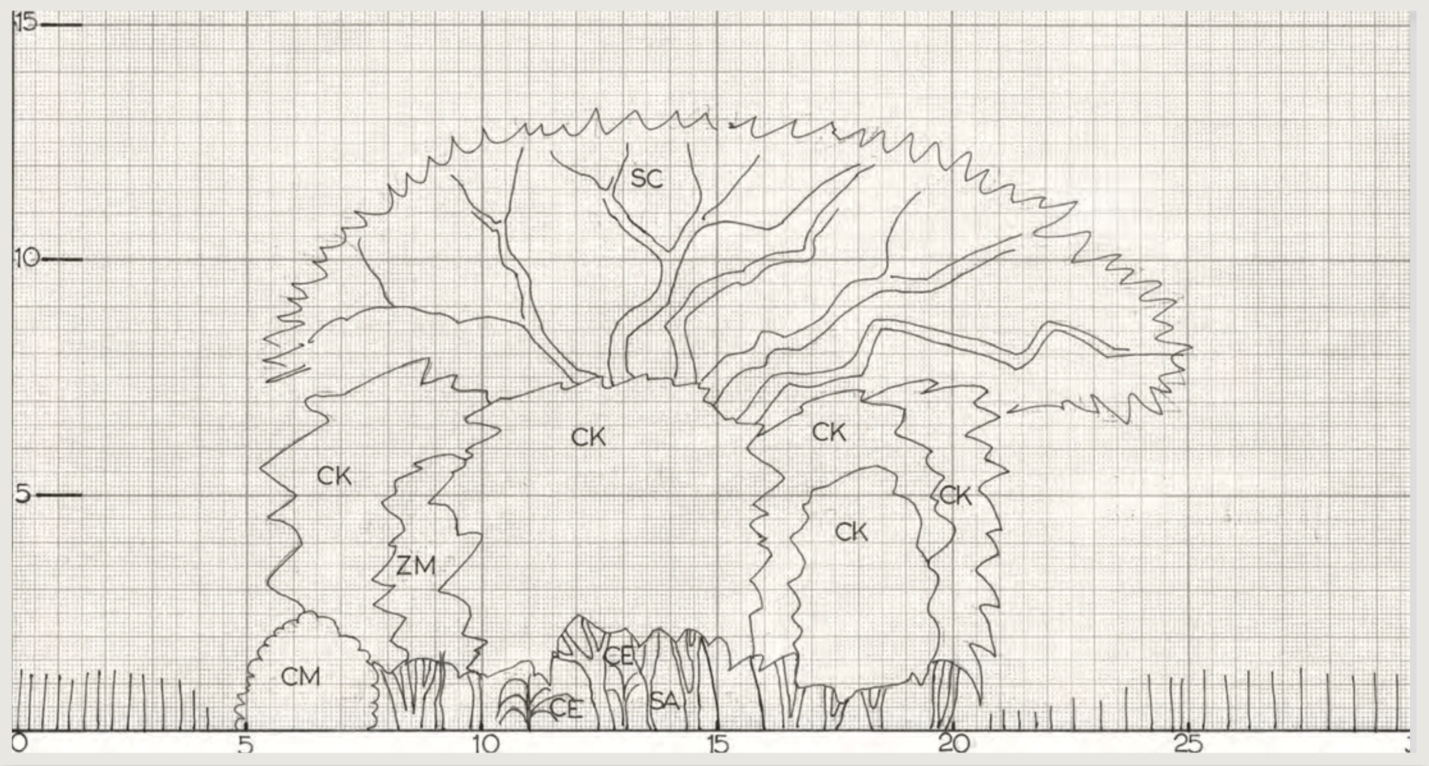


HYPHAENE BENGUELLENSIS
SAVANNA
Belt 10 m wide

AS *Acacia sieberana*
HB *Hyphaene benguellensis*

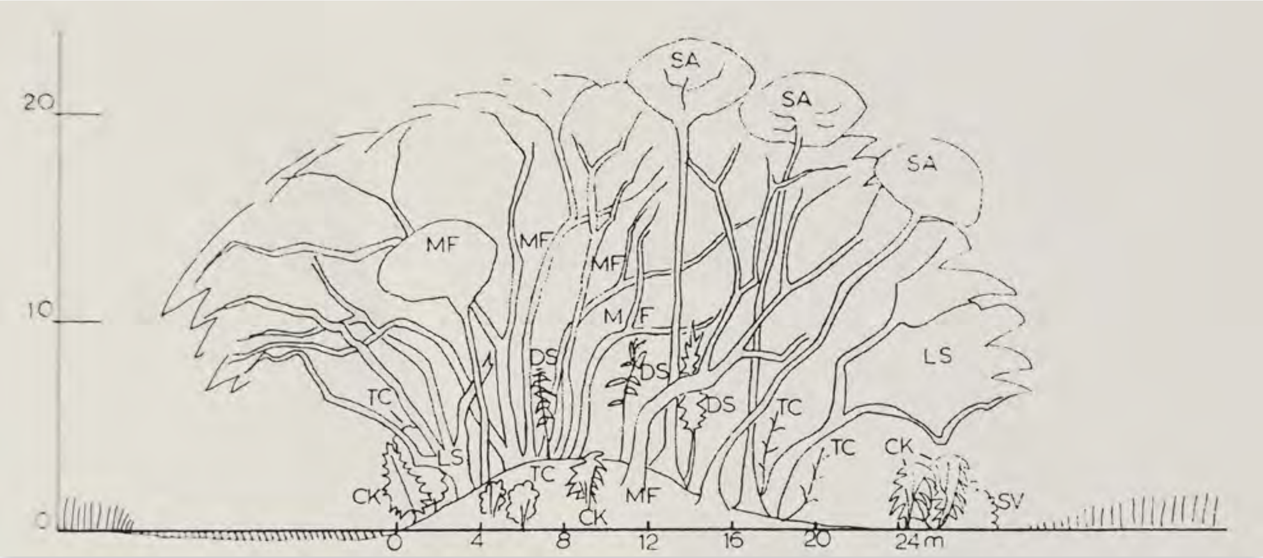
RIGHT: Figure 8.18

Profiles of treebase thicket and termitaria thicket.



TREE BASE THICKET
Belt 5 m wide

CE	*Capparis erythrocarpos*
CK	*Cleistochlamys kirkii*
CM	*Combretum mossambicensis*
SC	*Scelrocarya caffra*
SP	*Spirostachys africana*
ZM	*Ziziphus mucronata*



TERMITARIA THICKET
Belt 10 m wide

CK	*Cleistochlamys kirkii*
DS	*Diospyros senensis*
LK	*Lannea kirkii*
MF	*Mimusops fruiticosa*
SA	*Sterculia appendiculata*
SV	*Securinega virosa*
TC	*Trichilia capitata*

DRY FOREST

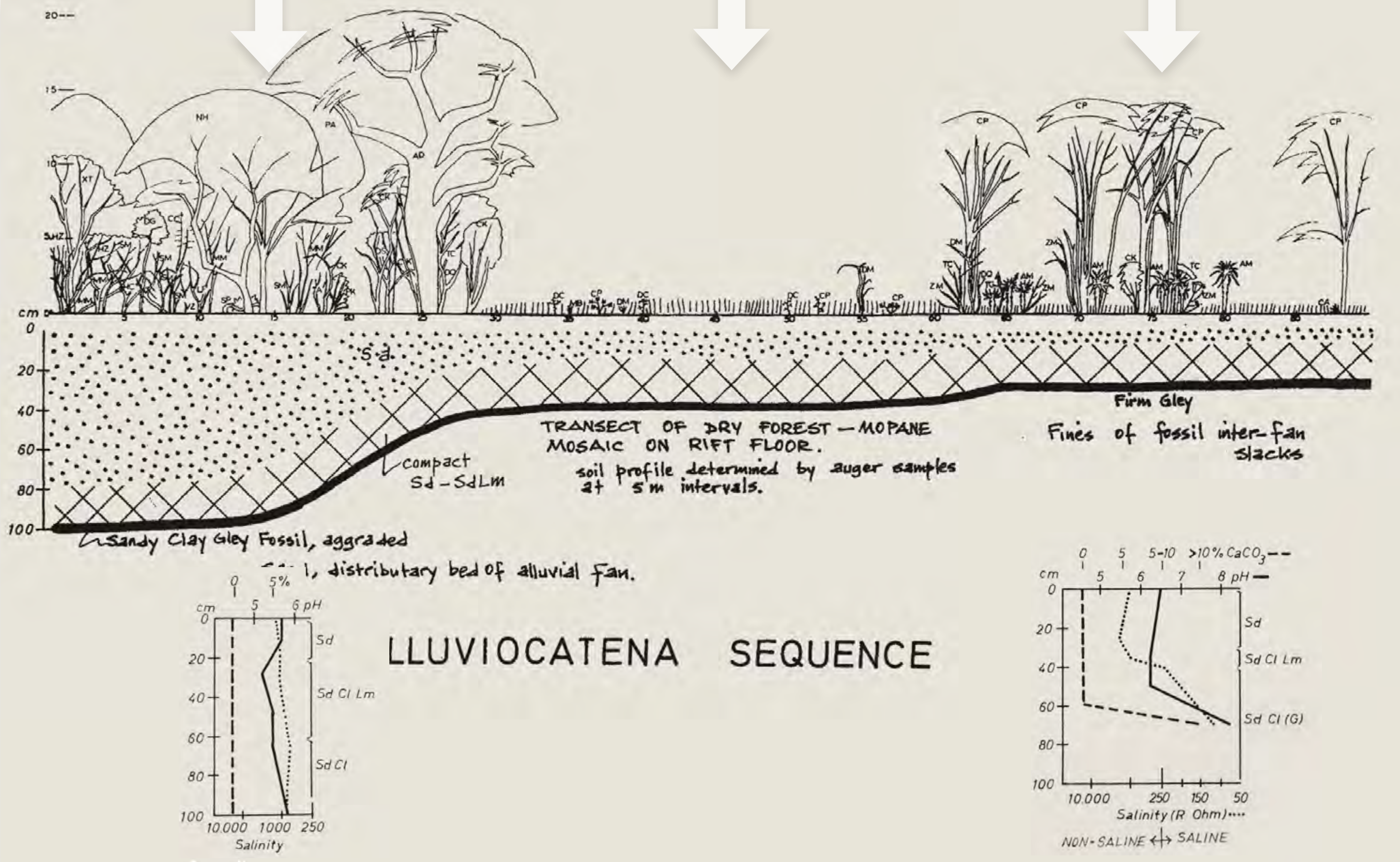
AD	*Adansonia digitata*
CC	*Canthium crassum*
CK	*Cleistochlamys kirkii*
CM	*Canthium martinii*
DS	*Diospyros senensis*
DG	*Drypetes gerrardii*
DQ	*Diospyros quiloensis*
HC	*Heinsia crinita*
HZ	*Hunteria zeylanica*
LF	*Lecanodiscus fraxinifolia*
MM	*Millettia mossambicensis*
NH	*Newtonia hildebrandtii*
PA	*Pterocarpus antonesii*
PK	*Phyllanthus kirkianus*
SM	*Strychnos mitis*
SP	*Salvadora persica*
TA	*Thilachium africanum*
TC	*Trichilia capitata*
VZ	*Vepris zambesiaca*

DAMBO GRASSLAND

CP	*Colophospermum mopane*
DC	*Dichrostachys cinerea*
DM	*Dalbergia melanoxylon*
MB	*Maerua brunnescens*

MOPANE SAVANNA WOODLAND

AM	*Aloe marlothii*
CA	*Commiphora africana*
CK	*Cleistochlamys kirkii*
CP	*Colophospermum mopane*
DM	*Dalbergia melanoxylon*
DQ	*Diospyros quiloensis*
TC	*Trichilia capitata*
ZM	*Ziziphus mucronata*



LEFT: Figure 8.18

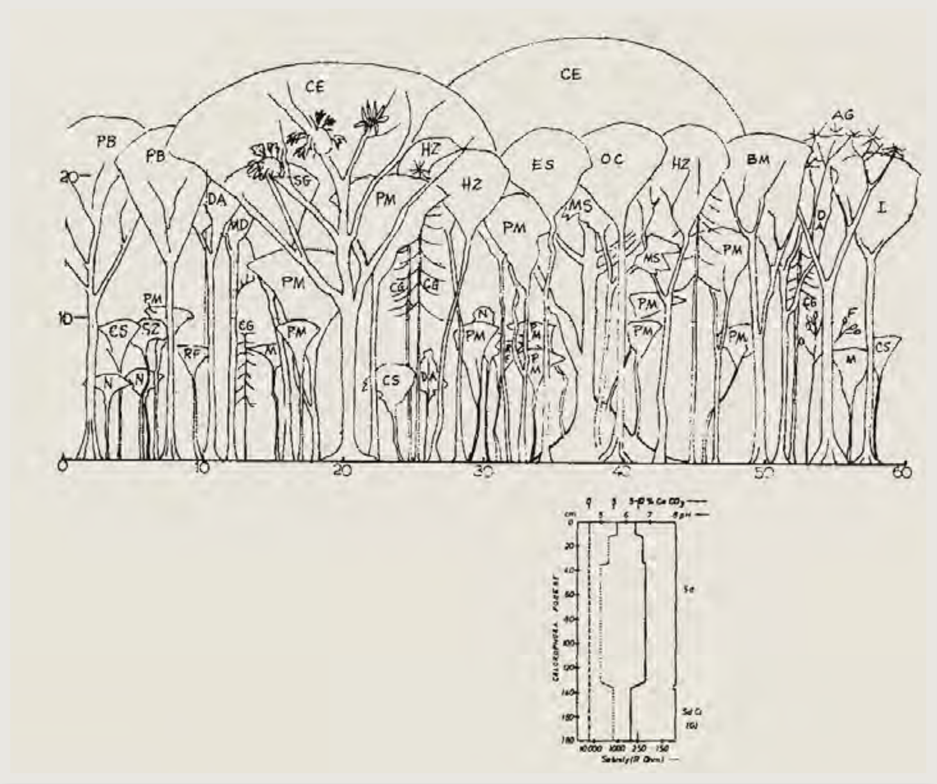
Profile of dry forest-mopane alluviocatena sequence on the Rift floor.

RIGHT, FAR RIGHT AND OPPOSITE:
Figure 8.19

Profiles of forest, thicket and heath on the Cheringoma Coast.

BRACHYSTEGIA SAVANNA CANOPY RELICS IN SUB-MATURE MOIST EVERGREEN FOREST
Belt 5 m wide

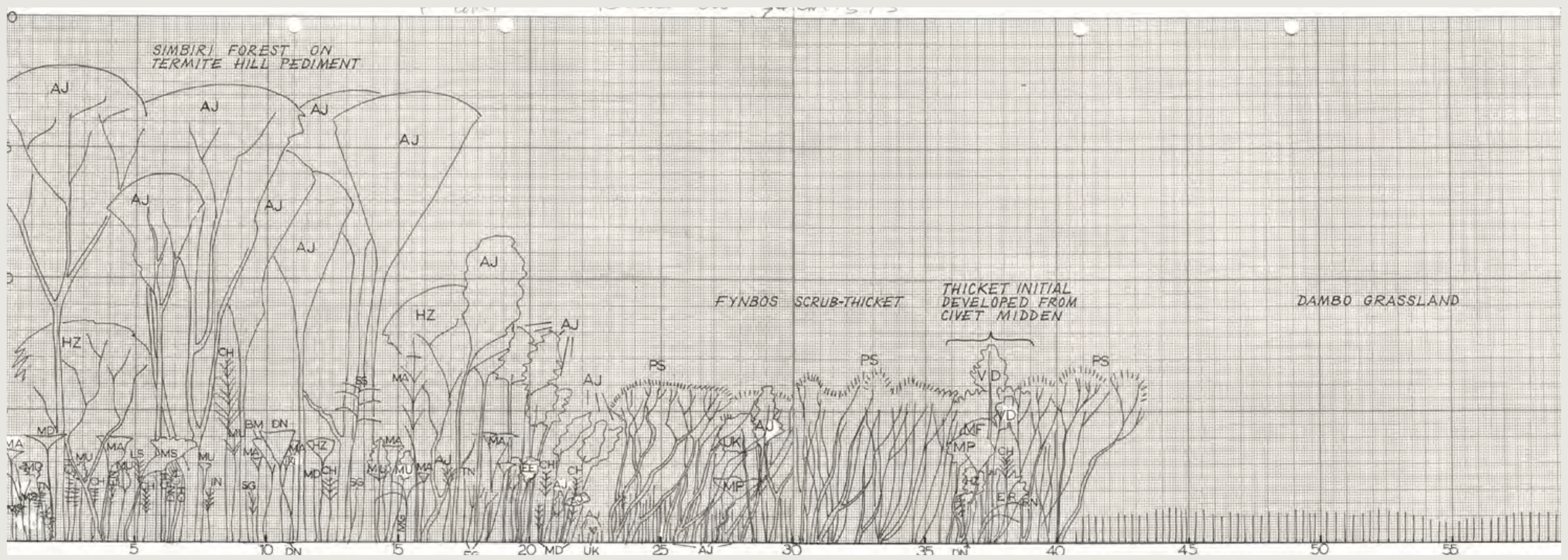
BS	*Brachystegia spiciformis*
CG	*Cassiopourea gummiflua*
CL	*Clestanthus schlechterii*
CZ	*Craibia zimmermannii*
DG	*Drypetes gerrardii*
ES	*Erythrophyllum sauveolens*
GT	*Grewia transzambesiaca*
HZ	*Hirtella zanzibarica*
MB	*Mermecylon sansibaricum*
MD	*Manilcara discolor*
MS	*Millettia stuhlmanii*
PB	*Pachystela brevipes*
PL	*Pteleopsie myrtifolia*
PM	*Pseudobersama mossambicensis*
PS	*Paropsia schliebeniana*
SG	*Syzigium guineense*
SZ	*Suregada zanzibariensis*
UK	*Uapaca kirkiana*
UN	*Uapaca nitida*
VP	*Vincentella passargei*

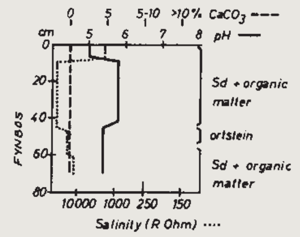


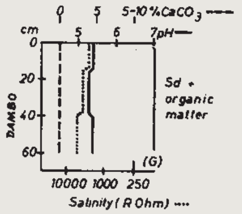
MOIST EVERGREEEN FOREST ON DUPLEX SANDS
Belt 5 m wide

AG	*Anthocleista grandiflora*
BM	*Balanites maughamii*
CE	*Chlorophora exelsa*
CG	*Cassipourea gummifera*
CS	*Craterispermum schweinfurthii*
DA	*Diospyros abyssinica?* (nkomanghamba)
ES	*Erythrophleum sauveolens*
F	*Ficus* sp. (large oval leaves)
HZ	*Hirtella zanguebarensis*
I	Indet.
M	*Memecylon sansibaricum*
MD	*Manilkara discolor*
MS	*Millettia stuhlmanii*
N	'ndambanhati' Indet.
OC	*Olea capensis*
PB	*Pachystela brevipes*
PM	*Pseudo bersama mossambicensis*
RF	*Rothmannia fischeri*
SG	*Syzigium guineense*
SZ	*Suregada zanzibariensis*

Field layer 2 to 4 m in height dominated by *Sloetiopsis usambarensis*







TRANSECT THROUGH FOREST, FYNBOS & DAMBO GRASSLAND SEQUENCE ON TERMITE HILL PEDIMENT
Belt 2 m wide on white podsolized sands

AJ	*Androstachys johnsonii*	HZ	*Hirtella zanguebarica*	MU	*Maytenus undata*
BM	*Brexia madagascariensis*	LS	*Lannea stuhlmannii*	PS	*Philippia simii*
CH	*Canthium huillense*	MA	*Mascarenhasia arborescens*	RN	*Rhus natalensis*
CP	*Croton pseudopulchellus*	MD	*Manilkara discolor*	SG	*Syzigium guineense*
DN	*Diospyros natalensis*	MF	*Mimusops fruticosa*	SS	*Scolopia stolzii*
EE	*Erythroxylum emarginatum*	MG	*Melodorum gracile*	TN	*Tarenna neurophylla*
EG	*E. gerrardii*	MP	*Myrica pilulifera*	UK	*Uapaca kirkiana*
EN	*Euclea natalensis*	MS	*Memecylon sansibaricum*	VD	*Vitex doniana*

RIGHT: Figure 8.20

Profiles of swamp forest, termitaria thicket and littoral communities.

SWAMP FOREST

Belt 5 m wide

AG	*Anthocleista grandiflora*
AM	*Adena microcephala*
BM	*Bridelia micrantha*
BR	*Barringtonia racemosa*
CF	*Clappertonia ficifolia*
CG	*Cassipourea gummiflua*
CS	*Craterispermum schweinfurthii*
EG	*Erythroxylum gerrardii*
FT	*Ficus trichpoda*
HA	*Homalium abdessammadi*
HM	*Harungana madagascariensis*
KN	*Khaya nyasica*
MA	*Mascarenhasia arborescens*
PB	*Pachystela brevipes*
PF	*Parkia filicoidea*
SA	*Scleria angusta*
SG	*Syzigium guineense*

DAMBO THIOCKET ISLANDS ON TERMITE HILLS

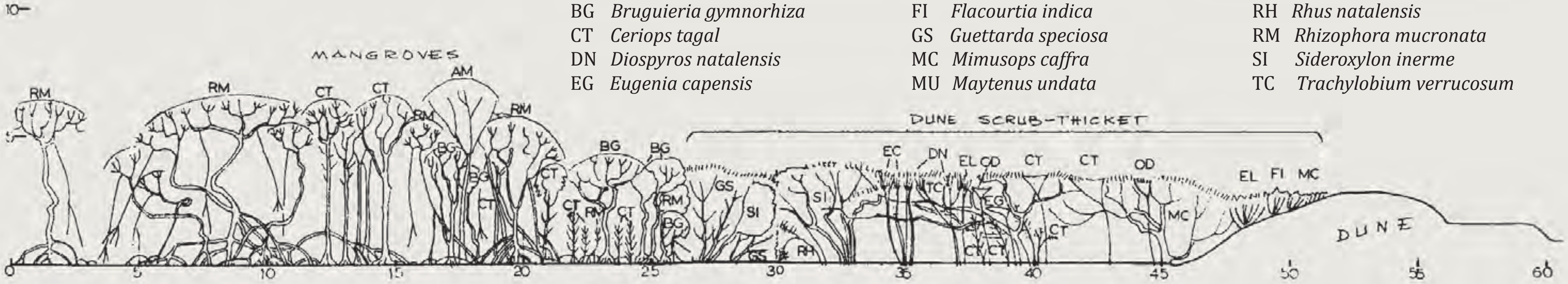
Belt 10 m wide

AC	*Afzelia quanzensis*
AV	*Antidesma venosum*
CL	*Cleistanthus schlechterii*
CS	*Craterispermum schweinfurthii*
ES	*Erythrophleum suaveolens*
GT	*Grewia transzambeziaca*
HC	*Hiensia crinita*
HZ	*Hirtella zanzibarica*
MD	*Manikara discolor*
MP	*Maprounea africana*
MF	*Mimusops fruitcosa*
MS	*Millettia stuhlmanii*
OA	*Oxytenanthera abyssinica*
PB	*Pachystela brevipes*
PC	*Paranari curatellifolia*
PL	*Polysphaeria lanceolata*
SG	*Syzigium guineense*
TE	*Tabernaemontana elegans*
UK	*Uapaca kirkiana*
UN	*U. nitida*
RM	*Rhizophora mucronata*
SI	*Sideroxylon inerme*
TC	*Trachylobium verrucosum*

PROFILE OF ESTUARINE MANGROVE & DUNE Scrub thicket SEQUENCE

Belt 2 m wide

AM	*Avicenna marina*
BG	*Bruguieria gymnorhiza*
CT	*Ceriops tagal*
DN	*Diospyros natalensis*
EG	*Eugenia capensis*
EL	*Enterospermum littorale*
FI	*Flacourtia indica*
GS	*Guettarda speciosa*
MC	*Mimusops caffra*
MU	*Maytenus undata*
OD	*Olax dissitiflora*
RH	*Rhus natalensis*
RM	*Rhizophora mucronata*
SI	*Sideroxylon inerme*
TC	*Trachylobium verrucosum*



REFERENCES / CORRELATION VEGETATION

AETFAT / UNESCO 1959. *Vegetation map of Africa 1:10 million, explanatory notes by E.W.J. Keay.* Oxford University Press.

Aubreville, A. 1947. *The disappearance of the tropical forests of Africa.* Unasylva, No. 1, pp. 5–11.
—1949a. *Climats, forêts et desertification de l'Afrique tropicale.* Soc. d'Edit. Geogr. Marit et Colon, Paris.
—1949b. *Contribution a la paléohistoire des forêts de l'Afrique tropicale.* Soc. d'Edit. Geogr. Marit et Colon, Paris.

Bayer, A.W. 1955. 'The ecology of grasslands'. In *The grasses and pastures of South Africa* edited by D. Meredith, C.N.A., pp. 539–550.

Boaler, S.B. 1966. *Ecology of a miombo site, Lupa North Forest Reserve, Tanzania II: plant communities and seasonal variation in the vegetation.* J. Ecology, vol. 54, pp. 465–479.

Bonsma, J. C. 1940. *The influence of climatological factors on cattle, observations on cattle in tropical regions.* Farming in South. Africa 15: 373-385,

Cain, S.A. & Castro, G.M. De Oliveira 1959. *Manual of vegetation analysis.* Harper, NY.

Chapman, J.D. & White, F. 1970. *The evergreen forests of Malawi.* Commonwealth Forestry Institute, University of Oxford.

Curtis, J.T. 1959. *The vegetation of Wisconsin.* University of Wisconsin Press, Madison, USA.

Curtis, J.T. & Cottam, G. 1962. *Plant ecology workbook.* Burgess, Minnesota, USA.

Davis, T.A.W. & Richards, P.W. 1933/34. *The vegetation of Moraballi Creek, British Guiana.* Parts I & II. J. Ecology, vol. 21, pp. 350–384, vol. 22, pp.106–155.

Dutton, T.P. & Dutton, Ann 1973. *A preliminary survey of the Chimanimani Mountains and adjoining area with a view to its creation as a conservation area.* Report to Vet. Dept. of Moz. Govt. mimeo.

Fanshawe, D. 1971. *The vegetation of Zambia.* For. Res. Bull. Min. Rural Devel. Zambia, vol. 7, pp. 1–67.

Fernandes, J.F. 1968a. *Os solos da Serra da Gorongosa e sua capacidade de utilização.* I.I.A.M. Communicações, No 7.
—1968b. *Os solos do Parque Nacional da Gorongosa.* I.I.A.M. Communicações, No. 19.7

Glover, P.E., Glover, J. & Gwynne, M.D. 1962. *Light rainfall and plant survival in East Africa.* J. Ecology, vol. 50, pp. 199–206.

Hall-Martin, A.J. 1972. *Aspects of the plant ecology of the Lengwe National Park, Malawi.* M.Sc. Thesis, University of Pretoria.

Hopkins, B. 1968. *Vegetation of the Olokemeji Forest Reserve, Nigeria V: the vegetation on the savanna site with special reference to its seasonal changes.* J. Ecology, vol. 56, pp. 97–115.

Komarek, E.V. 1964. *The natural history of lightning*. Proc. 3rd. Ann. Tall Timbers Fire Ecology Conf., pp. 139–183.
—1965. *Fire ecology – grasslands and man*. Proc. 4th Ann. Tall Timbers Fire Ecology Conf., pp.169–220.

Lawton, R.M. 1963. *Palaeoecological and ecological studies in the northern province of Northern Rhodesia.* Kirkia, vol. 3, pp. 46-77.

Lebrun, J. 1935. *Les essences forestieres des regions montagneuses du Congo oriental.* Publ. Inst. Agron. Congo Belge, Ser. Sci. 1.

Lemon, P.C. 1968. *Effects of fire on an African Plateau grassland.* Ecology, vol. 49 (2), pp. 317–322.

Malaisse F.P. 1974. Phenology of the Zambezian woodland area with emphasis on the miombo ecosystem. In *Phenology and seasonality modelling*. Edited by H. Leith, Ecological Studies, vol. 8, Springer-Verlag. Berlin and NY.

Macedo, J.M. De Aguiar 1966. *Relatório preliminar da dilligência ao Parque Nacional e á Serra da Gorongosa.* Part I, Part II, roneoed, I.I.A.M. Lourenco Marques.

—1970a. *Serra de Gorongosa necessidade e bases da sua protecção.* I.I.A.M. Communicações, No. 44.
—1970b. *Carta de vegetação da Serra da Gorongosa.* I.I.A.M. Communicações, No. 50, incl. vegetation map 1:75,000.

Malaisse, F.P. 1974. 'Phenology of the Zambezian Woodland area with emphasis on the miombo ecosystem'. In *Phenology and seasonality modelling.* H. Leith edit., Ecological Studies, vol. 8, Springer-Verlag, Berlin & NY.

Monod, T. 1957. *Les grandes divisions chorologigues de l'Afrique.* CSA/CCTA Publ., No. 24, London.

Pedro, J. Gomes & Barbosa, L. A. Grandvaux 1955. 'A vegetação'. In *Esboço do reconhecimento ecologico-agricola de Mozambique.* vol. 2 CICA (JEA) Mem. e Trab. No. 23, pp. 69–224 + vegetation map 1:2 million.

Phillips, J.F.V. 1931 *Forest succession and ecology in the Knysna region.* Bot. Survey of S. Afr. Memoir No. 14.
—1965. *Fire—as master and servant: its influence in bioclimatic regions of trans-Saharan Africa.* Proc. 4th Ann. Tall Timbers Fire Ecology Conf., Tall Timbers Research Station, Tallahassee, No. 71a, pp. 7–109.

Rees, A.R. 1964a. *Some observations on the flowering behaviour of Coffea rupestris in southern Nigeria.* J. Ecology, vol. 52 (1), pp. 1–7.
—1964b. *The flowering behaviour of Clerodendrum incisum in southern Nigeria.* J. Ecology, vol. 52 (1), pp. 9-17.

Ridley, H.N. 1930. *The dispersal of plants throughout the world.* Reeve Co., Ashford, England.

Schelpe, E.A.C.L.E. 1966. *The Pteridophyta of Gorongosa Mountain, southern Mozambique.* Bol. Soc. Broteriana, vol. 40 (2), pp. 149–79.

Smithers, R.H.N. & Tello, J.L.P. 1976. *Check list and atlas of the mammals of Mozambique.* National Museums of Rhodesia, Memoir No. 8, Mardon, Salisbury.

Trapnell, C.G. 1959. *Ecological results of woodland burning experiments in Northern Rhodesia.* J. Ecology, vol. 47 (1), pp. 129–168.

Tinley, K.L. 1966. *An ecological reconnaissance of the Moremi Wildlife Reserve, Botswana.* Okavango Wildlife Soc., Gothic, Cape Town.

Tinley, K.L. 1975. ‘Habitat physiognomy, structure and relationships’ in *The Mammal Research Institute 1966-1975. Symposium Proceedings,* University of Pretoria Publ., New Series No. 97, pp. 69–71.

Turnbull, C.M. 1961. *The forest people.* Chatto & Windus, London.

Van der Pijl, L . 1972. *Principles of dispersal in higher plants.* 2nd. ed., Springer-Verlag.

Walter, H. 1971. *Ecology of tropical and subtropical vegetation.* Oliver & Boyd, London.
—1973. *Vegetation of the Earth.* Heidelberg Science Library, vol. 15. Springer-Verlag.

West, O. 1965. *Fire in vegetation and its use in pasture management with special reference to tropical and subtropical vegetation.* C.A.B. Publ. No. 1/1965.

White, F. 1965. *The savanna woodlands of the Zambezian and Sudanian domains: an ecological and phytogeographical comparison.* Webbia, vol. 19 (2), pp. 651–681.
—1971. *The taxonomic and ecological basis of chorology.* Bot. Staatssamml Mitt. München, No. 10, pp. 91–112.

Wild, H. 1952. *The vegetation of Southern Rhodesian termitaria.* Rhod. Agric. J. 49: 280–292.

Wild, H. & Barbosa, La Grandvaux 1967/8. *Vegetation map of the Flora Zambeziaca area, 1:2.5 million.* Explantory supplement edited by H. Wild & A. Fernandes, M.O. Collins,

PART 2

CORRELATION

Chapter 9

Wildlife

Wildlife

9.1 INTRODUCTION

The term wildlife is used here mainly in relation to the larger indigenous mammals (Table 9.1), but some reference is also made to the avifauna in the context of diversity, seed dispersal, succession, seasonality and associations with mammals.

In Gorongosa, a large faunal diversity matches landscape variety and the multiplicity of ecosystems, habitats and ecotones produced by the juxtaposition and overlap of different substrates as elucidated in the preceding chapters. The greatest abundance and diversity of larger mammals is concentrated in the Rift Valley, where buffalo are numerically dominant (in 1977 c. 15,000). The largest species spectrum is contributed by neotragids (five) followed by three each of cephalophids, tragelaphids and alcephalids (with tsessebe recently extinct from the region) (see Table 9.1 for explanation). A total of 27 ungulates (two recently extinct locally) occur in the system, with nine larger carnivores (Fig. 9.1).

The spectacularly rich wildlife of the Rift Valley is a consequence of the mosaic evolution of forest, thicket and savanna, abutted against a floodplain grassland ecosystem of high primary productivity on base saturated soils. Habitat and faunal diversity can also be gauged by the recorded occurrence of 800 species of birds in the montane to mangrove transect of the Gorongosa–Cheringoma area (vide checklists of Rosa Pinto 1968, Clancey 1971).

TABLE 9.1
Larger mammal spectrum of the Gorongosa ecosystem > 5 kg mass

LARGE MAMMALS			GRAZER	MIXED	BROWSER	OMNIVORE	CARNIVORE	INSECTIVORE
Primates	Cercopithecids	Yellow baboon *Papio cynocephalus*				●		
		Samango monkey *Cercopithecus albogularis*				●		
		Vervet monkey *Cercopithecus pygerythrus*				●		
Pholidote	Manid	Pangolin *Manis teminki*						●
Carnivores	Hyaenids	Spotted hyaena *Crocuta crocuta*					●	
	Felids	*Cheetah *Acinonyx jubatus*					●	
		Leopard *Panthera pardis*					●	
		Lion *Panthera leo*					●	
		Serval *Felis serval*					●	
		Wildcat *Felis lybica*					●	
	Canids	Wild dog *Lycaon pictus*					●	
		Side-striped jackal *Canis adustus*				●		
	Mustellids	Cape clawless otter *Aonyx capensis*					●	
		Spotted-necked otter *Lutra maculicollis*					●	
		Honey badger *Mellivora capensis*				●		
	Viverrids	Civet *Viverra civetta*				●		
Tubulidentata	Orycteropids	Aardvark *Orycteropus afer*						●
Herbivores	Elephantids	Elephant *Loxodonta africana*		●				
	Equids	Zebra *Equus burchelli* subsp. *selousi*	●					
	Rhinocerids	*White rhino *Ceratotherium simum*	●					
		Black rhino *Diceros bicornis*			●			
	Suids	Bushpig *Potamochoerus porcus*				●		
		Warthog *Phacochoerus aethiopicus*	●					
	Hippopotamids	Hippo *Hippopotamus amphibius*	●					
	Tragelaphids	Eland *Taurotragus oryx*						
		Kudu *Tragelaphus strepciceros*			●			
		Nyala *Tragelaphus angasi*		●				
		Bushbuck *Tragelaphus scriptus* (vars*: sylvaticus & ornatus*)			●			
	Hippotragids	#Roan *Hippotragus equinus*						

(cont.)

LARGE MAMMALS			GRAZER	MIXED	BROWSER	OMNIVORE	CARNIVORE	INSECTIVORE
Herbivores cont.		Sable *Hippotragus niger*	●					
	Reduncids	Reedbuck *Redunca arundinum*	●					
		Waterbuck *Kobus ellipsiprymnus*	●					
	Alcephalids	Lichtenstein's or Miombo hartebeest *Alcephalus lichtensteinii*	●					
		#Tsessebe *Damaliscus lunatus*	●					
		Wildebeest *Connochaetes taurinus*	●					
	Antilopids	Impala *Aepyceros melampis*		●				
	Cephalophids	Red duiker *Cephalophus natalensis*			●			
		Blue duiker *Cephalophus monicola*			●			
		Grey duiker *Sylvicapra grimmia*			●			
	Neotragids	Suni *Neotragus moschatus*			●			
		Oribi *Ourebia ourebia*		●				
		Klipspringer *Oreotragus oreotragus*			●			
		Steenbok *Raphicerus campestris*			●			
		Sharpe's grysbok *Raphicerus sharpei*			●			
	Bovinid	Buffalo *Syncerus caffer*	●					
Rodents	*Hystricids*	Porcupine *Hystrix africaaustralis*				●		
	Thrynomids	Greater cane rat *Thryonomys swinderianus*	●					
		Total (44)	11	4	10	8	9	2
		Percent	25	9	23	18	20	5

KEY
#Recently locally extinct (between 1950 and 1970)
*Recently reintroduced: 1973 cheetah,
1970 white rhino (extinct c. 1940 NW of Gorongosa Mountain)

The larger fauna, which are associated with four major habitats: (a) forest/thicket, (b) savanna/grassland, (c) wetlands, and (d) rock outcrops, are composed of elements from eight zoo-geographic ranges of larger herbivores as derived from the distributional data in Dorst & Dandelot (1970).

(1) Widespread savanna (e.g. elephant, buffalo, warthog, oribi, black rhino, grey duiker)
(2) Widespread forest (e.g. tree dassie, bushpig, blue duiker, bushbuck)
(3) Widespread wetlands (e.g. hippopotamus)
(4) Widespread rock outcrops (e.g. klipspringer, rock dassie)
(5) Eastern and southern savannas (e.g wildebeest, plains zebra, impala, Lichtenstein's hartebeest, sable, steenbok)
(6) Eastern forest/thicket (e.g. nyala, suni, Sharpe's grysbok)
(7) Southern (tsessebe — recently extinct in area).
(8) Marine Indo-Pacific–estuarine and littoral (e.g. dugong).

Of these the first, third and fifth groups contribute the greatest zoomass in the Gorongosa ecosystem. The primates are represented by only two galagos, two monkeys and one baboon. In addition to the blue duiker, another equatorial rain forest element, Fraser's flying squirrel *Anomalurus derbianus*, occurs nearby in Zambezia District (Smithers & Tello 1976, p.136), and may well occur in the east of the system where it should be looked for in the ravine forests of the Cheringoma Plateau.

In a biome context only four of the seven major biomes (Tinley 1975) are represented by the larger mammals. These are: (1) Aquatic (eg. hippo), (2) Forest (e.g. blue duiker), (3) Moist Savanna (e.g. Lichtenstein's hartebeest, sable) and (4) Arid Savanna (e.g. steenbok). The flora and avifauna however contribute elements representative of the remaining three biomes: Afro-temperate, Desert and Palaearctic Temperate (e.g. Palaearctic bird migrants). Lechwe are confined to the floodplain systems of the Interior Continental Plateau; however another riverine ungulate, the sitatunga, may occur along the Zambezi in Mozambique (Smithers & Tello 1976, pp. 171–172).

Of the large faunal components, the nyala has the smallest geographic range and is endemic chiefly to the Mozambique lowlands. Greater endemism in the Eastern Forest Thicket Domain is exhibited by the flora and avifauna.

Until the arrival of the author at Gorongosa in August 1968, most of the faunal work in the region had been dedicated to building up collections for museum research, and the continued discovery of new records showed that much more field collecting was still required. These expeditions are summarised by Clancey (1971) for the avifauna and by Smithers & Tello (1976) for mammals. As a basis to the first stage ecological studies presented in this thesis, air surveys of the ecosystem and air counts of the large ungulates were completed twice a year at the height of the dry season (October) and in the wet season peak (February or March) for five consecutive years. However, due to pilot problems, only six out of 10 were complete counts across the whole ecosystem. As wildlife conservation and the administration of natural parks and reserves was the responsibility of a Fauna Branch of the Veterinary Department in Mozambique, all disease aspects were left to veterinary staff. A detailed study of lion prey in Gorongosa was initiated including the collection and cataloging of all skulls and lower jaws recovered from kills. This study was taken over by José Tello, ex-chief warden of Gorongosa, now with the Ecological Studies Section of the Veterinary Institute in Lourenço Marques (Maputo).

RIGHT: Figure 9.1

Species composition of mammal trophic groups.

FAR RIGHT: Figure 9.2

Biomass contribution of the three large herbivore trophic groups in the Rift Valley (Urema Trough).

Fig 9.1 SPECIES COMPOSITION OF MAMMAL TROPHIC GROUPS.
% of total ≥ 5kg mass

Fig 9.2 ZOOMASS CONTRIBUTION OF THE THREE LARGE HERBIVORE TROPHIC GROUPS IN THE RIFT VALLEY (UREMA TROUGH).
Percent of total zoomass derived from air counts & rough estimates purely browsing group.

9.2 EXTINCT, RARE OR ANOMALOUS

The tsessebe and roan antelope are recently extinct from the Gorongosa area, disappearing in the period between 1950 and 1970. Both species were recorded by Vaughan-Kirby (1899) and Vasse (1909) in the midland Rift Valley and Cheringoma sectors of the ecosystem, and the latter author includes a photograph of a shot tsessebe on the Urema Plains. Up to my arrival in Gorongosa in 1968, persistent reports of several black 'gondonga' (gondonga is the local tribal name for Lichtenstein's hartebeest) were received from the chief living in the Rift Valley savannas south of the Park between the Pungue River and the Rhodesia–Beira main road. During my time, several small herds were reported by professional hunters from the adjoining Lower Pungue–Buzi floodplain margins. In the summer of 1969/70 Dr. Donald Broadley from the Umtali Museum encountered a single roan male in the Inhamitanga area of the Cheringoma Plateau. Both these ungulates are threatened with extinction in Mozambique and tsessebe may already be extinct in the country.

White rhino occurred throughout central Mozambique west of the Cheringoma Plateau until fairly recently. One of the last was shot northwest of Gorongosa Mountain in the Macossa area of the Midlands in 1935 (Sydney 1965, p. 61, Fig. 10). This species must have become extinct in the 1940s. The Macossa area is hill and valley terrain with 'sand rivers', similar to that of their last stronghold in Umfolozi, Zululand. Six white rhino from Umfolosi Game Reserve were reintroduced to the Rift Valley sector of Gorongosa in midwinter of 1970.

Black rhino are recorded from all physiographic units in Gorongosa but the occurrence of only three to five individuals could be ascertained. It was estimated from reports by professional and tribal hunters, plus our own field work, that not more than eight individuals occurred in the whole region.

Cheetah is another species recorded from the area, but was extinct from about 1950. Six were reintroduced to the northern sector of the park in 1973. No recent data are available on their status.

The steenbok, which is abundant in the arid savannas of southern Africa, is recorded from central Mozambique only from the Macossa area (Smithers & Tello 1976, p. 122), and by the writer from one small area of the northern sector of the Rift Valley near the Lunga drainage in *Acacia borleae* scrub on a sheet eroded site. The species was first recorded from the Gorongosa area by Vaughan-Kirby (1899, p. 289) who shot a steenbok 2 km south of the Nhandue River on the Rift floor, judged to be some 8 km southwest of the Lunga site.

The Zambezi Valley is roughly the line separating two races of the wildebeest, *Connochaetes t. taurinus* to the south and the Niassa or Johnston wildebeest, *C. t. johnstoni* with white facial band, to the north. However, small populations of Niassa wildebeest occur amongst the nominate form in the Save Valley (Smithers & Tello 1976, pp. 131–132).

Perhaps the most anomalous distributions pattern in Mozambique is that of giraffe. There are no records in historical times, or amongst old tribal hunters, of giraffe occurring north of the Save River environs. The Chegorongosa tribe does not have a name for giraffe. Nor has the entire area of the Middle and Lower Zambezi Valley any historical record of their occurrence, despite expeditions such as those of Livingstone in 1856. The supposed record of giraffe near Tete noted by Du Plessis (1969, pp. 76–77) is a misinterpretation of a discussion on giraffe that Livingstone included whilst relating his traverse from Zumbo (Zambezi–Luangua confluence) to Tete. As a rinderpest outbreak in Kenya in 1960 resulted in the death of an estimated 70% of eland, buffalo and giraffe, this virus disease is a likely suspect. However, Livingstone's route from Zumbo was south of the river through ideal giraffe habitats interspersed with large areas of mopane, more than 30 years prior to the 1889–1896 rinderpest pandemic.

Ideal giraffe habitat, composed of arid savanna elements (*Acacia*, mopane, *Ziziphus, Combretum*) occurs from the Save area up the Buzi Valley to the Urema Trough thence to the arid valley of the Lower and Middle Zambezi in Mozambique and to beyond the confluence of the Luangua River. Yet a totally isolated population of giraffe occurs in the lower Luangua Trough (Ansell 1960, map D) with a suitable habitat link all the way south to the Limpopo.

In Chapter 7 the antiquity of concentrated human activity in Central Mozambique for gold, ivory and slaves was traced back to at least 1,400 BP, if not 2,400 BP. The major access routes to the interior and the Monomatapa Empire were up the Zambezi Valley and its tributary the Luenha-Mazoe which rises in Rhodesia. Other routes followed the Pungue and Revue valleys and spurs adjacent to Sofala. Giraffe 'riems' and meat were a major resource in the history of Africa and, as the tribesmen of this region all used arrows tipped with *Strophanthus kombe* poison, it is possible that this great gap in giraffe distribution is a long standing human artifact.

A similar anomalous gap in giraffe distribution existed in the vast thorn savanna area between Windhoek and Etosha in Namibia even at the time of Shortridge's first expeditions in the 1920s (1934, map facing p. 612). Vedder's (1966) historical record shows that Damaraland (then known as Hereroland) was a major route for ox wagons, and the southern sector down to Windhoek was the main theatre for the 20 year war between the Nama and Herero which ended in 1820. In addition, perusal of the series of wall maps exhibited in the Windhoek museum, depicting the growth of road and railway communications in the early 1900s radiating from Walvis Bay port and from the capital of Windhoek through Damaraland to Tsumeb, shows clearly that the Damaraland gap in many ungulate distribution patterns is probably a human artifact. The piles of bones at trlbal hunters' camps in northern Namibia and the Botswana border attest to giraffe being their most preferred prey, followed by eland (P. Stark pers. com.). These hunters used bow and arrows, with or without the aid of a plant poison derived from the latex of *Adenium boehmianum*, usually from horseback which made them doubly efficient.

In the early 1950s a few giraffe (about six) were introduced into Gorongosa National Park but were apparently all eventually taken by lions.

9.3 DISTRIBUTION, HABITAT, NUMBERS, BIOMASS

The salient feature of wild ungulate distribution to the ecosystem is their perennial concentration on the Rift Valley floor. In contrast, the adjacent miombo savanna and dambos of the Midlands and Cheringoma Plateau are extremely lightly stocked despite the presence of perennial water and the lack of human habitation over large areas. The miombo is however used more at certain seasons than at others by ungulates from the Rift floor.

The major ecosystem patterns (Fig. 6.1) and field data show that the main distribution of forest and thicket species is in the northern sector of the Rift floor and along the Riftward slopes of the Cheringoma Plateau. Nyala, suni and Sharpe's grysbok are commonest in these sectors, whilst bushbuck and red duiker are more ubiquitous, occurring in the forest areas as well as through all thicket patches in the Rift Valley savannas. Bushbuck are also abundant in the dense palm scrub thickets south of the Urema Plains. Blue duiker occur in the rainforest on Gorongosa Mountain with suni and red duiker in the forests on the Cheringoma cuesta.

Savanna and grassland ungulates are concentrated along riverine zones, and especially on the floodplain grasslands on the Rift floor. Waterbuck is one species that maintains a high year-round linear concentration on the flood and ebb margins of the Urema Lake and other waters.

Forest/Thicket Components

Bushbuck and red duiker are the most abundant dense-cover species throughout the ecosystem. In this area the southern (*Tragelaphus s. sylvaticus*) and western (*T. s. scriptus*) races of the bushbuck overlap with interesting habitat separation. The southern race is most common in the forested areas whilst the western race is characteristic of the palm thickets.

Suni occur in the smaller isolated dry forests, on the duplex sand patches of the Rift floor, but only where the field and ground layers are undamaged. In such areas suni typically occur within the forest precincts and red duiker occupy the forest margins and move out from one termitarium thicket to another. In the Zinave area of the Save River no red duiker occur and suni use all thicket habitats as do red duiker in Gorongosa (J.L.P.L. Tello pers. com.).

Kudu are uncommon but widely dispersed over the Rift floor and Midland valleys and hill areas. Nyala by contrast are confined to the dry forest and thickets of the Rift floor and to the Riftward foot slopes of the Cheringoma cuesta. They are most common from the centre of the Park northwards. Bushpig are abundant throughout the system from the mountain summits to mangrove margins, and are only absent (at least in the day) from the largest grasslands of the Urema floodplains and those on the coast.

Unfortunately, no quantitative data are available for the forest and thicket ungulates but a rough estimate of their zoomass contribution is included in Fig. 9.2. These species are mainly browsers (bushbuck, suni, red duiker, blue duiker, Sharpe's grysbok). The nyala is ditrophic and can be classified a browser (Tello & Van Gelder 1975) as in the Save area, or a mixed feeder as in Zululand (J. Anderson pers. com.). Mixed feeders are species in which grass is included as a major component of their diet in addition to browse. The bushpig is omnivorous as is the forest samango monkey. This primate occurs in all forest areas of the system, and in the Rift Valley uses the tall riverine thickets as well as venturing out from larger forest areas to feed or pass through the archipelagos of termitaria thickets. The most important predators in closed habitats are leopards which abound throughout the entire Gorongosa–Cheringoma area.

Savanna and Grassland Components

The large ungulate spectrum which inhabits both the savannas and the grasslands comprises 14 species of which the eight major species are listed in the biomass table (Table 9.2). The remainder includes grey duiker, impala, oribi, reedbuck, warthog and white rhino (re-introduced). Grey duiker are confined to the miombo savannas and are absent on the Rift Valley floor, at least within the bounds of the ecosystem. Impala are fairly common in the Rift Valley particularly in the southern sector at the junction of the Urema Plains with the marginal savannas. Oribi and reedbuck are abundant throughout the Rift Valley and sparse in the miombo–dambo terrain on either side. Warthog, though common and widespread on the Rift Valley floor, are nowhere abundant. A few occur in the adjacent miombo savannas particularly during the post-fire flush of grasses. After release in the southern sector of the park, the white rhino utilized both floodplain and savanna grasslands and were commonly observed on the ecotones between the two.

The most important predator in the open habitats of the ecosystem is the lion with an estimated population of about 200. Their greatest concentration is related to that of the large ungulates in the Rift Valley where prides of up to 30 individuals occur on the margins of the Urema Plains. Spotted hyaena are widespread but uncommon. Leopards, whilst being more commonly associated with closed habitats, are also found in any open terrain where tall grass patches or thicket clumps occur. They are the most ubiquitous of the carnivores, extending throughout the montane to mangrove transect. Wild dog, though rare, range through all the savannas and grassland areas except the mountain.

The major large ungulates, including elephant, are discussed individually in their order of biomass contribution (Table 9.2) but hippo are treated separately under a section on Aquatic Components. The zoomass contribution of the three large herbivore trophic groups is shown in Fig. 9.2.

TABLE 9.2
Total numbers of the major large herbivores recorded in six total air counts across the Gorongosa ecosystem.

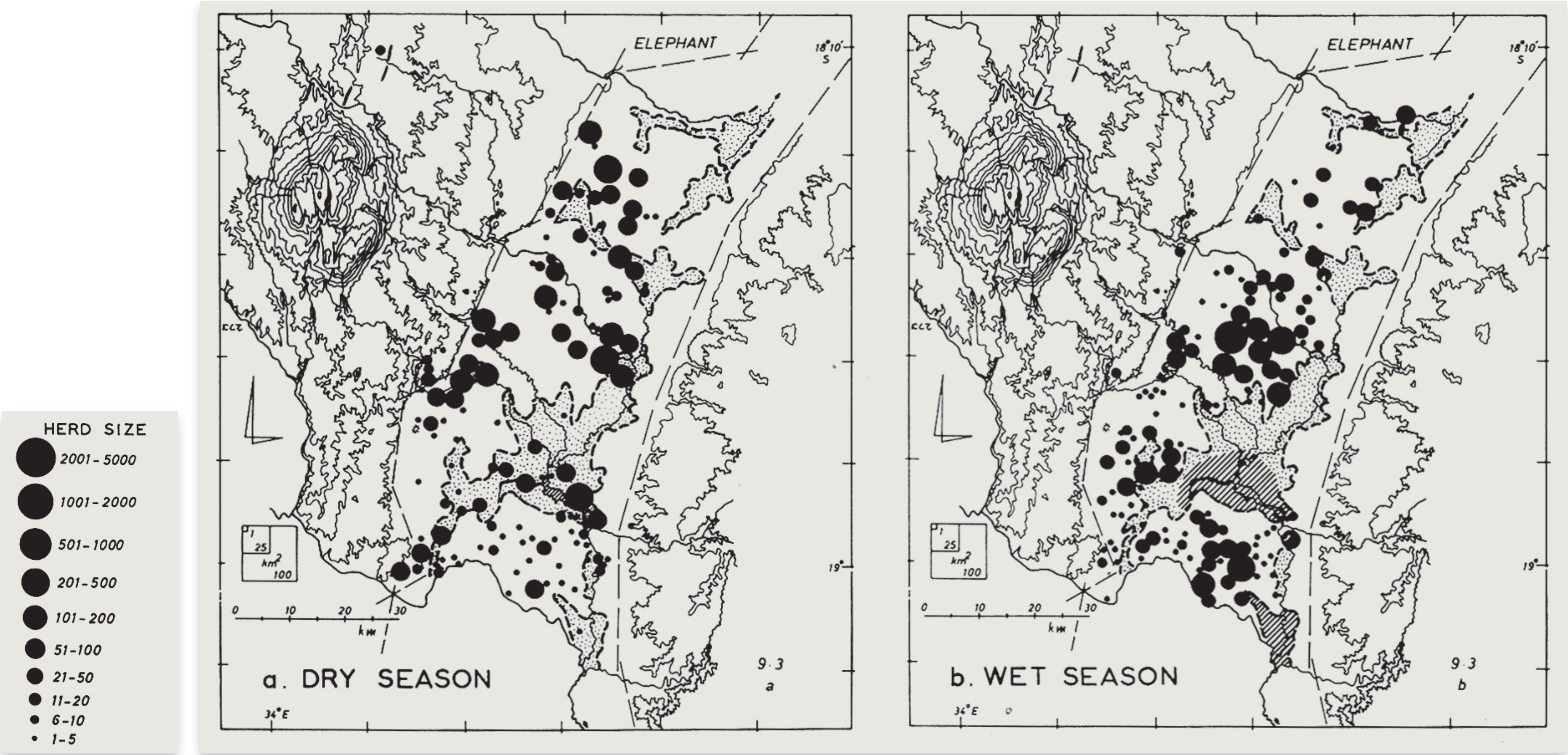
	DRY SEASON 1 NOV. 1968	WET SEASON 1 FEB. 1969	DRY SEASON 2 OCT. 1969	WET SEASON 2 JAN. 1970	WET SEASON 3 MAR. 1971	DRY SEASON 3 OCT. 1972
Elephant	1,555	1,634	2,072	2,185	1,401(?)	2,542
Buffalo	10,928	11,214	11,168	11,756	12,953	13,295
Wildebeest	3,020	2,989	2,734	7,060	5,618	6,427
Waterbuck	1,930	1,604	3,557	2,223	2,697	3,362
Zebra	1,196	2,899	2,391	3,583	2,938	3,331
Eland	134	226	342	429	356	126
Sable	436	84	628	361	352	483
Hartebeest	87	352	472	839	603	344
Hippo	2,972					3,483

Author’s co-observers in the air counts: J.L.P.L. Tello; F.C. Costa; S.J. Liversidge; T.P. Dutton

Elephant

Although grouped with open habitat species, elephant range through and utilize almost every habitat listed in the montane to mangrove transect. Their greatest year-round density is however associated with the tall grass *Acacia* savannas and riverine areas of the Rift Valley. Here three main riverine-associated concentration areas are habitually used over both dry and wet season peak periods: (1) Nhandue riverine zone, (2) western Vundudzl–Mucodza–Mupuaze riverine zones (western central margin of Rift floor below the Rift Sides), (3) Urema–Pungue riverine zone (Fig. 9.3).

These three areas take the brunt of high density and biomass for most of the year, attaining figures of three elephant/km^2 (or 10 tonnes/km^2). Habitat diversity in the three areas is similar, comprising a mosaic of tall acacia and mixed tree savanna with a tall *Panicum maximum* (robust form) herb layer and well developed termitaria thickets (3/ha), interspersed with seasonal pans, and the riverine strips of the rivers noted above. Marshes are confined to the riverine meander belt margins, the largest being the Mucodza marsh near the western margin of the Rift. This spectrum provides an abundance and diversity of fruit, browse and grazing. With the advent of fire the grass stratum is totally eliminated for several months over extensive areas, and excessive use or damage to the other habitats is buffered by the availability of green pastures in marsh areas.



RIGHT: Figure 9.3

Elephant—seasonal distribution and abundance.

LEFT:

Paul Dutton, ecologist and pilot, José Tello, Chief Warden, and myself with Paul's Super Cub, September 1968. Preparing for the first aerial census of big game in Gorongosa.

Unseasonal early thunder showers at the height of the dry season (Aug–Oct.) cause an almost overnight emigration to the areas where rain has fallen. If grasslands are previously burnt and beginning to show a post-fire flush, an unseasonal rain of more than 10 mm induces a magnified leaf production, but wilting can follow if no further precipitation occurs. The elephant then withdraw to the riverine zones again or move into the adjacent hill miombo. Examples of elephant feeding in miombo and on the Rift floor are included in Figs 9.17a, 9.18, 9.19a, 9.20a.

Figure 9.4
RIGHT:

Buffalo—seasonal distribution and abundance.

FAR RIGHT:

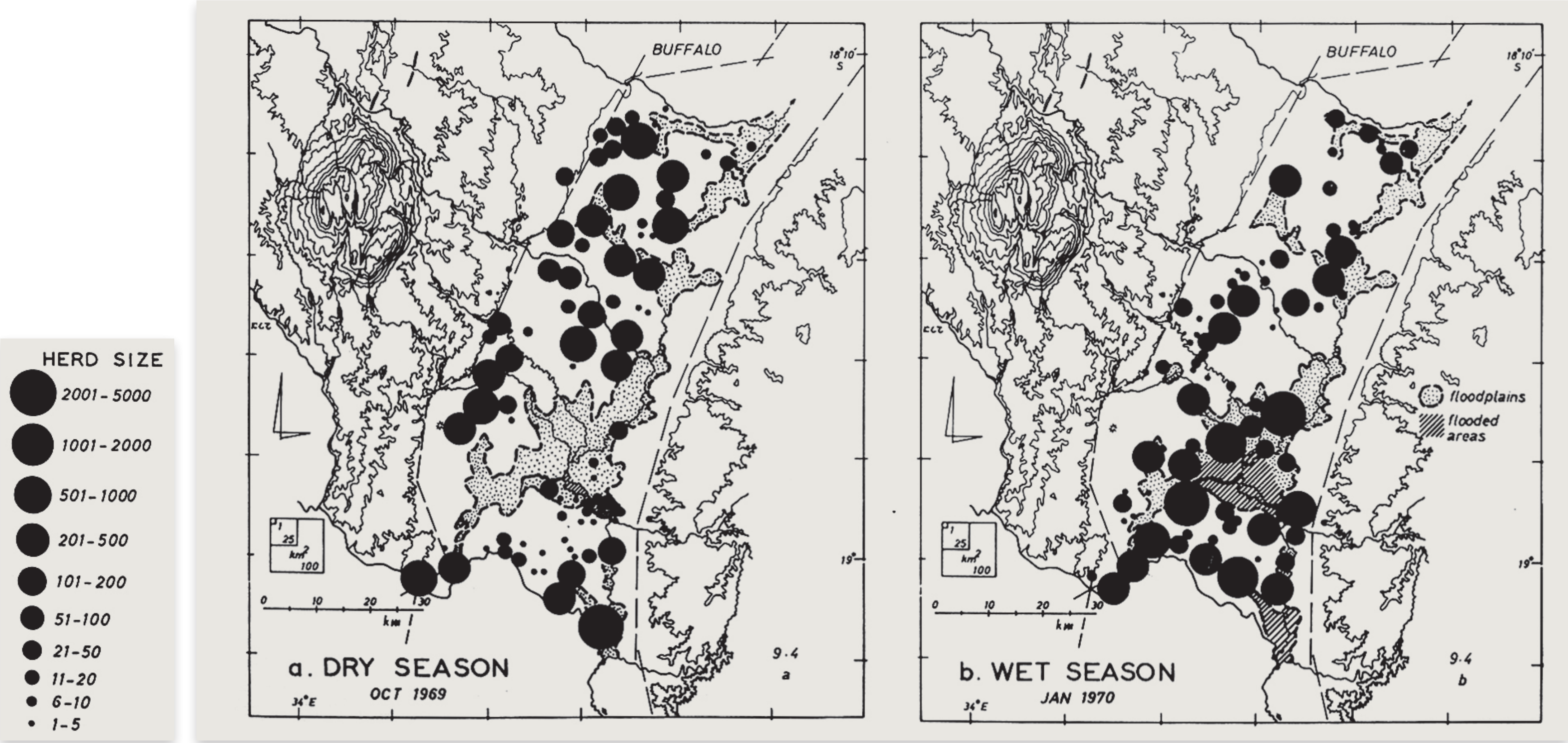
Buffalo and egrets, north of the lake.

Buffalo

The distribution and concentration areas of buffalo in the Rift Valley are remarkably similar to those of elephant (Fig. 9.4). In the dry season there are three main areas of concentration: (a) Nhandue riverine zone and adjacent Nhamisangu floodplain grassland area, (b) Mucodza marsh area (western Vundudzi–Mucodza–Mupuaze riverine zones in the west central sector of the Rift), (c) Dingedinge marsh in the Urema–Pungue confluence area (Fig. 9.4a). With the autumnal ebb of floodwaters a herd of nearly 2,000 buffalo becomes a permanent feature of the Goinha Plains (immediately north of the Urema Lake) which are *Setaria* floodplain grasslands. When these have dried out sufficiently to admit fire, in about June or July, the large herd breaks up into smaller groups which graze in the wooded margins of the plains and up onto the Cheringoma Plateau.

In the wet season a similar concentration is maintained with two main shifts. The Mucodza Marsh concentration fades and a major wet season centre is on the converging delta of the Mucodza and Vundudzi at the head of the Urema Lake, and on the median height floodplain grasslands west (Sungue) and southwest (Nhauranga) between the Sungue and Pungue River (Fig. 9.4b).

Between one and four herds containing more than 1,000 animals normally occur in both the dry and wet seasons. In contrast between three and six herds of this dimension are recorded in the Marromeu sector of the



Zambezi Delta grasslands (Tinley 1969b and unpublished air counts). Thus in the main concentration areas, buffalo biomass exceeds 1,600 tonnes/km^2 for the period in which herds up to 2,000 strong remain intact, moving and feeding through the median and tall grass pastures. The largest herds are all associated with marsh and riverine grasslands and move to adjacent sites in long columns.

Like elephant there is an immediate response by buffalo, in the dry season and first rains period, to move to any area where isolated thunderstorm rains have fallen. This is clearly portrayed by the spread of smaller herds into the waterless northern sector of the system between the Nhandue and Nhampaza Rivers after a thundershower; recorded by the air counts of November 1968 and October 1969. The exact limit of the isolated rain was demarcated by the limit of the herds, the adjacent unburnt and rainless area being quite devoid of large ungulates.

Buffalo are the most susceptible to starvation and high mortality when their pastures are dried out early in the autumn by drought conditions, and especially when the annual event of uncontrolled fires sweeps across the Rift floor. Elephant can turn to browse, and the other major species obtain sufficient nutrition from the remaining green zones of short microperennial grasses (*Cynodon dactylon* and *Digitaria swazilandensis*) in waters-edge zones. Due to an excessive population, hippo are the only exception to this amongst the short-grass feeders (see following section). Post-fire flush and wilted regrowth appear to be a main cause of excessive scouring (diarrhoea) in buffalo followed by death (possibly from prussic acid poisoning, also known as 'geilsiekte'—refer to section on mortality factors).

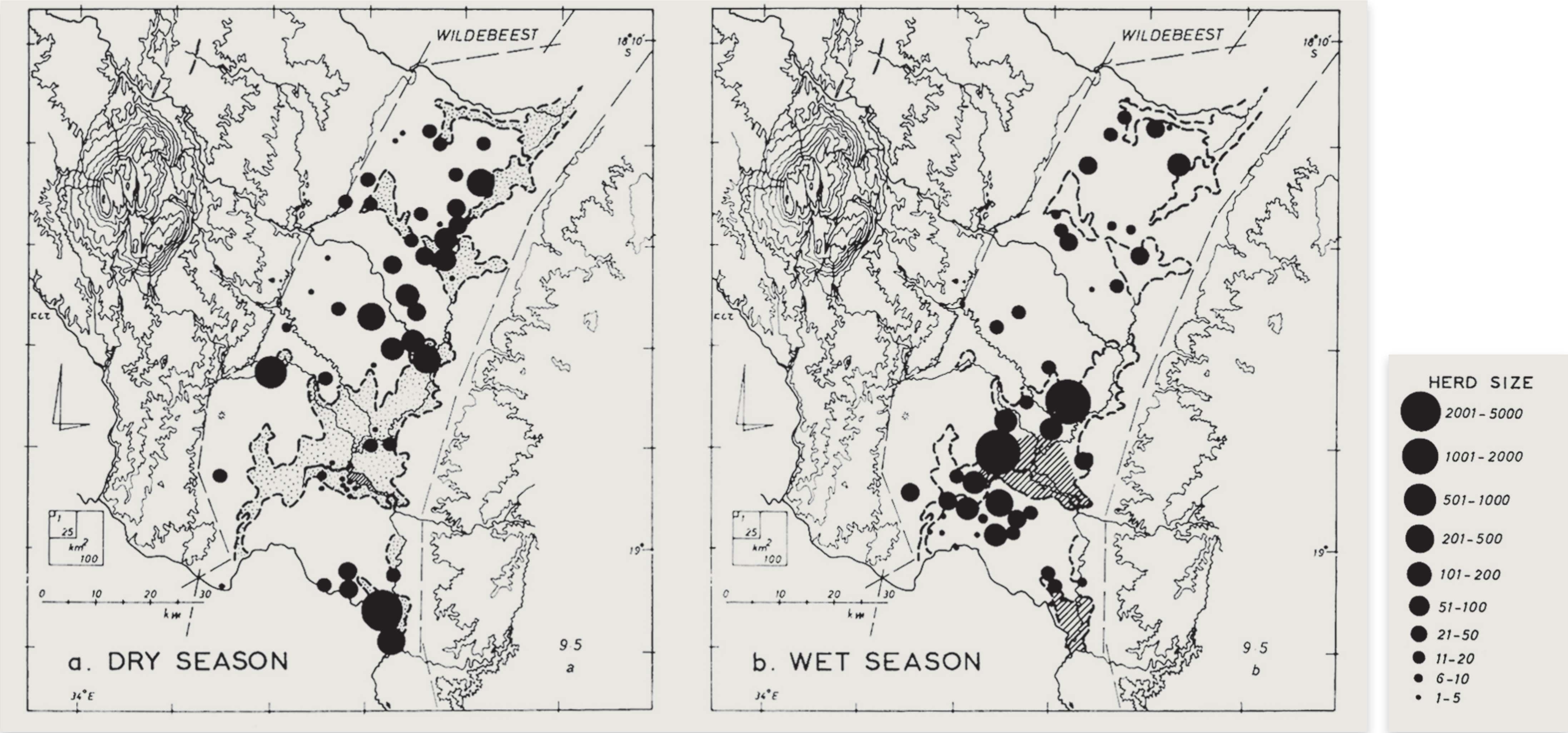
During midsummer whole buffalo herds often rest in pans and marshes from about 09h00 to 16h00 before moving out to graze for the night. However, in addition to ruminating, some local feeding takes place as the animals are lying amongst some of their important grass foods, *Echinochloa stagnina* and *Vossia cuspidata*. Two examples of buffalo grazing are included in Figs. 9.16a, b.

Wildebeest and zebra

As short and medium height pastures form a mosaic, and the short grasslands are taller during the rains, the distribution and concentration areas of wildebeest and zebra are generally coincident.

The major dry season concentration area for both species is the Dingedinge floodplain marshes (slacks) at the Urema–Pungue confluence. Other concentration areas centre about the Mucodza marsh in the central western margin of the Rift floor (Vundudzi–Mucodza–Mupuaze riverine areas), and alternate between the Macoreia Plains and those of the converging delta at the head of the Urema Lake (Figs. 9.5, 9.6). In some years the Nhandue riverine area (particularly where it enters the top end of the Macoreia Plain) and the adjacent Nhamisangu floodplain are important.

The wet season concentration patterns depend on the extent of flooding. Maximum spread of floods results in a linear concentration pattern in the abutting savannas, e.g. in the *Urochloa* median savanna grasslands between the Urema Plains and the Pungue (e.g. Jan. 1970). At this time zebra show separate concentrations on the Macoreia Plains, and on the margins of the Goinha Plains (Fig. 9.6b). In the north, other concentrations form in the lower Nhandue riverine zone and the grassland areas adjacent to the Lunga drainage and near the northern Nhamapaza River boundary. In wet seasons, with median to low flood, the main areas of concentration of both species is on the short grass plains south,



LEFT: Figure 9.5

Wildebeest—seasonal distribution and abundance.

RIGHT:

Wildebeest and impala on the floodplain.

FAR RIGHT:

Zebra in a mixed heard on the floodplain.

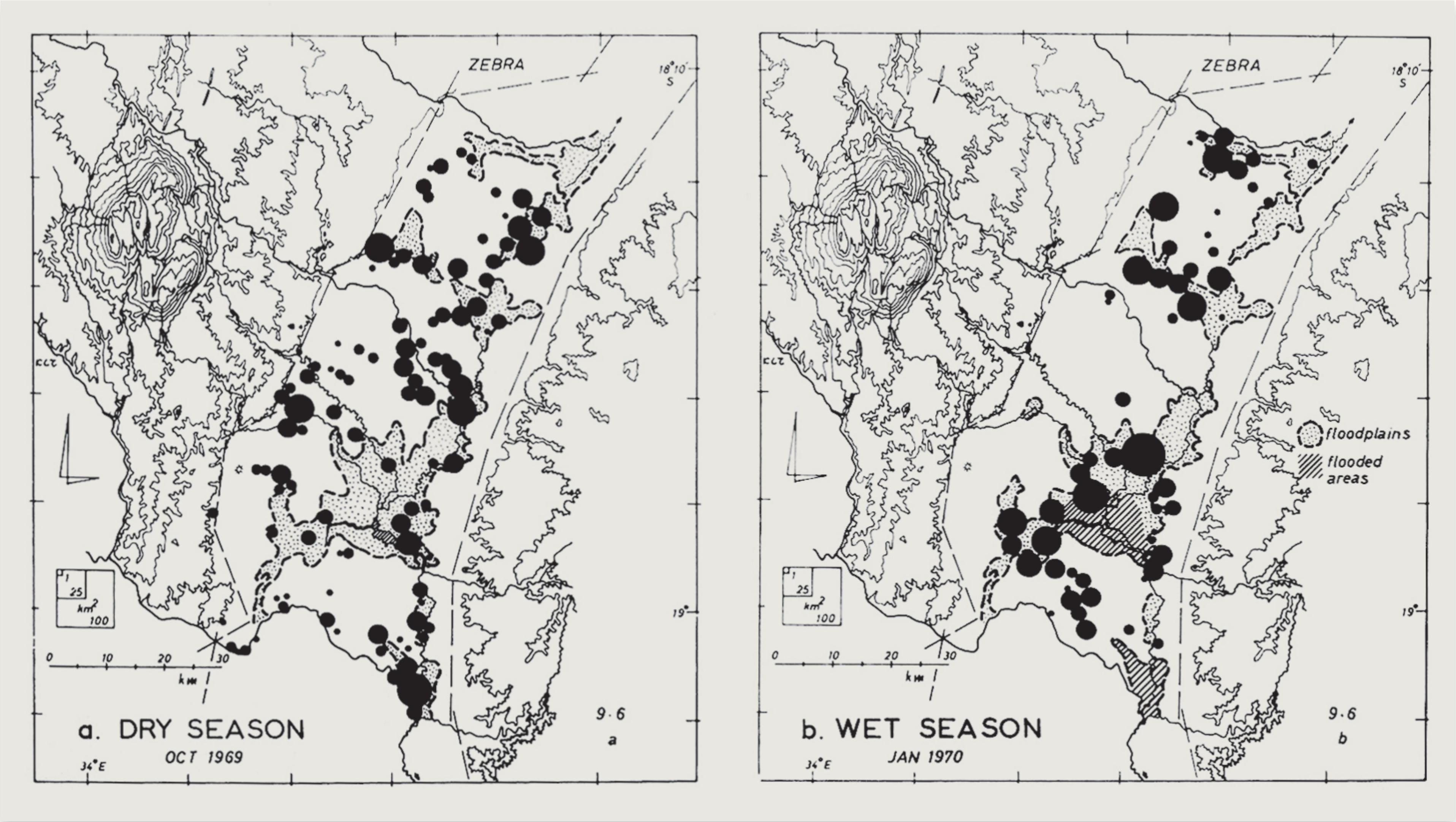
west and northwest of the Urema Lake (including the converging delta area and Macoreia).

Wildebeest and zebra, with Lichtenstein's hartebeest, are the first large herbivores to invade new areas of post-fire flush in the dry season, and like the species already dealt with, show an immediate migratory response to the occurrence of isolated, unseasonal rain. If the rain was too little to provide an adequate grass flush and surface water, the herds return to the riverine zones.

In numbers wildebeest have increased from about 3,000 in November 1968 to 7,000 in October 1972 (Table 9.2). In October 1969 the least number were counted (2,391) followed by a large influx in the dry 1969/70 summer to give the highest count of 7,060 animals in January 1970. Although inaccuracies are an inevitable artifact of total counts, these changes in number reflect immigration into the park and emigration from the remainder of the Rift Valley sector between the park and the Zambezi Valley, which is much drier and with rare surface water. Small localized herds, or no wildebeest, occur south of the Pungue or in the Midlands. In the summer rain months wildebeest densities attain 4.3 tonnes/km^2, and at the height of the dry season a quarter of this, 1.5 tonnes/km^2. Like waterbuck, wildebeest form concentrations of more than 100 animals at the two seasonal extremes, on marshland green zones in the dry season, and on the rains and/or flood-ebb flush of the short floodplain grasslands in summer and autumn.

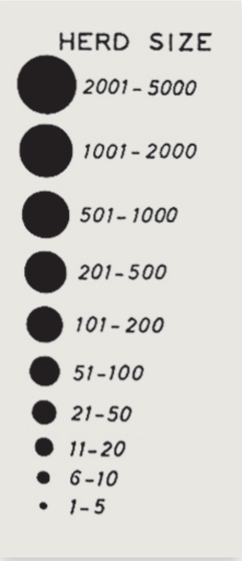
No wildebeest occur in the Zambezi Delta or on the Riftward slopes of the Cheringoma cuesta, nor is there any historical record of their having done so. Wildebeest migrations thus appear to be confined mainly to lengthwise movements along the Rift Valley. In the past they moved southward to the vast floodplain grasslands of the Pungue–Buzi confluence area, but now mostly northward to Dimba Marsh and possibly northwest up the Nhandue and other Midland valleys.

Zebra numbers in the five year period increased from about 1,196 (Nov. 1968) to 3,331 (October 1972). A regular pattern of greater numbers in the wet season and less in the dry season featured in every pair of dry-wet



LEFT: Figure 9.6

Zebra—seasonal distribution and abundance.



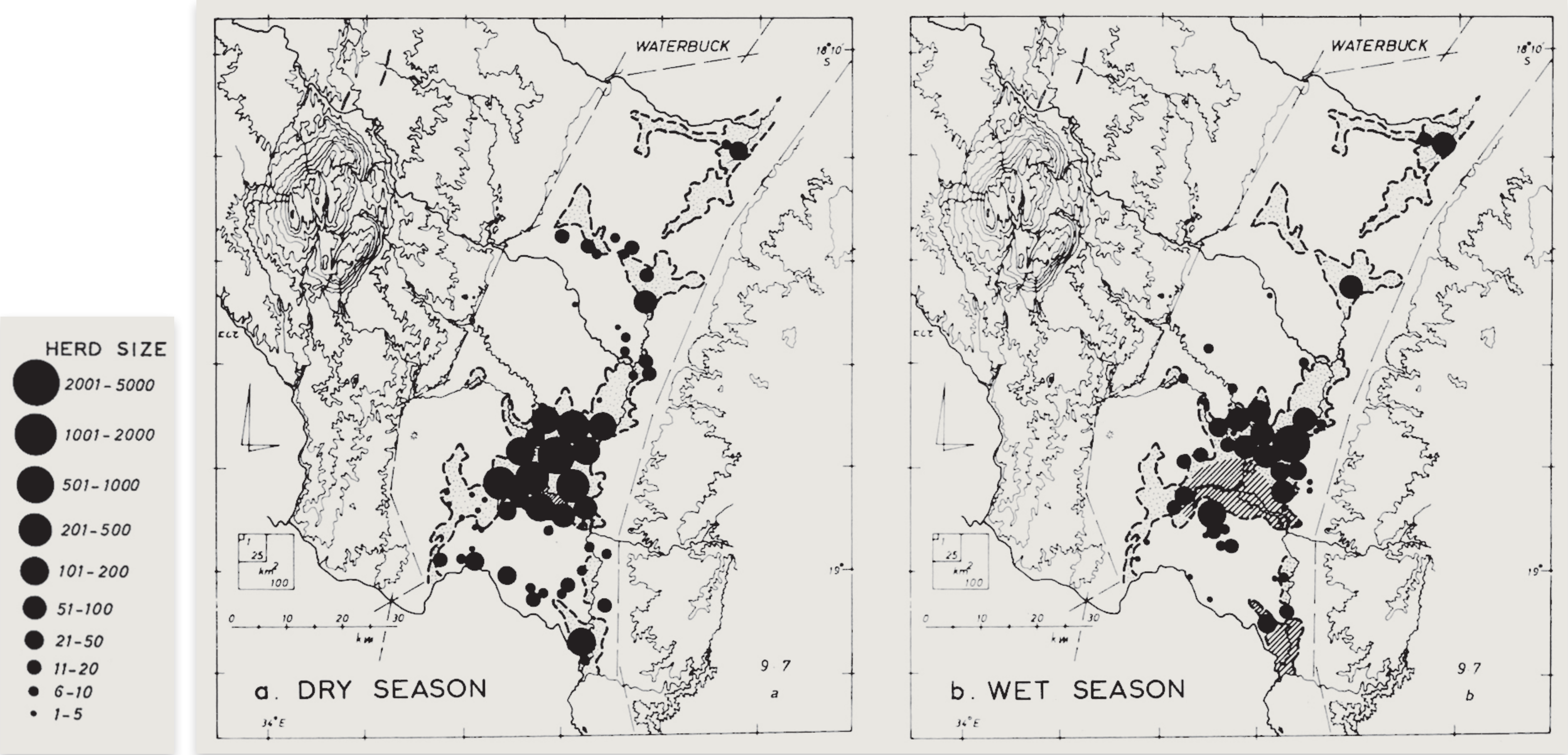
season counts. Certainly their merging more easily with the substrate in the dry season would have been a contributory factor to lower numbers being counted at this time. However this concentration pattern contrasts with that of waterbuck, which show greater numbers in the dry season and lowest in the rains although they are the most difficult species of all to count from the air in the dry season without the aid of oblique (early or late) sunlight.

In the rains period, zebra biomass attains 2 tonnes/km^2, and a third of this in the dry season, 0.6 tonnes/km^2. Unlike wildebeest and waterbuck, zebra only form large aggregations of more than a hundred animals on the rainy season pastures. In the dry season, concentrations in riverine and marshland areas seldom exceed groups of 30 animals. Zebra also move into post-fire flush areas of miombo and dambos on the adjacent plateaux in the late dry season, particularly if good unseasonal rains occur on the Midlands. It is suspected, but not known for certain, that there is a movement of zebra groups between the approximately 1,000 strong population of the Marromeu Buffalo Reserve in the Zambezi Delta and those on the Rift Valley, along the dambos of the Cheringoma Plateau during the dry season, particularly in the post-fire flush period in August.

Waterbuck

With the exception of hippo, which are tied to open waters, waterbuck have the most restricted dispersion of all the ungulates in the system. The major part of the population is confined to the green zone pastures which expand and contract with flood and ebb of the Urema Lake. Equally high concentrations of waterbuck are found at both seasonal extremes in a zone around the Urema Lake, especially in the converging delta area of the Mucodza, Vundudzi and Mucombeze streams (Fig. 9.7). This area supported the greatest densities in the dry season peak of 1968 and the following rains peak in February 1969, and again in October 1969 (Fig. 9.7a). Very few waterbuck occurred in the Dingedinge marsh area until the 1969 dry season, when large numbers were recorded for the first time in the dry season peaks of that year (Oct. 1969) and again in 1972.

During the rains and flood period there is a shift of concentration to the Macoreia tando (Feb. 1969) or to either side of the Mucombeze drainage on the Macoreia and Goinha tandos (Jan. 1970), and along the Sungue branch of the Urema Lake, (seasonally flooded or waterlogged grass plains or drainage lines are known locally as 'tandos'). There is also an outward radiation of herds from the Urema concentration area to the northern chain of tandos of Lunga, Nhamisangu and Tengane (Fig. 9.7b). Some herds move along the Rift Valley drainage as far as Dimba Marsh, 120 km north of the Urema and 40 km south of the



RIGHT: Figure 9.7

Waterbuck—seasonal distribution and abundance.

Zambezi River. The Dimba Marsh area has a flood and ebb regime similar to the Urema, but since the advent of Kariba Dam, it is totally reliant on summer rains. Had this marsh fallen within a protected zone, instead of forming part of the open hunting concession area, it would probably have been a centre of a major concentration area. However, during dry years the waters dry up altogether and this would force waterbuck and species such as buffalo, wildebeest, and zebra to move south to the Urema or to parts of the Zambezi River less settled by people.

As noted above, waterbuck numbers in the system are greatest during the dry season when there are lowest zebra numbers. Air counts showed an increase of waterbuck from 1,856 (Nov. 1968) to 3,382 (Oct. 1972) with the highest total of 3,557 animals recorded in February 1969 (Table 9.2). In the summer rains, season densities attain biomasses between 1 tonne and 2 tonnes/km^2 and the dry season concentrations only slightly less, 0.8 tonnes/km$^{2.}$

LEFT:

Waterbuck

© C Haagner

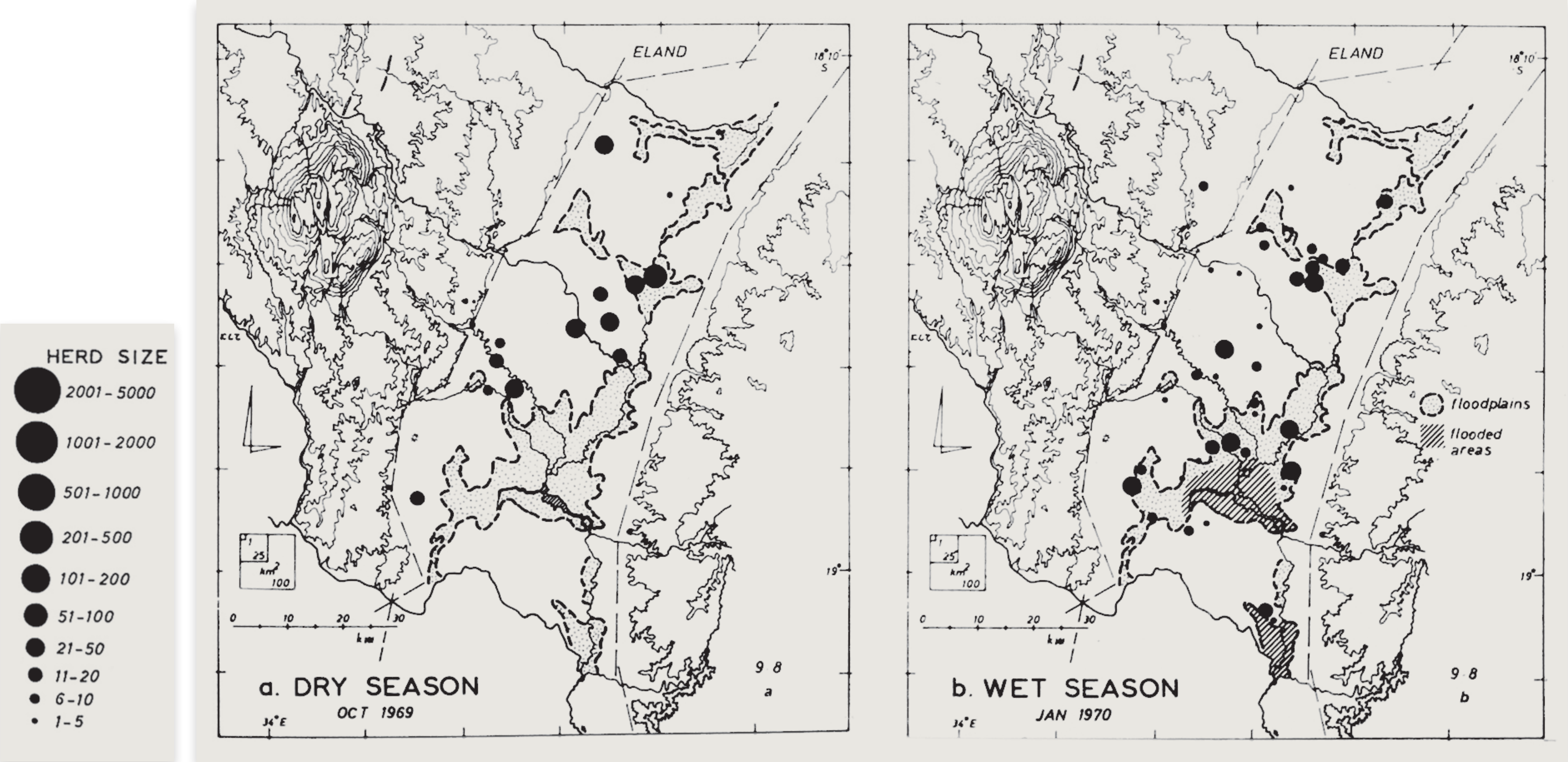
RIGHT: Figure 9.8

Eland—seasonal distribution and abundance.

Eland

Like sable and Lichtenstein's hartebeest, eland are found mainly down the central and western part of the Rift floor in the savannas and their tando grassland ecotones. Eland show large seasonal change in numbers, the most occurring in the summer rains period, and the least in the dry season when they are suspected to be north and northwest of the park in the dry Midland valleys such as those of the Macossa area (Fig. 9.8).

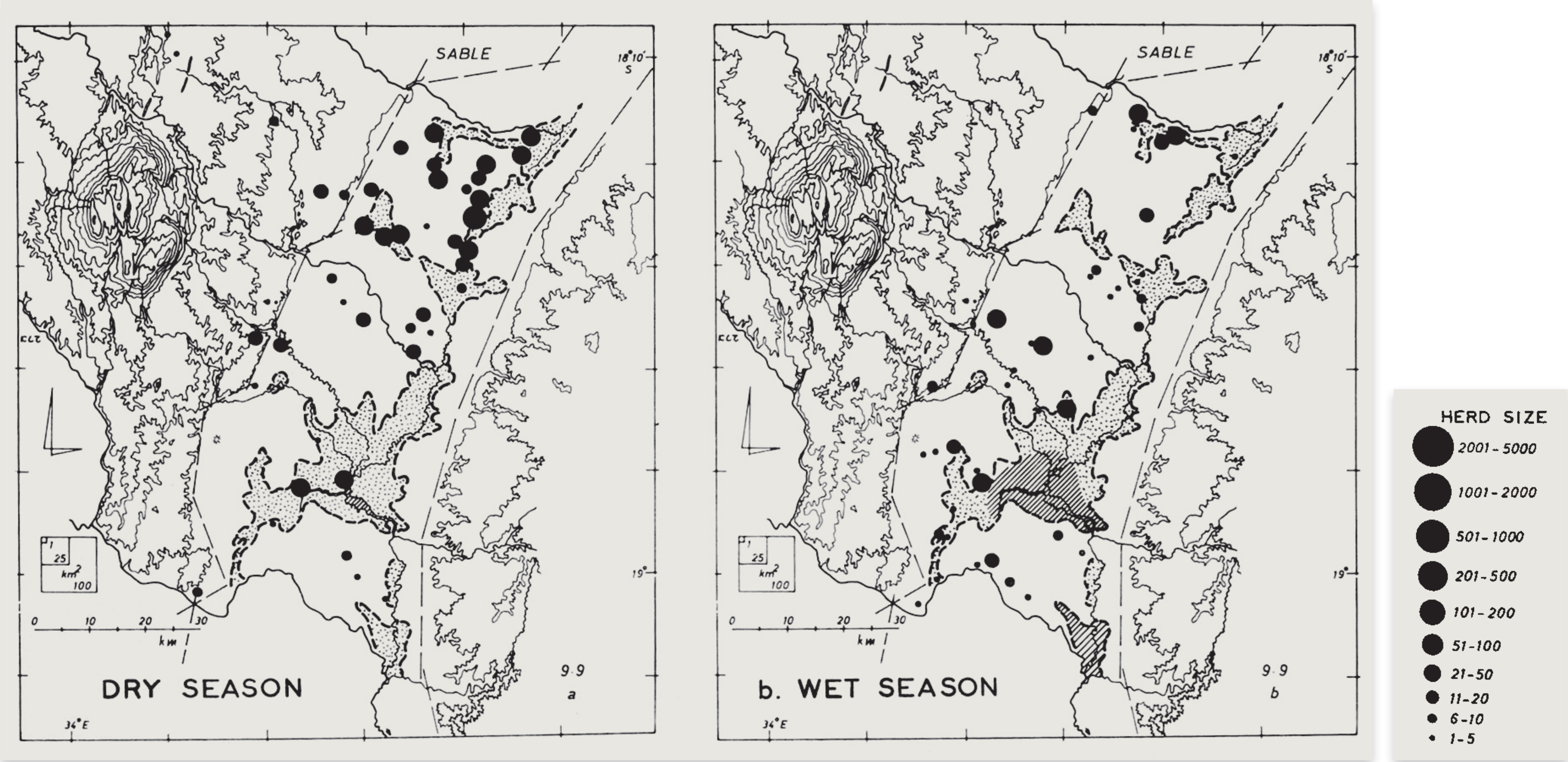
The largest herds (up to 90 animals) were encountered in the dry season but herds up to 50 strong are recorded at other seasons. In two dry season periods the majority of eland occurred in the lower Nhandue–Lunga–Nhamisangu tando area, below the Bunga inselbergs near the Vundudzi River, and across to the Mucodza Marsh area (Fig. 9.8a). In the wet season large numbers remained on the Lunga–Nhamisangu tando area and the remainder were in the savannas south of the Nhandue River to the Sungue tando west of the Urema Lake (Fig 9.8b). The largest herds contribute a zoomass of over 40 tonnes/ha when feeding in a group, or extending over some five hectares when spread out.



Sable and Lichtenstein's hartebeest

The largest numbers of sable occur on the Rift Valley floor in the dry season and the least in the wet season (Table 9.2, Fig 9.9). Sable and Lichtenstein's hartebeest untilize similar habitats preferring ecotones of savanna with dambos and floodplain grasslands. They also feed on the same grass species and the same parts of grasses. Unlike sable, however, the hartebeest are inveterate followers of burnt grassland, feeding on toasted basal parts and the first post-fire flush.

In the wet season there is a lateral upward movement of sable from the Rift into the miombo savannas of the Midlands and the Cheringoma Plateau. About the same time there is a downward movement of Lichtenstein's hartebeest from the uplands onto the Rift Valley floor resulting in a maximum of their numbers in the wet season, opposite to that of sable (Fig. 9.10). In the dry season the hartebeest move back into the the miombo and dambos of the uplands on either side of the Rift Valley—an opposing altidudinal movement similar to transhumance. Unfortunately no quantitative data from the uplands are available.

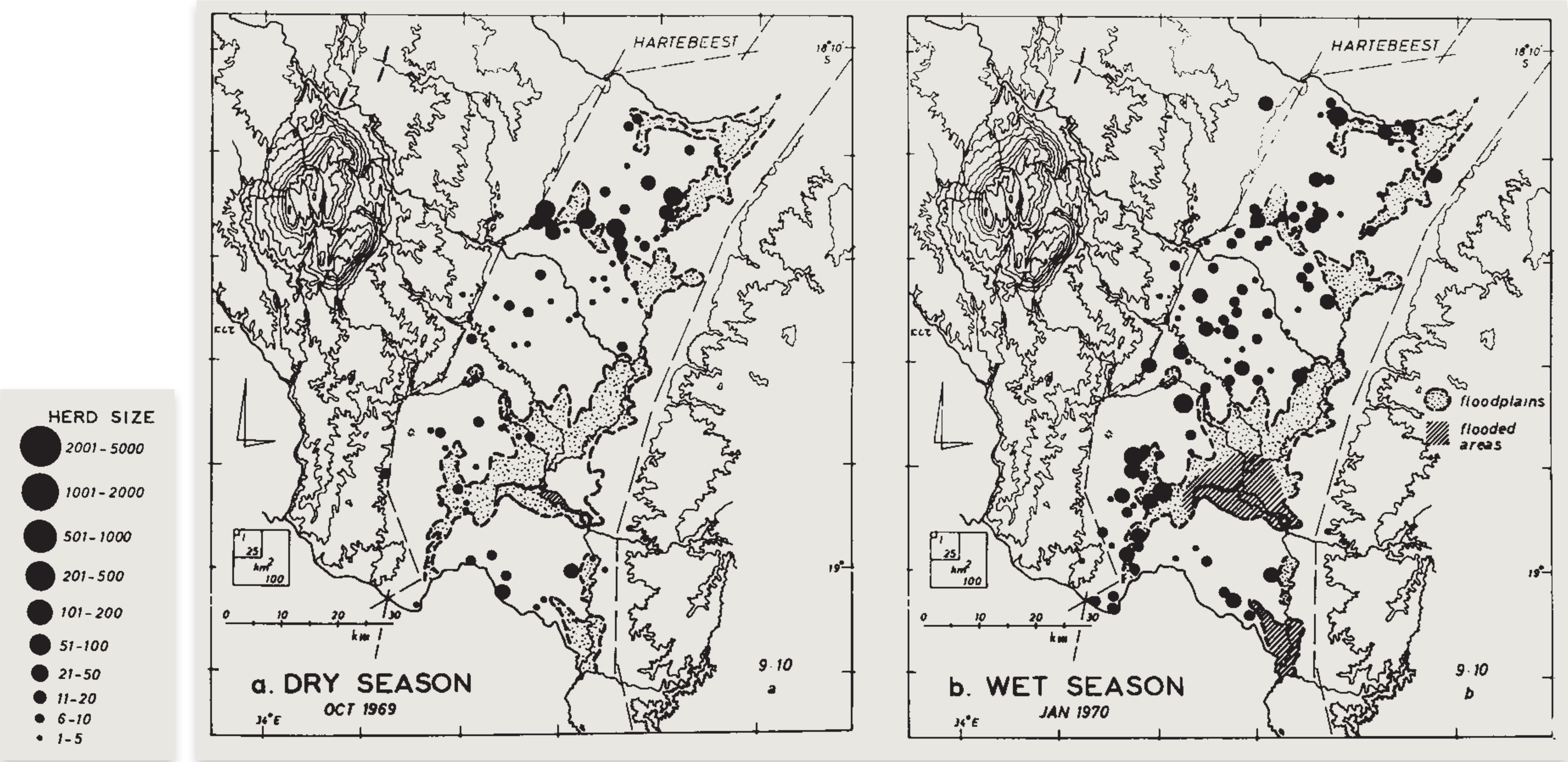


LEFT: Figure 9.9

Sable—seasonal distribution and abundance.

Although two herd sizes, 11 and 30, are most frequent amongst sable, groups containing up to 83 animals are recorded (October 1972), giving a biomass of some 6 tonnes/ha over the period they remain together. Lichtenstein's hartebeest also have two high, frequent herd size peaks of six and 12 but occasionally large gatherings of up to 72 animals occur (October 1972), providing about 3 tonnes/ha.

© Trail camera – Gorongosa monitoring network 2012



RIGHT: Figure 9.8

Lichtenstein's Hartebeest—seasonal distribution and abundance.

Impala

A first attempt was made to count impala from the air in February 1969 resulting in a total of 908. However this was discontinued as it proved too distracting for the observers to search out smaller animals whilst nine larger species were being recorded. Subsequently, in the October 1969 and January 1970 counts, only distribution of impala was noted. It was estimated that the impala population was between 1,500 and 2,000 in 1972.

In the autumn and dry season, large aggregations of impala occur on the micro-perennial floodplain grasslands to the south and west of the Urema Lake. Elsewhere they are in scattered groups on the savannas between the Urema and Pungue Rivers and on floodplain ecotones in Macoreia and Lunga in the centre and north. The wet season record shows impala herds spread out and scattered over most of the Rift Valley floor.

A more detailed account of the seasonal changes in impala numbers on a floodplain savanna junction is related in the section on floodplain rhythms. An example of impala grazing is included in Fig. 9.16d.

Distribution of impala in central Mozambique is in scattered herds up the Rift Valley to the Zambezi River and westward up the Zambezi Valley. Some are recorded slightly west of the Rift, up the dry valleys which lead into the trough from the Midlands. In 1970, professional hunters reported the first sightings of some impala in the southern (Marromeu) sector of the Zambezi Delta. These animals could only have moved downriver from where the Rift Valley crosses the Zambezi area near Vila Fantes. It is not known whether these animals have become established, or what the sex and age composition was of the first colonizers. In other areas subadult males are recorded as the first colonists of new locales.

Oribi

Quantitative data for small ungulates are available only for oribi which were counted from a vehicle whilst traversing floodplains and their ecotones with the marginal savannas south and west of the Urema Lake. A total of 390 oribi were encountered in 132 km^2 giving 3 oribi/km^2, or an approximate population of 11,000 for the Rift Valley floor alone, if a similar density is presumed throughout.

In the Urema sector, oribi exhibit an interesting but unexplained seasonal local movement in some years. From April until November family groups of two to three animals (65% of 145 groups) occur throughout both savannas and the floodplain grasslands. In some rainy seasons, from the end of November until March, oribi are totally absent from the floodplains irrespective of the level of flooding. At this time they are to be found in the adjacent tall grass savanna peripheral to the grassplains. It is suspected that this movement may be related to plagues of biting flies. The traverse of the floodplains and their savanna margins showed a higher density of oribi related to the ecotones between open grassland and savanna, the abrupt junctions of riverine thicket or termitaria thicket islands with the surrounding grassland, and junctions between short and long grassland.

Aquatic Components

Of the five ungulates in Africa which are tied strictly to water though they feed out from this base, only hippo occur in Mozambique. The others are pygmy hippo, water chevrotain, lechwe and sitatunga. The latter two occur within 200 km and 80 km respectively from the north-western corner of Mozambique (Tete District) above the Muchinga–Gwembe escarpment of the Luangwa–Middle Zambezi Trough.

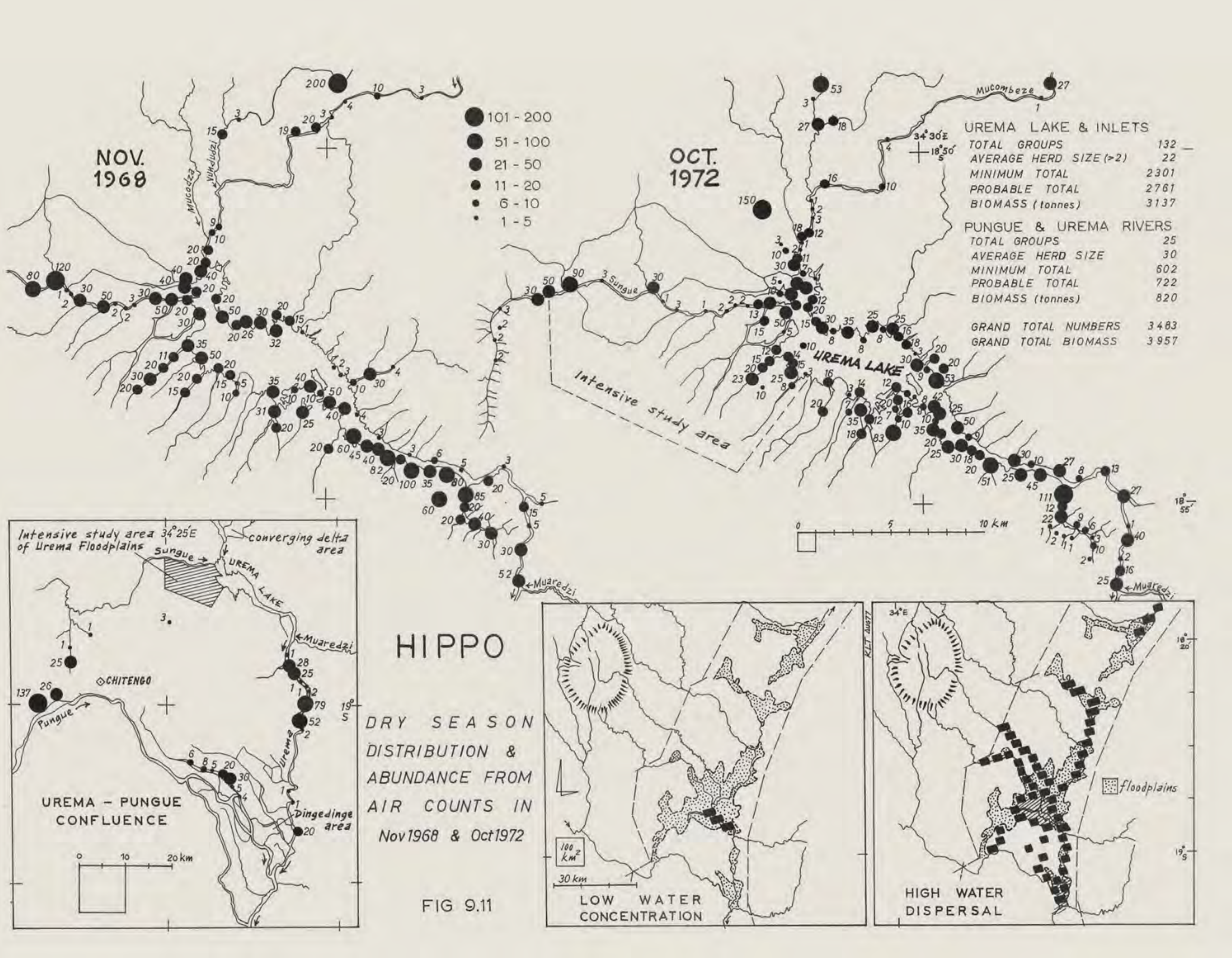
Some 3,500 hippo occur in the Gorongosa ecosystem of which 2,761 (80%) are confined to the margins of Urema Lake. This represents the single largest hippo population remaining in Mozambique today. A first air count of hippo in the Urema Lake in November 1968 realized a minimum total of 2,250 (Fig 9.11). The steady state of the Urema populations, in which little change had occurred after a five-year interval, is significant.

A second air count five years later, in October 1972, recorded a minimum total of 2,301 hippo in the Urema Lake and a probable total of 2,761, as corrected from vertical air photographs. This gives 209 tonnes/km^2 of lake or 3,316 tonnes biomass in a lake area of 15 km^2. In the last count of all the waterways in Gorongosa an additional 722 (820 tonnes biomass) occurred in the Urema and Pungue Rivers and their old meanders realising a grand total of 3,483 (Fig 9.11). The steady state of the Urema populations, in which little change had occurred after a five year interval, is significant.

The distribution of hippo at the dry season peak in November 1968 and October 1972 contrasts with the situation in the rains and flood period (Fig. 9.11). At this time an extensive spread of hippo occurs outward from the

RIGHT: Figure 9.11

Hippo—seasonal distribution and abundance.



HIPPO

DRY SEASON DISTRIBUTION & ABUNDANCE FROM AIR COUNTS IN Nov1968 & Oct1972

FIG 9.11

Urema Lake up the Mucodza, Vundudzi and Mucombeze rivers as far north as Lunga Pan, and single animals occupy rain-filled pans in the savannas. During high floods, hippo herds are still distributed peripherally along the floodplain–savanna junction where they trample depressions in their favourite lying-up sites which form pans when floodwaters ebb, and are rain-filled in low flood years.

In November 1968 the average herd size in the Urema Lake was 35, and 25 in October 1972, as opposed to the larger average herd size in the rivers. Hippo paths radiate 10 km out from permanent waters, which includes virtually all the country between the lake and the Pungue River as grazing grounds.

Rock Outcrop Components

Four wild ungulates in Africa are closely associated with rock outcrop habitats: Barbary sheep, beira, ibex and klipspringer. Of these only the last occurs in Africa south of Abyssinia, accompanied by the rock dassie *Procavia capensis* and yellow-spotted dassie *Heterohyrax brucei* (Dorst & Dandelot 1970).

In Gorongosa, klipspringer occur on the mountain and its satellite inselbergs as well as on inconspicuous outcrops within the Midland miombo. There is no record of them from east of the Rift Valley in the ravines of the Cheringoma cuesta. The two dassies occur on the mountain, where they were collected from the same outcrop on Gogogo summit, as well as on the inselbergs. Klipspringer spoor were found in savanna plains-land between inselbergs and they and dassie must move between isolated rock outcrops, which are within sight, and so they are probably more explorative than is generally realised.

Summary of Distribution and Density Patterns

Four main distributional and density (high biomass) patterns are exhibited by the large wild ungulates in the ecosystem, each pattern shared by at least one pair of species due to similar trophic and habitat requirements (Figs 9.12, 9.13).

(1) Riverine zones and medium to tall grass marsh areas characterized by elephant and buffalo. Four main localities for this distributional pattern occur on the Rift Floor: (a) Nhandue River, (b) Vundudzi–Mucodza–Mupuaze Riverine area on the western margin of the Rift Floor, (c) Urema –Pungue, and (d) the Mucodza, Goinha (northern margin of Urema Lake) and Dingedinge slack marshes.

(2) Medium to short floodplain grasslands (including marsh areas which dry out late in the dry season) characterised by wildebeest and zebra which form a concentration pattern related to the nutritional status of the floodplain grasslands. These animals migrate between floodplain areas higher or lower in the flood-ebb catena. Main dry season concentration areas are all the tandos surrounding the Urema Lake and the rivers entering it from the north (i.e. Macoreia, converging delta, Sungue, South Urema) and, especially, the Dingedinge slack grasslands at the Urema–Pungue confluence. In the wet season the main congregations of wildebeest and zebra occur on the higher levels of the floodplain grasslands, again associated with the Urema Lake and the rivers entering it, as well as on the tando between the Nhandue and Nhamapaza Rivers in the north (Nhamisangu, Tengane, Lunga). In the wet season, inundation of the Dingedinge area excludes most wildlife but only in exceptional flood years (e.g. 1966/67, 1969/70, 1973/74) are the herds excluded from the other floodplains during which time they form a linear concentration in the adjacent savannas.

(3) Circum-Urema Lake floodplain grasslands; an all year concentration of waterbuck and hippo, which expands and contracts with the spread and ebb of flood waters. Waterbuck exhibit a periodic change of concentration around the lake and its associated tandos, rotating their grazing grounds. They also exhibit a seasonally contrasting population density pattern to zebra, due perhaps more to migratory flux of the latter. The largest number of waterbuck occur on the Rift floor during the dry season when there are the least number of zebra—in the wet season it is the opposite.

(4) Savanna dambo mosaic of medium to tall grasslands with seasonally reversed density patterns on the topocatena of the Rift floor and adjacent plateaux. Characterised by sable and Lichtenstein's hartebeest, the most sable occurring on the Rift floor in the dry season and the most hartebeest in the same area in the wet season, with reciprocal changes of abundance in the adjacent miombo hill country.

Two lesser patterns are related to (a) the forest/thicket ecosystem-type and (b) to rock outcrops. These habitats may assume considerable areal importance but, due to the territorial behaviour of the ungulates which inhabit them, groups are spaced and rarely assume more than local high density. However, kudu and nyala are two closed-cover components which can attain high population densities resulting in habitat damage, thus the term 'local' depends on the dimension of the closed cover habitat.

(a) The forest/thicket pattern is relatively the most sedentary compared to the extensive movement and migrations undertaken by some of the larger open country ungulates. However, considerable local movement occurs outward from larger forest/thicket areas along riverine zones with 'island hopping' through the archipelagos of termitaria thickets. In this pattern, kudu show the most extensive mobility and exploration.

(b) Rock Outcrop pattern. Gorongosa Mountain and its satellite inselbergs on the west of the system, characterised by klipspringer and rock dassies.

The total patterns of the principal large wild ungulates for the two seasonal extremes are shown in Figs 9.12 and 9.13 which emphasize the fundamental role of riverine zones, floodplain grasslands and marshes at both extremes. The major biomass concentrations are thus supported by the pastures of the base saturated alluvial soils (**Ah**). In the rains there is a spread from these high density areas to the intervening savanna-termitaria thicket-rain pan complexes, mostly on the better drained sandy clay loam **Chd** and **Cd** soils with medium to high phosphorus content and poor base status. If midsummer droughts occur, the herds return to the hygrophilous grasslands. Biomass figures of the principal large ungulates is given in Table 10.3

9.4 FLOODPLAIN FLUCTUATIONS

The series of maps depicting seasonal changes in distribution and density of the principal large ungulates emphasizes the key role of floodplain and riverine zones as a food base. The drought conditions experienced in 1968, exacerbated by a midsummer drought (Feb. 1969), were followed by extreme flood conditions in the summer of 1969/70 when the Urema Plains were flooded into the peripheral savanna tree-line for nearly two months.

After this extreme sequence, a 20 km^2 section of the Urema floodplain was chosen for its year-round accessibility on which to record the effects of fluctuations in the life-supporting floodplain ecosystem. This intensive study area extended from the southwestern shores of the Urema Lake and its Sungue arm, south to the marginal woods of fever tree and winter thorn. Total counts of all ungulates were made at two-weekly intervals for one year (3 Feb. 1969 to 11 March 1970) with December 1969 omitted. As this study area fell within the sector most frequented by tourist vehicles, the animals were conditioned to close approach and this allowed for easy counting. Counting was done from the roof of a Land Rover station wagon with the aid of x10 binoculars. As various parts of the floodplain are clearly demarcated by incised hippo paths, and the mosaic of shallow slack areas supporting taller hygrophilous grasses within the larger areas of micro-perennial swards, no problems of double counting arose. As warthog were rare to absent, they were omitted from the final analysis (Fig. 9.14), as were oribi which show only local seasonal movement.

Features

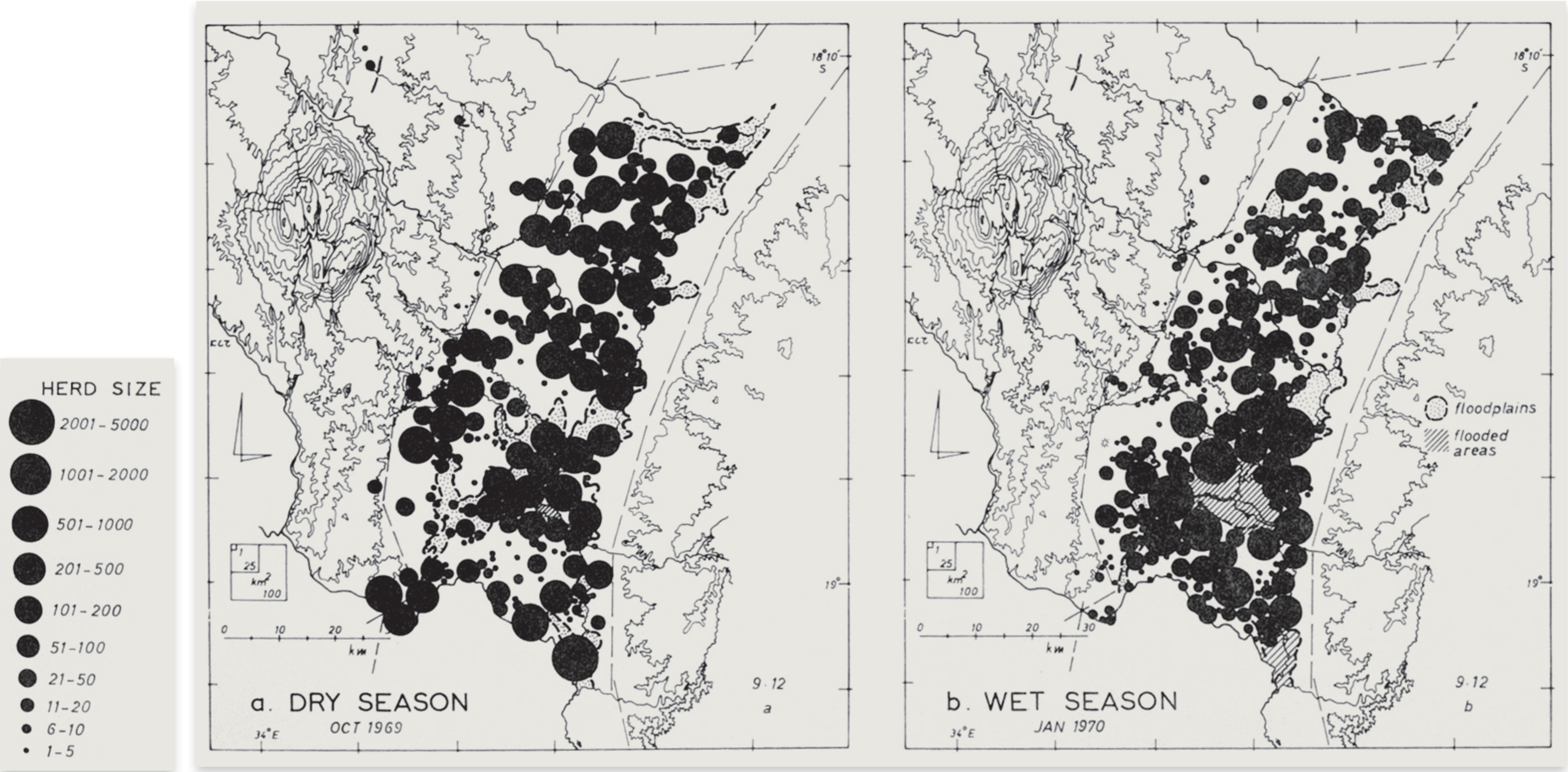
The floodplains dip at about 1^0 from the tree line to the lake margin and this is traversed by seven major hippo paths, which are more deeply cut towards the lake and less so on the upper margins of the floodplain. The greater part of the plain surface is flat to faintly undulating and covered by two short perennial creeping grasses *Cynodon dactylon* and *Digitaria swazilandensis* with an average height of 5 cm over the greater part of the year, but attaining 20 cm during the rains and when flooded. Several shallow basins, from a quarter to half a hectare in extent, occur in the upper sector and these support the aquatic hygrophilous grasses *Echinochloa stagnina* and *Vossia cuspidata,* which attain more than 50 cm in height in the rains. If flooded, the two species form floating meadows over extensive areas of the floodwaters. These basins are joined to the similar lower lake shore zone by shallow drainage line depressions, mostly incised by hippo paths. The channels formed by the paths are rounded along their edges by erosion and support dense growths of the two aquatic grasses. In total the poorly drained sites with taller grass cover occupy about 8 km^2, and the well drained short grass area about 12 km^2. On the southwest margin small patches of tufted *Eragrostis atrovirens* occur, and in the west, adjoining the Sungue, is a dense sward of *Panicum coloratum* over 1 m high in summer and lodging to half this height in the dry season. See Section 8.5 for a detailed analysis of this floodplain sector. The degree of pasture utilization by ungulates in the same area is dealt with in this section, and that following, on food, feeding and condition (Section 9.5).

Fluctuations

Floodplain ecosystems are in a constant state of flux as seasonal changes vary from year to year in intensity and duration. Unlike dry land systems, which totally depend on direct rainfall and the moisture balance achieved with a particular substrate, floodplain dynamics are controlled by runoff from afar as well as by direct precipitation. The wetting and drying sequence on floodplains is thus a function of: (a) fluctuations in precipitation and runoff in distant catchments, (b) their own dimensions and (c) their drainage status.

In large floodplain systems, such as the Okavango Delta and Kafue Flats, there is a much longer time lag between the peak in flooding at the top end of the system and that at the lower end. In the Okavango, peak flooding at the beginning of the delta occurs in February/March and five months later in July/August at Maun, 256 km downstream at the termination of the delta (Wellington 1955, Tinley 1966). Although the Kafue Flats are of the same order of length as the Okavango Delta, they are only 45 km at their broadest compared to 176 km in the Okavango Delta, hence there is half the time lag. There is about 2.5 months lag between peak flooding at the flats' commencement in March and at its lower end in May/June (Sheppe & Osborn 1971). The ebb is also of much longer duration in the larger systems as the drying sequence follows after the flood peaks from the upper to the lower end of the system. Because of their dimensions alone therefore, large floodplains have a built-in inertia to water loss and thus provide green pastures throughout the dry season and into the torrid pre-rains period, August to October. Only exceptionally high floods exclude the majority of ungulates from these floodplain pastures in mid-winter.

The effectivity of smaller floodplain systems such as the Urema in providing unseasonal green pastures for wildlife are thus most critically related to the drainage status of their depressions. If they are unbreached, shallow bodies of water of various dimensions are left behind which provide a contracting zone of green flush as the waters dry up. However, if they are breached by channels, both the amount and temporal spread of hygrophilous grassland productivity is greatly reduced to little better than that of the adjoining savannas.



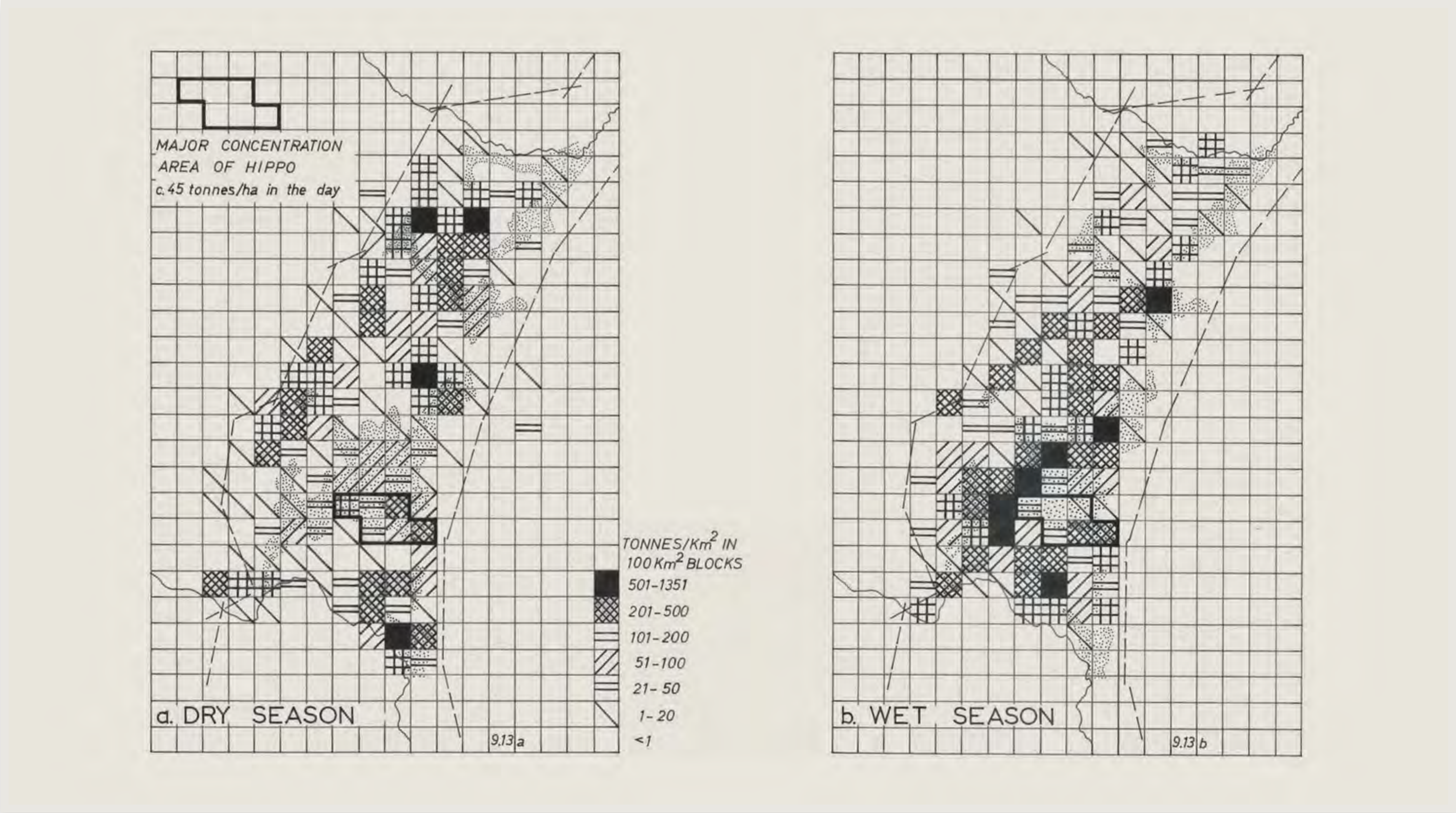
RIGHT: Figure 9.12

Total concentration patterns of the wild ungulates.

The wetting and drying sequence over floodplain microrelief is the reverse of that which the system experiences as a whole, described above for the Okavango and Kafue. The lowest parts are flooded first and are exposed last on the ebb, whereas the highest parts are flooded last and exposed first. Thus a spatial sequence is superimposed on a micro-topographic sequence. The intensity and duration of this superimposed sequence influences primary productivity, plant and animal phenological events, phyto-zoomass relationships, and successional dynamics of floodplain and dry land components.

Due to their relatively small size and close proximity to the Gorongosa Mountain catchment, flood and ebb responses on the Urema Plains are sensitive to changes in precipitation and runoff from the Mountain and in the Rift Valley itself. Maximal flooding on the Urema Plains, lasting from eight to 10 weeks in the period January to March, occurs some two months after the beginning of the rains. Compared to the rapid flood rise to a maximal spread, the ebb lasts for twice as long from two to five months (the latter in the lowest slack areas) depending on how slow or rapid rains tail-off on the Mountain in the autumn.

When the Urema Lake floods, water spreads outward up all the channels and basins first and inundates the upper depressions before coalescing across the short



LEFT: Figure 9.13

Biomass during the dry and wet season.

Water to the horizon of the Urema Plains in high flood years (summer 1969/70)

grasslands and extending up to 300 m into the marginal fever tree, winter thorn and palm savannas. The ebb sequence is in reverse, the first sites to be exposed are the upper margins and convex surfaces which flush first in response to re-exposure. The last to be exposed are the floating mats of aquatic grasses, which are left stranded on top of the short grasses, but are soon eaten back to the receding water's edge. Termite hills usually remain exposed as small islands during high floods but the lower eroded hills are flooded. Depending on extent of flooding and speed of ebb, through rapid loss of water along channels, the drying sequence can be fast (2 months) or slower when the lowest slack areas dry out only at the most arid part of the year, providing a last green flush before the rains. However, as pointed out in the chapter on hydrography (Ch. 5.6), most of the depressions in the Gorongosa ecosystems are breached by hippo paths if not by natural headward erosion of nickpoints. Thus the areal extent of unseasonal green pastures has been reduced to a very narrow margin or edge in most sectors, except the flattest mudflats adjoining the dry season level of the Urema Lake. On the other hand, floodwaters which are too deep, or lie too long, kill off the inundated grass cover if this is not composed of hygrophilous species, resulting in extensive bare mudflats. These bare areas are then invaded by dense swards of mudflat weed communities, (components of which are used by some of the herbivores), and later by the creeping *Cynodon* and *Digitaria* from the margins or from root bases which had survived long flooding.

Grassland and Grazing Succession

Flood and ebb of varying intensity in every year imposes a succession of flush and availability of different grassland types to which is a closely related succession of large ungulates. The succession of grazers is a function of the feeding level preferences in each species and thus the growth form of each stage in the grasslands.

By grazing down rank pastures, the coarse grass feeders, elephant and buffalo, enhance grazing conditions for the medium to short grass feeders. First described by Vesey-Fitzgerald (1960, pp. 161–172) from floodplains of the Rukwa Trough, this relationship has been neatly quantified by Gwynne and Bell (1968, pp. 390–393) for the sequence zebra, wildebeest, Thomson's gazelle in the Serengeti ecosystem, Tanzania. In Gorongosa the grazing succession of species is elephant and buffalo first, on rank or coarse pastures, followed by zebra, then wildebeest, waterbuck and impala.

Where the passage of elephant or buffalo herds have flattened swathes through 3 m high grassland, the same succession of species occurs following the exposure of two subordinate soft-leaved grasses and the basal regrowth of the large grasses. These areas are also attractive to sable, Lichtenstein's hartebeest, reedbuck and oribi.

High flood patterns

All the grasslands in the system flush with the first rains in November, although extensive areas of post-fire growth wither in the torrid period. For the first two months of the rains the floodplains support high concentrations of large herbivores—elephant and buffalo on the margins of depressions and channels, zebra on the medium swards and wildebeest and waterbuck on the shorter grasslands, in a mosaic fitting that of the different pasture types.

As the floodwaters spread outwards, the herds move back in linear concentration using the still exposed floodplain margins, or they are forced back into the adjoining savannas. In the adjacent savannas the pastures used most by the herds are those dominated by *Urochloa mosambicensis, Digitaria milanjiana, Panicum coloratum* and *P. maximum*. The coarse grass feeders also concentrate on the hygrophilous grasses of depressions in the savanna. Some of these grasses, particularly *Urochloa,* become dominant in basal area, if not in quantity, by heavy ungulate use. In such circumstances there is a change in growth form, the flowering culms are procumbent as opposed to the usual erect growth form when there is no grazing pressure, and vegetative growth is maximal. The short *Cynodon dactylon–Digitaria swazilandensis* grassland become

RIGHT:

View west of the southern margin of the Urema Plains from above the lake's eastern end. In the foreground shallowly flooded short grass *Cynodon-Digitaria* grassland on a concave surface traversed by hippo paths. Leafless winterthorn woodlands in middle distance and Road 4 area in background.

CENTRE:

View north of the Urema Plains from above its southern margin (Road 4 area). Floating pastures of *Echinocloa stagnina* and *Vossia cuspidata* in the background. In the foreground termite hill islands, winterthorn on sand, and palm on saline clay convexities of alluvio-catena.

FAR RIGHT:

View northeast of inundated marginal floodplain fever tree woodland. Southern margin of Urema Plains (Road 3-4 junction area). Dark patches in floodwater are floating meadows of aquatic grasses.

completely inundated and the aquatic *Vossia cuspidata* and *Echinochloa stagnina* grasses rooted in depressions on the floodplains grow through the aerial parts on buoyant stoloniferous culms forming extensive floating meadows.

As the floodwater is from a few centimetres to 60 cm in depth over large areas, the micro-perennial grasses are not killed by a two month submergence and in the shallower parts grow up towards the water surface. Deeper than 60 cm the *Cynodon* and *Digitaria* die back (or are grazed by fish?) to their largest tufts from which they grow out and recolonize the mudflats when they are exposed. Rafts of varying dimensions of the floating aquatic *Eichhornia crassipes* form islands which are moved by changes in wind or are carried down the Urema to the Pungue and the sea.

The extreme floods recorded in January and February 1970 inundated some 200 km^2 of the Urema Plains and the entire Urema–Pungue confluence area for

Water to the horizon of the Urema Plains in high flood years (summer 1969/70) *(cont.)*

LEFT:

View north to Goinha sector of Urema Plains from near 'Lagoa Paraiso' (flooded slack on right). Southeast margin of lake in the foreground *Hyphaene benguellensis* scrub thicket and winterthorn on leaves of fossil Pungue River distributary fan in middle distance.

two months. At the end of February and beginning of March the waters slowly receded, stranding the floating meadows and rafts of *Eichhornia*, and the short *Cynodon–Digitaria* grasses flushed a second time on re-exposure.

The herds move back onto the still wet plains following the ebb, and large herds of elephant, buffalo and zebra graze down the stranded *Vossia* and *Echinochloa* to the edge of the depressions. The channels and depressions choked with these two aquatic grasses plus *Paspalidium obtusifolium* are increasingly used as the autumn advances, first by the coarse grass feeders and in mid and late dry season by the short grass feeders. The first ungulates to stake their territory on the re-exposed ground are lone wildebeest bulls. They, and small wildebeest herds, often walk through extensive areas of shallows to take up a post or graze on low rounded exposed termite hills.

The high primary production and mosaic of grass types, as the floods abate, support the heaviest concentrations of large ungulates and also a diversity of species including eland, impala, oribi and large baboon troops, in addition to the species noted above. The exclusion of the herds from the floodplains by intervention of high floods results in a bimodal maximum and minimum of ungulate density and biomass. One maximum occurs on the rain-flushed pastures until February, followed by total exclusion of animals (except hippo), with a second high peak in the autumn on the ebb flush. This is followed by a second extreme low in animals (total ebb) in October (inset in Fig 9.14).

From here on the sequence is similar to that detailed in the following section for medium to low flood years.

Medium to low flood patterns

After the maximal spread of flood waters from mid-February to mid-March in 1970, a detailed study of a 20 km^2 section of the Urema Plains was initiated in February 1971 during low flood conditions, and extended through until March 1972 when medium floods occurred.

The composition and numbers of species at two-week intervals, expressed as a percentage of total animals and correlated with the rainfall of the 10 days preceding each count, clearly illustrates a number of salient features (Figs 9.14, 9.15).

On the environmental side, the total reliance of floodplain and aquatic grasses (in unflooded depressions) on rain-drought sequences is marked. The rapidity of drying or wilting is a characteristic of the short *Cynodon–Digitaria* grasslands which occur on the better drained convex surfaces of the base saturated vertisols. The excessive soil moisture in the depressions permits these pastures to remain greener longer, overriding the rapid aridifying effects of highly saline soils. These moisture and pasture fluctuations are depicted by means of contrasting symbols for clouds and grass in Fig 9.14. The short grasslands show a regrowth flush about 10 days after rain, if no further rain occurs the grasses wither quickly but take another 10 days to discolour.

On the animal side, the grassland and grazing sequence is clearly depicted by the change in species dominance through the annual cycle (Figs. 9.14, 9.15). Elephant and buffalo are rare within the intensive study area due to the predominance of short grasslands; the *Vossia* and *Echinochloa* depressions are however used mainly at the height of the rains when these areas have been partially inundated by direct rainfall and runoff. If the aquatic grasses only attain about 50 cm in height, zebra are first in the grazing sequence, as shown by their abundance in the 4 February count. At the same time the wildebeest herds are mostly on the intervening short grasslands, but move into the grazed-down depressions after the zebra, and whenever the short grasslands wither or discolour. Zebra numbers decrease, with some fluctuations by movement to and from the adjacent savannas, whenever regrowth occurs after rain. This pattern continues until mid-May when almost all zebra leave the Urema Plains for the slack pastures in the Dingedinge area at the Urema–Pungue confluence. A maximum in wildebeest numbers occurs in April and May due to influx of herds migrating from central and northern pastures to Dingedinge via the southern margins of the Urema. The arrival and length of time spent by these herds on the south Urema Plains varies with the state of the pastures in each autumn.

Following the ebb line is a zone of changing widths, dependent on microrelief at each level, of moist soil supporting a green flush (the ‘green zone’) which moves down the alluvio-catena followed by drying out (browning) on its upper margins. The herds follow the green zone and vacate all the upper margins where the grasslands have turned brown. Large concentrations of wildebeest stay on the narrowing green zone for more than a month after the zebra have left, then disperse south to the Dingedinge area where the slacks choked by *Vossia* and *Echinochloa* growth have been grazed down first by buffalo and elephant, and then zebra, to a short pasture.

With the departure of the majority of wildebeest, waterbuck and impala become the dominant species on the green zone from mid-dry season (June) until the first rains in November. The small changes in wildebeest and zebra numbers during this period is related to the effect of unseasonal showers on *Vossia* and *Echinochloa* grasses of the lower-lying sectors, attracting animals from the adjacent savannas for short periods.

The green zone at the height of the dry season is a mosaic of large mudflat areas covered in seasonal weeds, which are at the height of their development in September, green stubs of the aquatic grasses, and *Cynodon* and *Digitaria* recolonizing the drying mudflats and shooting through the mulch of stranded *Eichornia* rafts. This narrow zone supports almost the entire waterbuck population, large herds of impala and 80% (2,7611) of the hippo population during the torrid period (3-4 months). The hippo, however, also graze *Cynodon* that has turned brown if the culms are still green. Nevertheless, a large number of hippo are forced to graze out to nearly 10 km at night in the adjoining savannas and the entire population are extremely emaciated for the greater part of the year (Fig. 9.22).

As the waterbuck and impala are confined to the narrow green zone near the water's edge in the mid and late dry season, the view from the tree line from July on is of vast floodplains of sere grass and mirages, devoid of all herds, and which remain an empty quarter until the onset of the first rains, unless revitalised by unseasonal showers.

A marked break in impala numbers on the floodplains occurs in the first half of November, when herds return to the adjacent savannas and bush where the females drop their young. In the last part of November the impala herds and their newborn lambs return to the green zone on the floodplains (Figs 9.14 and 9.15 compare counts between 19 October and 25 November).

Some ten days after the first significant spring rains (> 20 mm) have fallen, the wildebeest herds are the first to arrive on the new growth flush of *Cynodon–Digitaria* grassland of the Urema Plains from their dry season concentration area in Dingedinge (Figs 9.14, 9.15 compare the contrast in counts on 13 November and 25 November). Zebra arrive in large numbers later, when some grass areas have attained a medium height, having spent the interim period grazing in the intervening savanna grasslands.

Dimensions of the Succession

On the macroscale the grassland and grazing sequence, following the catenal changes in soil moisture, and thus in green pastures, is shown by sable which move down from the adjacent miombo savanna uplands into the Rift floor where green shoots can be obtained throughout the dry season, in contrast to the coarse grass stratum on over-drained sands in the miombo. Lichtenstein's hartebeest show an opposite movement to sable apparently due to their preference for burnt grasslands. Fires usually begin earlier in the miombo than on the Rift floor due to the dense human populations along the Park boundaries. The spectacular regional migrations of wild ungulates in the Serengeti is probably the best African example of macroscale sequences (Bell 1971).

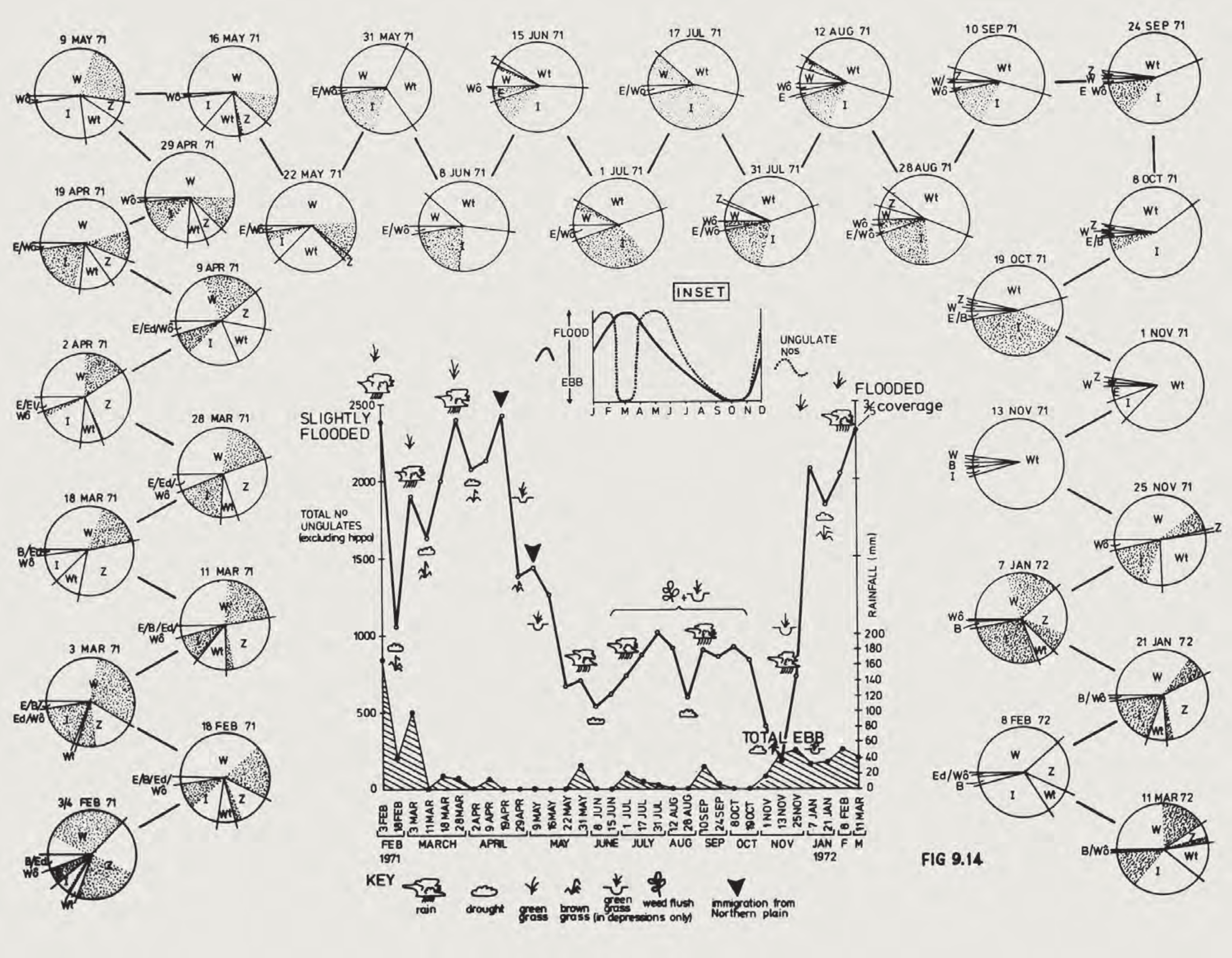
The wetting and drying sequences, outlined above, of floodplain grassland and grazing succession are mesoscale examples of the substrate sequences utilized by ungulates, as is the movement from miombo to the dambos traversing them in the upland areas. The relation between the dry savannas and their local pan and drainage line systems is on a similar scale.

A singular example of the grass and grazing succession on the microscale is that exhibited by and on the gilgai micro-basins on bottomland vertisols. Whether inundated by rain or river flooding, these circular depressions, of about 3 m diameter, remain wetter longer into the dry season than the intervening micro-ridges. The microbasins support the hygrophilous *Echinochloa, Paspilidium* and *Vossia* grasses and the microridges support either median height *Panicum coloratum* or the micro-perennials *Cynodon dactylon* and *Digitaria swazilandensis*. Buffalo and elephant graze the *Panicum* and then the lush aquatic growth of the microbasins, followed by zebra and wildebeest. Waterbuck are present in these gilgai areas throughout the annual cycle. As the microbasins dry out, stoloniferous invasion by *Cynodon* and *Digitaria* of the basin occurs from the browned microridges. Hence in mid-dry season, groups of wildebeest, centred on the microbasins, can be seen grazing the fresh green growth of invading micro-perennials.

The grasses in the microbasins, now comprising a mixture of aquatic and mesic species, are among the first sites of renewed and extended growth when unseasonal showers occur.

RIGHT:
Figure 9.14

Pattern of floodplain utilization by wild ungulates during low to medium flood conditions when pasture changes are almost totally controlled by the occurrence of rain.



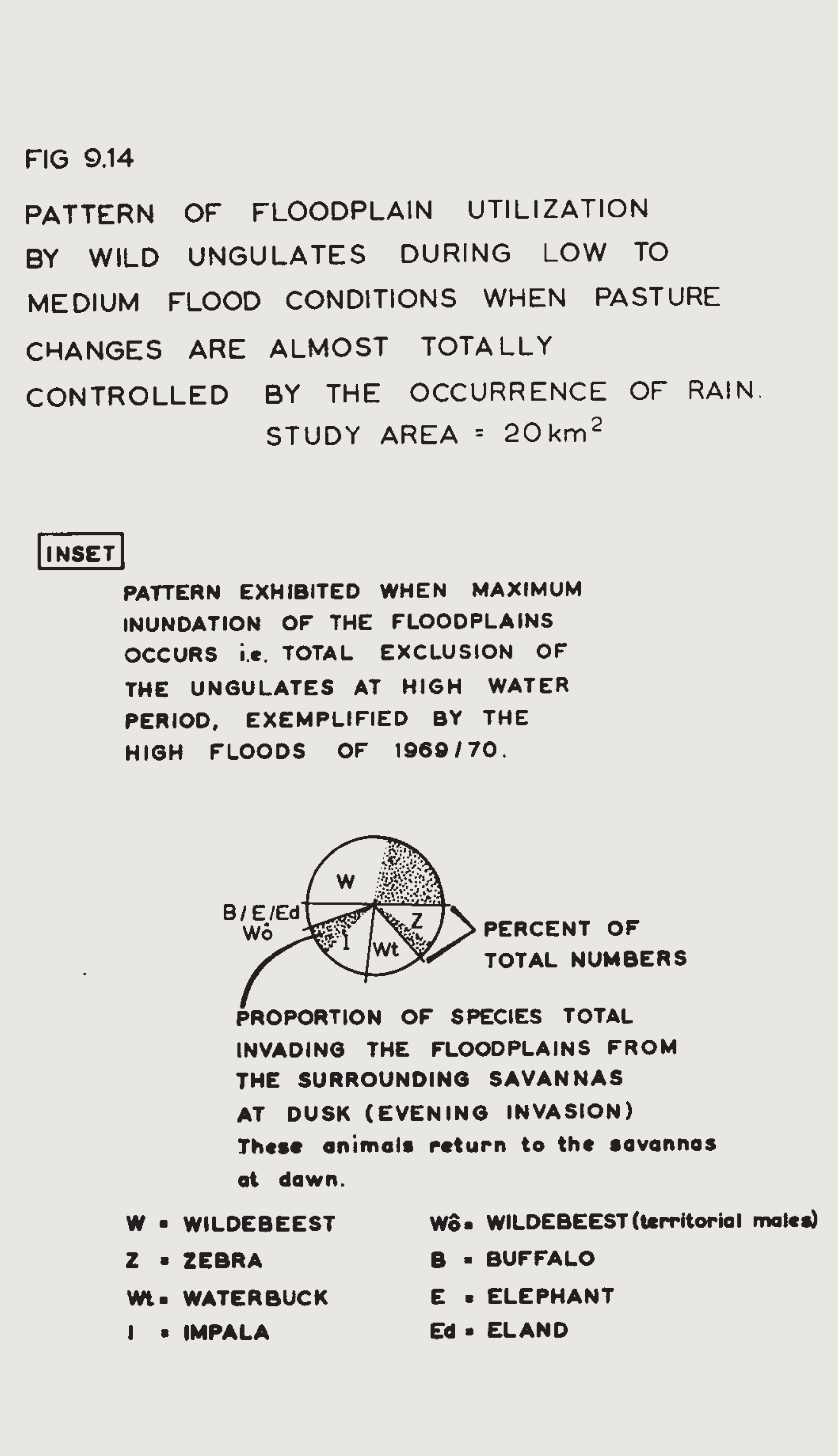


FIG 9.14

PATTERN OF FLOODPLAIN UTILIZATION BY WILD UNGULATES DURING LOW TO MEDIUM FLOOD CONDITIONS WHEN PASTURE CHANGES ARE ALMOST TOTALLY CONTROLLED BY THE OCCURRENCE OF RAIN.

STUDY AREA = 20 km^2

INSET

PATTERN EXHIBITED WHEN MAXIMUM INUNDATION OF THE FLOODPLAINS OCCURS i.e. TOTAL EXCLUSION OF THE UNGULATES AT HIGH WATER PERIOD, EXEMPLIFIED BY THE HIGH FLOODS OF 1969/70.

PROPORTION OF SPECIES TOTAL INVADING THE FLOODPLAINS FROM THE SURROUNDING SAVANNAS AT DUSK (EVENING INVASION)
These animals return to the savannas at dawn.

W = WILDEBEEST
Z = ZEBRA
Wt = WATERBUCK
I = IMPALA

Wô = WILDEBEEST (territorial males)
B = BUFFALO
E = ELEPHANT
Ed = ELAND

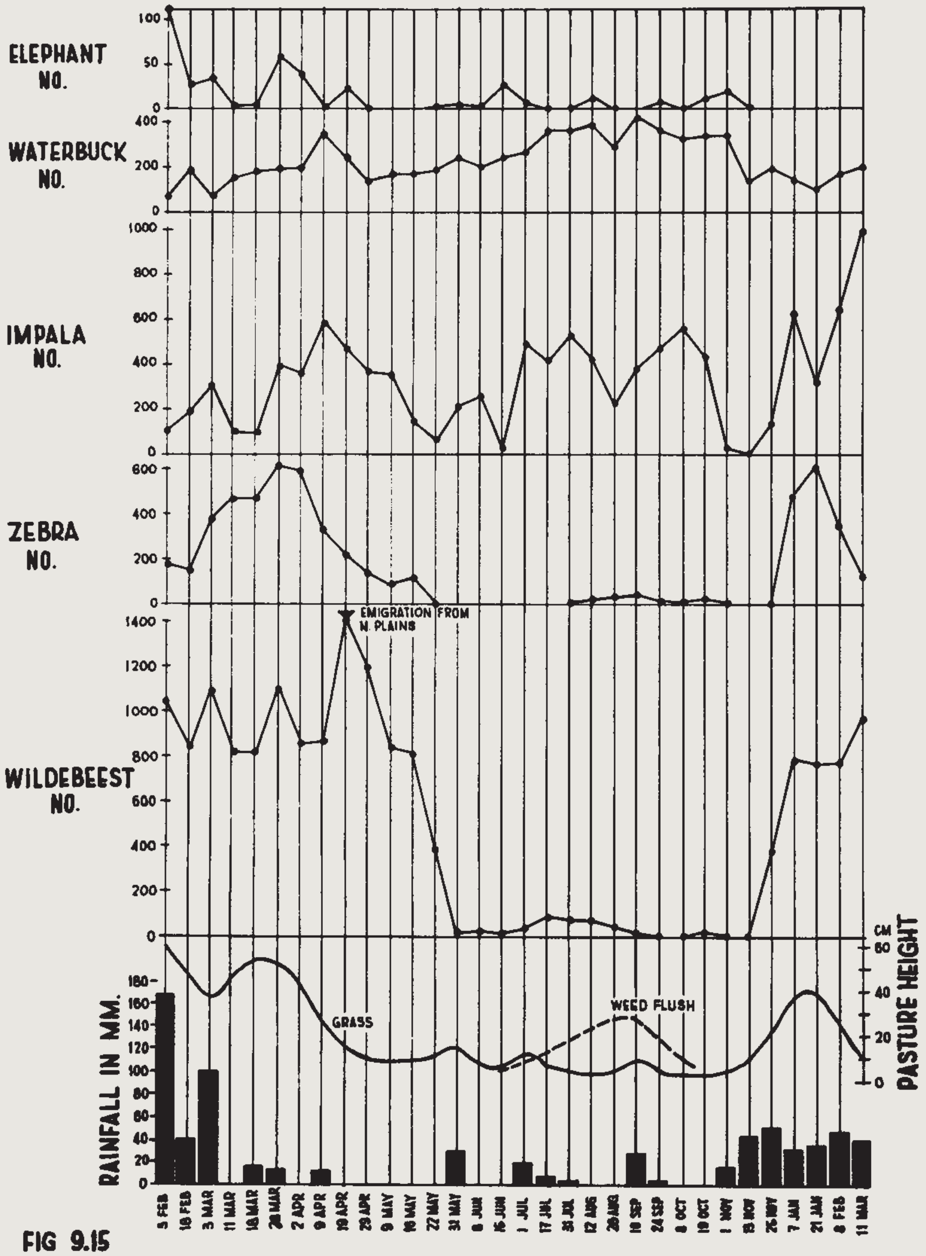


FIG 9.15

SEASONAL FLUCTUATIONS IN GRASSLAND AND GRAZING SUCCESSION ON 20KM^2 INTENSIVE STUDY AREA OF UREMA FLOODPLAINS

LEFT: Figure 9.15

Seasonal fluctuations in grassland and grazing succession on 20 km^2 intensive study area of Urema floodplains.

Savanna Sequences

As the interplay of utilization by wild ungulates of savannas and their pan and riverine sites is similar to the succession described for the floodplains, explanation is required of changes and differences in the savanna which influence ungulate movements between the two. Essentially the floodplain system is merely a greatly expanded riverine and pan system where microrelief influences on degree and duration of wetting override differences in soils.

Unlike the upland miombo savannas which occur on only a few soil types, the Rift Valley savannas occur as a mosaic on alluvio-catena patterns and their ecotones, which in itself is responsible for a whole chain of interactions. The soil properties in each affect the soil moisture balance and influence the occurrence of different types of grassland of varying height, density and structure. Thus, in the savannas and adjoining upper margins of the floodplains, a spectrum of pastures is available to the whole range of ungulate preferences which can be obtained merely by their moving from one site to another. Each of these habitats (plant-edaphic associations) has different responses and potentials to environmental change, though all are eventually affected by continued drought conditions. Many of the savanna grasslands of the Rift floor dry out and discolour with midsummer droughts and in the early autumn (March and April) and are then shunned by the wild ungulates for the remaining green pastures, though some species retain green leaves basally.

The inherent salient feature of alluvial grasslands is that single or few species dominate over extensive areas, alternating with other single dominants on adjacent substrates (vide Section 8.5), and either provide a superfluity of preferred grazing during the rains and autumn for many ungulates at its different stages of growth or, at the other extreme, are almost useless as pasture unless altered by lodging, trampling or fire, well exemplified by the 3 m to 4 m tall *Vetiveria, Hyparrhenia, Panicum* or *Setaria* swards over large sectors of the system.

Most of the tall grasslands, however, have a two (or three) tiered structure, the lower storey occupied by highly favoured soft-leaved grasses. In *Hyparrhenia* swards the subordinate layer is formed by *Urochloa mosambicensis* and *Digitaria milanjiana*, and in *Setaria* grassland *Panicum coloratum* and *Digitaria swazilandensis* form a lower layer with forbs. Thus the passage of buffalo and elephant through these grasslands whilst they are feeding on the second grass storey opens up the dense tall cover for a succession of other grazing species.

The extensive stands of 4 m high, giant form of *Panicum maximum,* which occur mostly in the shade of closed canopied *Piliostigma* tree savanna on the Rift floor, remain green until June when they are in full seed. They are used mostly by buffalo and elephant in the autumn before they become rank. Early fires also destroy these swards as there is an abundance of fuel from the accumulation of lower dead leaves. If no fire occurs these shade grasslands lodge, if not flattened by the large herbivores, and provide green shoots for medium to short grass feeders deep into the torrid season if unseasonal showers occur.

In the autumn when the median floodplain grasslands have been grazed down, the zebra move into the adjacent savannas where they concentrate in the areas of *Urochloa mosambicensis, Digitaria milanjiana, Panicum maximum* and *Heteropogon contortus* already topped by buffalo and elephant. In dry years this movement is earlier in the season and later in wet years. Either rapid drying out and fire, or both, make large areas of savanna unattractive and most of the ungulates congregate on the depressions in the savannas if the floodplain slack pasture area are still too wet. However, soon after the passage of fire, large herds of zebra and wildebeest are lured away from the bottomlands and are joined by Lichtenstein's hartebeest to feed on the burnt (toasted) culms and basal leaves. The post-fire regrowth is grazed until withering occurs, when the herds move back to the bottomland or slack grazing. It is at this time that small herds of zebra and wildebeest move up into the miombo savannas following the flush of grasses there from earlier fires.

Other fluctuations in numbers and composition of ungulates on the slack green zones are caused by unseasonal showers which results in different responses in the variety of grasslands, and within the same type, depending on whether they were burnt or not.

In the dry season, short grasslands of all kinds including the burnt and post-fire stages of tall and medium grasslands, whilst reacting rapidly to any unseasonal rain shower, also dry out the fastest due to lack of shade on the soil surface. In addition, leaf production in the micro-perennials is very small compared to the larger tufted grasses. Thus apart from slacklands, the most important pastures in the dry season are those savanna grass communities which have a mulch cover on the soil of lodged or trampled grass. The smallest unseasonal shower is then most effective, as the moisture is not lost by evaporation but penetrates the soil, and is deepest beneath the mulch and in the grass root zone of each tuft from increased runoff of rain down the grass stems (Table 5.3). For example, a shower of 4 mm on 27 August 1971 penetrated from 5 mm to 7 mm beneath median *Urochloa* grassland as well as in the micro-perennial cover, but the unburnt median grasses continued to produce green foliage long after the shorter species or burnt areas of the same cover had dried out.

For these reasons many of the herds stay on in the savannas where unburnt areas of *Urochloa* occur, and only decamp to the slack areas in the final part of the torrid period. Drought years aggravated by devastating fires leave only the dry hippo lawns and narrow green zones intact. This has tremendous repercussions on migration and animal condition. Herds from long distances away appear in the Park (noted by professional hunters for those areas), the riverine and slack areas are overutilized, and most ungulates lose condition rapidly in the early autumn resulting in mortality mainly of hippo and buffalo (see Section 5.7).

Daily Movement BetweenSavanna and Floodplain

Within the two major rhythms of the general annual cycle exhibited by ungulates—dispersion in the rains and and return to riverine zones in the dry season (with a seasonally fluctuating trophic sucessional pattern)—is a striking year-round, daily component involving the alternate use of savanna and floodplain.

The data from a year's study of one sector of the Urema Plains shows the regularity and dimension of this phenomenon (summarised in Figs. 9.14 and 9.15).

The stippled areas within each pyegram represent the proportion of the total percent of each species which invaded the floodplains in the late afternoon from the adjacent savannas. Wildebeest, zebra and impala in the rains and autumn, and mostly impala at the height of the dry season, provided the most spectacular display of this evening invasion. At the break of dawn and before, lines of zebra and wildebeest trek back into the adjacent savannas. What would be the grandest spectacle of all, if it were possible to see, would be the emergence of nearly 3,000 hippo from the Urema Lake out onto the surrounding floodplains every night.

In midsummer and autumn, herds of elephants also form part of the evening invasion to feed on floating mats of *Vossia* grass and *Mimosa pigra* shrubs in the shallows. They leave the floodplains before dawn. In the mid-dry season, lone territorial male wildebeest also take part in the evening invasion and return to the savanna. Waterbuck is the only species which remains on the surrounding floodplains every night.

No evening invasion of the floodplains was recorded on three of the 32 counts in the year, i.e. on 1 November 1971, 13 November 1971, 8 February 1972 (Fig. 9.14). Large baboon troops spend the nights sleeping in riverine or savanna trees marginal to the floodplains, and most of the day feeding either on the ecotone or far out on the plains, returning only at dusk.

In the torrid period and hot-wet midsummer period, there is some movement of individual herds to the floodplain margins for shade, elephant seeking shade as early as 09h00 in this season. The important feature is that about half the population of wildebeest and zebra remain on the plains all day, whilst the other half return to graze in the savanna at dawn. In the case of impala, though the proportion varied, the majority of the local population came onto the open plains in the late afternoons of summer and in autumn when good rains had occurred. In the dry season, however, the population showed a dimorphic activity, part remaining on the floodplains all the time and the remainder moving daily back and forth. As noted previously, the exodus of impala from the floodplains in the first three weeks of November relates to their calving in the bush of the savannas. Soon after giving birth the impala herds return to the *Cynodon* floodplain pastures.

These daily oscillatory movements were also observed between April and October on a smaller scale in most other floodplain or slack savanna junctions, including the areas: Tengane, Nhamisangu, Goinha, Mucodza, and Dingedinge. However no wet season data are available from these areas to verify the behaviour as a general year-round phenomenon everywhere.

Adjustments in drinking behaviour to tourist activities in Wankie National Park, Rhodesia were noted amongst elephant, buffalo and zebra (Weir & Davidson 1965). No definite data on this subject were obtained from my intensive study area, which fell within the southern sector of the Park open to tourism. Elephant, however, emerged later in the evenings in the tourist season between April and November, and eland left the area altogether. In the remainder of the Rift floor, closed to tourists, eland were often encountered in similar open floodplain areas during the dry season. As safari hunting areas adjoined the northern and eastern sections of the Park, eland may remain shy of vehicles due to their wide-ranging habit. With other species, however, the impression was that tourist activity formed part of a sanctuary effect furthest from the safari areas and where least poaching took place.

Similar daily movements, though apparently on a smaller scale, were recorded by Jarman (1972) in the mid-Zambezi valley below Kariba Dam and on the Chobe River in Botswana by Sheppe and Haas (1976). As the daily movements recorded in the mid-Zambezi Valley coincided with the drinking times noted for the same species in Wankie (Weir & Davidson 1965), Jarman suggested that 'at least part of the reason for the daily incursions onto the floodplain made by these species was to drink at the river.' (Jarman 1972, p. 291). In comparing the different patterns of floodplain use by the same wild ungulate species on the 20 km broad Kafue (Sheppe & Osborne 1971) with that on the narrow (1 km or less) Chobe floodplain in Botswana, Sheppe & Haas (1976) conclude that the different dimensions of the two floodplain areas was the determining factor. The size of the floodplain influences the flood regimen and thus the spatial and seasonal relations with their surroundings.

As oscillatory movements between the two major systems are exhibited throughout the annual cycle, from the time when surface water is abundant everywhere to the time when the Urema Lake is the only surface water in the area, several factors are probably at play. These factors probably act in concert or alone at different seasons, and influence each species differently.

In sum, the possibilities responsible tor this daily oscillatory movement between the floodplains and marginal wooded savannas include:

(1) Attraction of open places for feeding or spending the night (e.g. wildebeest, zebra, impala). This is shown by the attraction of animals to open saline areas in wooded savanna or airstrip cuttings. Recorded for impala elsewhere by Jarman (1972, p. 292).

(2) Shade seeking; moving onto marginal savanna on summer days and returning to open plains in the evening (e.g. buffalo and elephant).

(3) Movement from plains to marginal wooded savanna at night (opposite to shade seeking) as shown by baboon. Where floodplains are narrow, waterbuck (and lechwe in the Okavango, pers. data) also move into the marginal savanna at night.

(4) (a) Surface water availability and preferred drinking times.
    (b) Availability of surface water as a result of elephant digging holes in sandy riverbeds. Local examples are the broad Nhandue and Nhamapaza 'sand rivers' which traverse the Rift floor in the north of the system.

(5) Evasion of large predators, by either the increased vigilance of several species occurring together in large numbers and/or the visual advantage of open terrain.

(6) Inadequacy of the plain's green zone in the dry season. Part of the local population of the same species remains all day and night on the plains. The remainder uses the adjacent savannas in the day and return to the floodplains at night. What determines which herds take part in this dimorphic behaviour is unknown.

(7) Change of feeding due to drying out (wilting) of floodplain pastures in the day when toxic amounts of hydrocyanic (prussic) acid are likely, particularly in *Cynodon*. Use of these pastures at night due to regained turgor and guttation, resulting in rapid reduction of prussic acid content after sunset. Rapid changes in prussic acid toxicity are recorded in many grasses, particularly *Cynodon dactylon,* in the torrid period after unseasonal showers or fire, in midsummer droughts and in autumn due to rapid dessication and/or frost on the inland plateau (Henrici 1926, pp. 494, 498; Steyn 1934, pp. 118–138). Savanna grasses in the shade of trees or the green zone pastures are used at these times.

(8) Possible local movement in summer imposed by intense irritation of bloodsucking flies (*Tabanidae* and *Glossina*) mostly in the daylight and crepuscular hours, and mosquitoes (*Culcidae*) at night. Mosquitoes are known to be far less numerous on the open floodplains at night than in the adjacent wooded savannas where the effect of the nocturnal katabatic breeze from the uplands is nullified. However, on still nights there may be no difference. Certainly some animal species and individuals are more sensitive than others to biting flies (e.g. lechwe pers. obs.) and to the irritation of non-bloodsucking muscids (locally referred to as 'wildebeest flies') which occur in swarms of almost

plague proportions at the height of the wet season. These flies appear to affect oribi most who take evasive action by secluding themselves in tall, dense grass patches. Evasive actions take by animals against biting flies are recorded by a number of authors (e.g. Fraser Darling 1937, pp. 131–140; Fosbrooke 1963, pp. 124-126; Glasgow 1963, pp. 97–99; Tinley 1964, pp. 73–75; 1966, p.106; 1969, p. 17).

(9) Adjustments of resource use patterns to human activities (including tourism, day hunting, night hunting, agriculture).

(10) Influence of the spatial dimensions of abutting systems on wetting and drying sequences, and thus the seasonal and daily sequences of utilisation by herbivores through proximity or remoteness of contrasting habitat resources (their qualitative and quantitative changes).

Grazing Succession: Summary and Comparisons

The migratory and local movements of wild ungulates are an opportunistic response to the availability and disposition of suitable ambient (physical and social) food resources and water. In the Gorongosa system, the coactive influences of substrate diversity, disparate wetting and drying sequences, grazing and fire, provide a year-round succession of resources in a relatively small area. However, this multiformity is lost during droughts when the drying out of even the lowest slacks, and uncontrolled fires, reduce the pasture resource to a seared homogeneity for several months.

The Gorongosa example shows further that close juxtaposition of diverse systems, particularly that of savanna with slack floodplains exhibiting heterogenous wetting and drying sequences, is a fundamental feature allowing attainment of year-round life requirements through the rotation of large concentrations of ungulates on a local scale, whereas migrations of geographic dimensions (exemplified by Serengeti) are required in order to sample a parallel sequence when systems are widely separated.

The grassland and grazing succession involving wild ungulates and floodplains (slack basins) of the Urema Trough (first described in Tinley 1969c) is almost identical with that recorded by Vesey-Fitzgerald (1960, 1965) further north in the Rukwa Trough sector of the Great Rift Valley. It is also similar to that in the Ngorongoro Crater, Tanzania (Estes 1968; Anderson & Herlocker 1973), and that of the Serengeti ecosystem (Bell 1971) except on a smaller scale. The pattern is, however, quite different to the typical relationship between savanna and riverine strips where there is a high concentration of ungulates along the riverine zones in the dry season only, followed by a dispersal away to the back country during the rains. This latter seasonal alternation is exemplified by the Luangwa Valley (Fraser Darling 1960, pp. 72–74; Dodds and Patton 1968), the mid-Zambezi Valley (Attwell 1963 and Jarman 1972 in Rhodesia; Tinley and Sousa Dias 1973 in Mozambique) and the Chobe River (Child 1968b; Sheppe and Haas 1976) to name a few.

Although there is a topocatenal grazing succession on the macroscale between the upland miombo savannas and the Rift Valley floor, the main difference in succession between interfan slack basins and the usual riverine situation given above is the local rotation of high concentrations of wild ungulates at all seasons across alluvio-catenas which are separated by small differences in microrelief. The microrelief differences, together with changes in soil properties and differential grazing, affect the composition, structure, productivity and availability (phenology) of pasture food resources.

The overlay of microrelief (micro-catenas) on laterally changing soils (alluvio-catenas), related to differential sorting and deposition by fluvial fan processes (as opposed to lateral deposition by a river traversing the bottomland), has provided a multiplicity of substrates from which the wildlife can obtain maximal use by opportunistic migratory responses; moving laterally, and up or down. For this reason the sequences in the Urema Trough simulate, on the meso and micro scale, that exhibited by the rotatory regional migrations of the Serengeti.

Whilst the fluctuating trophic succession in the Urema Trough is generally similar to that on two other large floodplain ecosystems in southern Africa, the Kafue Flats (Sheppe & Osborne 1971) and the Okavango Delta (Tinley 1966), these two areas have different sequential patterns of utilization imposed by their large dimensions and yearly fluctuations. In the Okavango especially, the lag in floodwater spread causes an anomalous flooding regime which forces most wildlife off the floodplain in the mid to late winter dry season. Thus, in this case the ebb regrowth flush occurs in the two remaining months of the torrid period (Sept.– Dec.) before the first rains dispersal to the backcountry, and the lowest slack areas of aquatic grasses are only exposed (if at all), in the autumn and early winter before the arrival of the midwinter floods. The Okavango Delta substrates have been formed in a similar manner to the fan sequences in the Rift Valley and Cheringoma Coast, whereas the deposits on the Kafue Flats appear to have been mostly laid by river meander sequences and other levee deposits. These latter are thus soils comprised mostly of fines, so that soft mud is a major feature excluding floodplain use for long periods (Sheppe & Osborne 1971).

A major feature emphasised by the year-long study of a sector of the Urema floodplains, though perhaps unremarkable when pointed out, is the total reliance of the floodplain system on direct occurrence in low to median flood years. In these low-water years, the hygrophilous grasslands are virtually reduced to the same status as savanna, causing far-reaching repercussions and implications as the dry season food base and buffer action of this system is then lost. These features will be dealt with under 'Management' (Chapter 10). As low water years have been more frequent (seven out of 10 years' records) and high floodwaters are drained off, major areas of floodplain grassland must now be considered functionally as part of the savanna system. The widespread invasion of these grasslands by scrub (sapling) phase of woody plant succession emphasises their changed status. The speed of invasion is dampened by the perched position of the old floodplain substrates above incised drainage. The change to savanna status means that the grassland exists as a unimodal pattern of productivity related to the incidence of rain, intensity and duration of dry periods and fire as opposed to a year-round gradient of productivity and availability typified by the floodplain system.

Another intrinsic feature of the Urema Trough is the prevalence of preferred food grasses as dominants over large areas (low diversity/maximal food base) which, under the constraints of soil moisture balance, can support massive biomass concentrations. The preferred grasses form a mosaic with grasslands dominated by species that are avoided by ungulates unless physically altered by trampling or fire. Contrasting with this feature is the medium to tall grass stratum of the adjacent miombo savannas which have a much higher diversity of grass species per unit area (up to 10x) than equal areas on the alluvia of the Rift floor. This implies a selection for low biomass and specialist grazing, even before their poor attributes as pasture are considered. Their substrates are acid sand or skeletal soils of low nutritional status, except where latosols occur on basic intrusions, and vegetative regrowth must be forced by cutting, firing or grazing. The herbivore populations which do use these grasslands are never in sufficient quantity to hold back the rank stage from being attained.

The relationships noted between ungulates and substrates on the Rift floor support Bell's (1971, p. 92) and Jarman's (1972, p. 298) generalisation that catenal sequences underlie differential distribution of ungulates, grassland and grazing patterns over much of Africa. If the whole spectrum of wildlife is taken into consideration, however, it can be shown that various other climo-edaphic gradients, or ecoclines, and spatial relations underlie the distribution, movements and patterns of utilisation. Jarman's (1972) rains dispersal / dry season riverine concentration is not the whole story.

Bell (1971, p. 92) and Jarman (1972, p. 298) list factors which may make riverine floodplain areas unfavourable habitats in the wet season, and higher catena levels more attractive, to attempt to explain why wild ungulates do disperse to the back country at this time when abundant herbage is available on the riverine areas. For the lowest part of the topocatena the factors included are excessively muddy conditions, rank grass of poor nutritional status, easy concealment of predators and re-infestation by parasites. In comparison, the higher catena levels are said to have shorter grasses, many of which are annuals considered to be of higher food value and which could more easily be kept at optimal vegetative growth by grazing pressure.

The factors listed by the above authors for the catenal migrations will probably be different in every situation and with different combinations of species and circumstances. For example, many of the mopane savanna clays are boggier in the rains than the floodplain soils, and the occurrence of annual grasses are common only where mopane savanna is adjacent to riverine floodplains. Elsewhere, dense, medium to tall, coarse perennial grasslands predominate on sandier soils and in miombo savannas, which have a greater diversity but dry out relatively quickly. The higher catena levels in southern Africa, whilst generally supporting shorter swards than the bottomlands, are of medium to tall height and are not depleted by grazing unless artificial water points are established.

The Gorongosa data, and that from the Save (Tello & Van Gelden 1975) and Zambezi (Tinley & Sousa Dias 1973) rivers in Mozambique, suggest that perhaps two other reasons are fundamental triggers to rain season dispersion to the higher catena levels or back country.

(1) The physical removal of animals from dangerous situations, i.e. from being swept away by river floodwaters. This would apply in the rushing, overwhelming flood regimes of the river floodplain systems e.g. Zambezi, Luangua, Save, Limpopo, Mkuze, Umfolozi, but not in slack or basin floodplain systems exemplified by Ngorongoro Crater, Rukwa, Okavango Delta, Banhine (in Gaza region of Mozambique) and the Urema, where flooding is a gentle spreading.

(2) The partial dispersal of some plains species in Gorongosa to the higher macro-topocatenas of the upland miombo savannas on either side of the Rift floor is directly related to regrowth flush of the otherwise rank sour miombo grasses. This movement occurs prior to the rains as well as during the first rains, when the major attraction of the back country is grass flush due either to fire and/or the first rains. After this initial stage of growth, the dispersed herds cannot easily maintain the swards in a utilisable state, except in local patches if surface water is available. If surface water is in unlimited supply (e.g. windpumps), the herds can maintain themselves on dry or sour pastures. The perennial grasslands of the higher catena levels can never be depleted unless artificial water is provided, thus the trigger enforcing return to lower levels appears to be moisture based, and to the rank status of pastures.

The work of Henrici (1928) shows that a bimodality in nutritional peaks occurs in most grasses during the growing season, one in the spring before or at the time of the first rains and the other in the autumn (Mar.–Apr.). The midsummer low is related to relocation of nutrients from the leaves to take part in maximal growth of the stems (culms). If adequate nutrient levels in riverine pastures are depleted by excessive cropping, this also would reinforce dispersal at the time of the first rains.

Another fundamental feature prompting animals to invade new areas and habitats is their innate exploratory drive. Shifts in this innate life force, enabling exploitation of available opportunities, can only be realised when the moisture constraint is broken by the incidence of rain. In moving into the backcountry the savanna–riverine relationship is, in fact, maintained by the use of rain-filled pans as island riverine zones. In this way a kaleidoscopic interplay of changing populations, species associations and habitat facets are intermeshed in different combinations through the annual cycle.

In sum, the differential wetting and drying (moisture status of forage and surface water) sequences underlie migrations and movements. The use and alteration of rank or dry grasslands for grazing sequences or semi-sedentary populations in non-riverine sites depends on the persistence of surface water. The riverine growth, once it has become rank, is utilisable because the confined water resource enforces concentration of ungulates large enough that they materially alter its structure, and thus maintain optimal vegetative growth on substrates that are still moist at the height of the dry season. However, even this life saving feature (and buffer to destruction of other habitats by mixed feeders) of the lowest part of a catena is lost if it is too quickly drained. The slacks or marshes are then reduced to the same status as the surrounding fast-drying savannas. The incidence of rain releases the exploratory drive of animals permitting wide ranging movements to occur which may result in new centres of population establishment, as shown in cases where artificial water has been provided far from the riverine zones. An example of this is wildebeest becoming established in the Kalahari National Park (Eloff 1966, pp. 34–36). The whole significance of dispersal is aptly described by Eloff (op. cit.).

Gwynne and Bell's (1968, p. 393) contention that the grazing succession is a facultative relationship between species, rather than a competitive one, fits the summer and autumn seasons in Gorongosa, but not the mid and late dry season period when there must be competition for suitable grazing.

Thus soil moisture balance—which is a function of cover and surface, porosity, drainage status of pans and lower catenal zones, and climatic fluctuations—is the intrinsic factor permeating social dynamics, migration, grassland and grazing patterns, and fluctuations in density and occurrence of ungulates. As shown in Chapter 6 (Process and Response) the moisture factor underlies all geoecological dynamics and should thus be the prime feature of any management programme.

9.5 FOOD, FEEDING, CONDITION

Food

The feeding sequences described in the previous section are corroborated by the seasonal food records for different species listed in Appendix 2, and the grass species which recur most in the diets of 13 ungulates (Table 9.3). The striking feature demonstrated by both the herbaceous and woody food records of wild ungulates, baboons and frugivores is the overlap of preferred plant foods in all trophic groups. Although these components are abundant, in different sites and different seasons they have different phenophase availabilities. Year-round utilisation may be obtained from them, however, by several strategies of ecological separation or facilitation: (a) by feeding sequences (temporal and structural succession), (b) and/or a spatial separation (use of different layers or mosaic facets), (c) aggregations of different species associations at feeding stations that have an abundant product (cornucopian resources) e.g. fruit trees, or merely through the differential mobility of different species and groups which permits opportunistic use of resource complexes as they are encountered.

Examples of feeding utilisation by wild ungulates of the main ecosystems is summarised in diagrammatic form (Figs. 9.16 to 9.20), showing the level of utilisation against frequency of occurrence of food species. Together these data illustrate availability and food preferences in each major system, and their various strata, indicating the kind of selection pressure that various plant components are subjected to by the wild ungulate consumer level. Whereas only fresh feeding utilisation was recorded for the herbaceous layers, a recency of use category for the woody strata differentiates between old use (c. >6 months) and new (c. <6 months). This separation indicates changes in utilisation intensity related to seasonal fluctuations in ungulate density or to upward or downward trends in browsing populations.

TABLE 9.3
Grass species that recur most in wet and dry season food records of 13 wild ungulate species, including buffalo, eland, elephant, hippo, impala, Lichtenstein's hartebeest, oribi, reedbuck, sable, warthog, waterbuck, wildebeest and zebra.

GRASS	DRY SEASON NO. UNGULATE SPP.	WET SEASON NO. UNGULATE SPP.	HABITAT
**Urochloa mosambicensis*	11	13	savanna
Vossia cuspidata	11	9	marsh
Panicum coloratum	11	9	floodplain/savanna
Echinochloa stagnina	10	9	marsh
Cynodon dactylon	8	10	floodplain/savanna
Digitaria swazilandensis	5	10	floodplain/savanna
Panicum maximum	9	6	savanna
Eriochloa stapfiana	6	7	floodplain
Setaria eylesii	10	3	floodplain
Digitaria milanjiana	5	8	savanna
Chloris gayana	6	7	floodplain/savanna
Paspalidium obtusifolium	6	7	marsh
Eriochloa fatmensis[1]	6	6	floodplain/savanna
Heteropogon contortus	7	4	savanna
Sporobolus pyramidalis	5	5	floodplain/savanna
15 spp.			

Key
* including *U. pullans*;
[1]= annual

All possible selection combinations are discernible in the examples provided. Certain trees such as *Berchemia discolor, Boscia salicifolia, Cleistochlamys kirkii, Sclerocarya caffra* and *Strychnos madagascariensis* are important fruit producers but are relatively little browsed, However, under certain circumstances, for example where *Cleistochlamys* occurs on termitaria, the adult trees are heavily browsed by elephant. Heavy utilisation of patches of miombo by elephant, interspersed with large areas of the same habitat which is hardly touched, is characteristic. These heavily used patches are returned to, often at long enough intervals to allow the torn edges of bark to heal completely. Such selection indicates that possibly 'sweet' trees relatively low in tannin (or other phenolics) are sought after, and once used, the feeding scars remain as indicators to future elephants.

The four basic combinations of abundant/rare—preferred/avoided are thus overtaken by other considerations. Many components are eaten during seasonal extremes apparently only because of their availability. An analysis comparing dispersal efficiency against level of utilisation may not expose, for example, why two animal-dispersed but little browsed trees such as *Boscia salicifolia* and *Euclea schimperi* should show such different dispersal results. The former remains relatively uncommon whilst the latter can assume weed proportions.

The phenomenon referred to earlier of nearly pure species abundance (low diversity) of preferred high biomass-supporting food plants over large areas on heavy, usually base saturated soils, is well exemplified by mopane and *Acacia* and by the grasses *Echinochloa stagnina, Vossia cuspidata, Cynodon dactylon, Urochloa mosambicensis* and *Panicum* species on the Rift Valley floor.

As their food lists show, bushbuck and impala are avid weed feeders mainly in midsummmer and autumn in the Rift Valley. Impala, however, also utilise the grass stratum heavily at this time. Both these species eat the same fruits as other species such as elephant, bushpig and baboon, and are consequently often associated with them at feeding stations (see Section 9.8).

Two important features emerge from the intensity of utilisation of woody strata by elephant, and of floodplain grasslands by other ungulates. All elephant feeding samples, even those where there was excessive damage, had been more heavily utilised in the past despite the elephant increase recorded in air counts from 1,555 in 1968 to 2,542 in 1972 (Table 9.2). This could imply that prior to 1968 much higher densities of elephant occurred throughout the park area. If this was the case, then judging by the present level of woody plant utilisation, past local densities must have been between two and three elephants/km^2 or about double the present total. Several interacting features could have been responsible for changes in density: (1) influence of consecutive drought years, (2) decimatlon of population by ivory hunters, and (3) changes in density patterns locally or involving the whole region. In 1894 the hunter-naturalist Vaughan-Kirby (1899) recorded large numbers of elephant on the Cheringoma Plateau where the best elephant hunting was to be had. But in more recent times, until about 1971, this mosaic of forest, miombo and dambos has been totally empty of elephants due to heavy hunting pressure. In fact only rare sigmoid-shaped trees, which could indicate long past elephant use, can be found. Past use of the tree layers contrasts with that of the shrub strata below 3 m which are, almost without exception, more heavily utilised at the time of study than previously, indicating a trend of overall increase in the low to median level browsing population (i.e. impala, and the tragelaphines: bushbuck, kudu and nyala) as well as preferred use of this stratum by elephants.

Measurement of the grazing pressure on floodplain grasslands of the Urema Plains indicate that more than 70% of the area is over-utilised, primarily by the over-population of hippo in the lake. The selection for *Cynodon dactylon* grass by hippo is exemplified by the data in Table 9.4. The interaction of canalisation by hippo and other factors on floodplain dynamics has been dealt with previously in Section 9.4. However there are several aspects here which may trap the unwary observer. Floodplain grasslands are renewed twice in the annual cycle to a greater or lesser extent—first by direct rainfall, and then by a flood and ebb sequence. Thus heavy utilisation is interspersed with an expanding and contracting green zone under heavy utilisation. Simultaneously, however, the floodplains are becoming increasingly over-drained hence the overall perennial hygrophilous system is shrinking and is being replaced by the seasonal savanna system. The over-used zone is thus moving inwards over time.

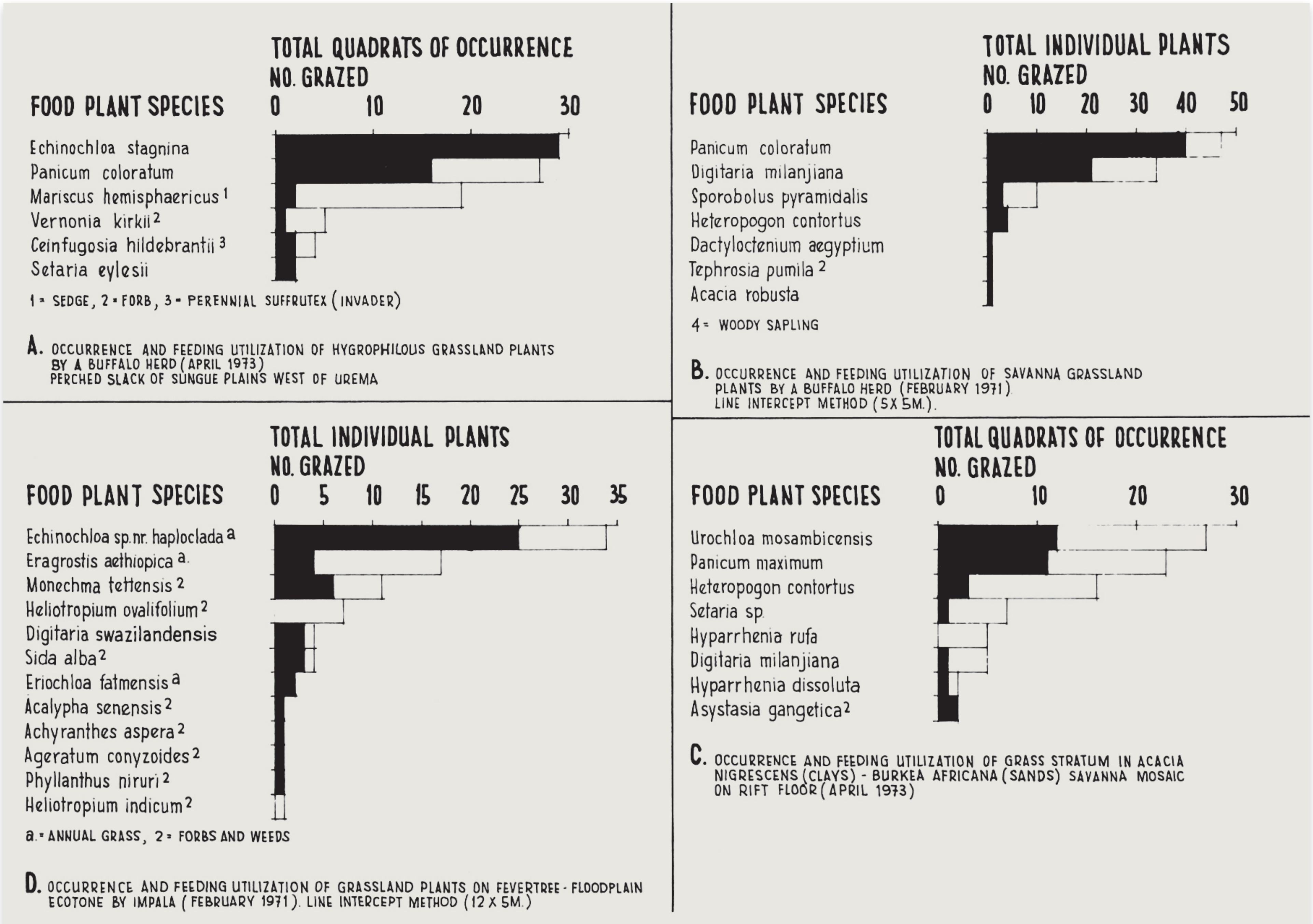
TABLE 9.4

Hippo grazing on the Urema Floodplains. Examples from a solitary male followed on two consecutive overcast days in adjacent parts of the plains. Only fresh bites recorded.

GRASS SPECIES	NO. TIMES GRAZED	% OF TOTAL
SAMPLE 1: 15 July 1970 (14h00–17h00)		
Cynodon dactylon	344	84.4
Glinus lotoides f	56	13.0
Heliotropium indicum f	3	0.7
Vossia cuspidata	2	0.5
Alternanthera sessilis f	1	0.2
Heliotropium ovalifolium f	1	0.2
	407	100%
SAMPLE 2: 16 July 1970 (13h00–17h50)		
Cynodon dactylon	333	87.3
Digitaria swazilandensis	27	7.1
Glinus lotoides	13	4.0
Eriochloa fatmensis	3	0.8
Heliotropium ovalifolium f	2	0.5
Heliotropium indicum f	1	0.3
KEY f = forbs and weeds	379	100%

RIGHT: Figure 9.16

Examples of grassland feeding utilization by wild ungulates.



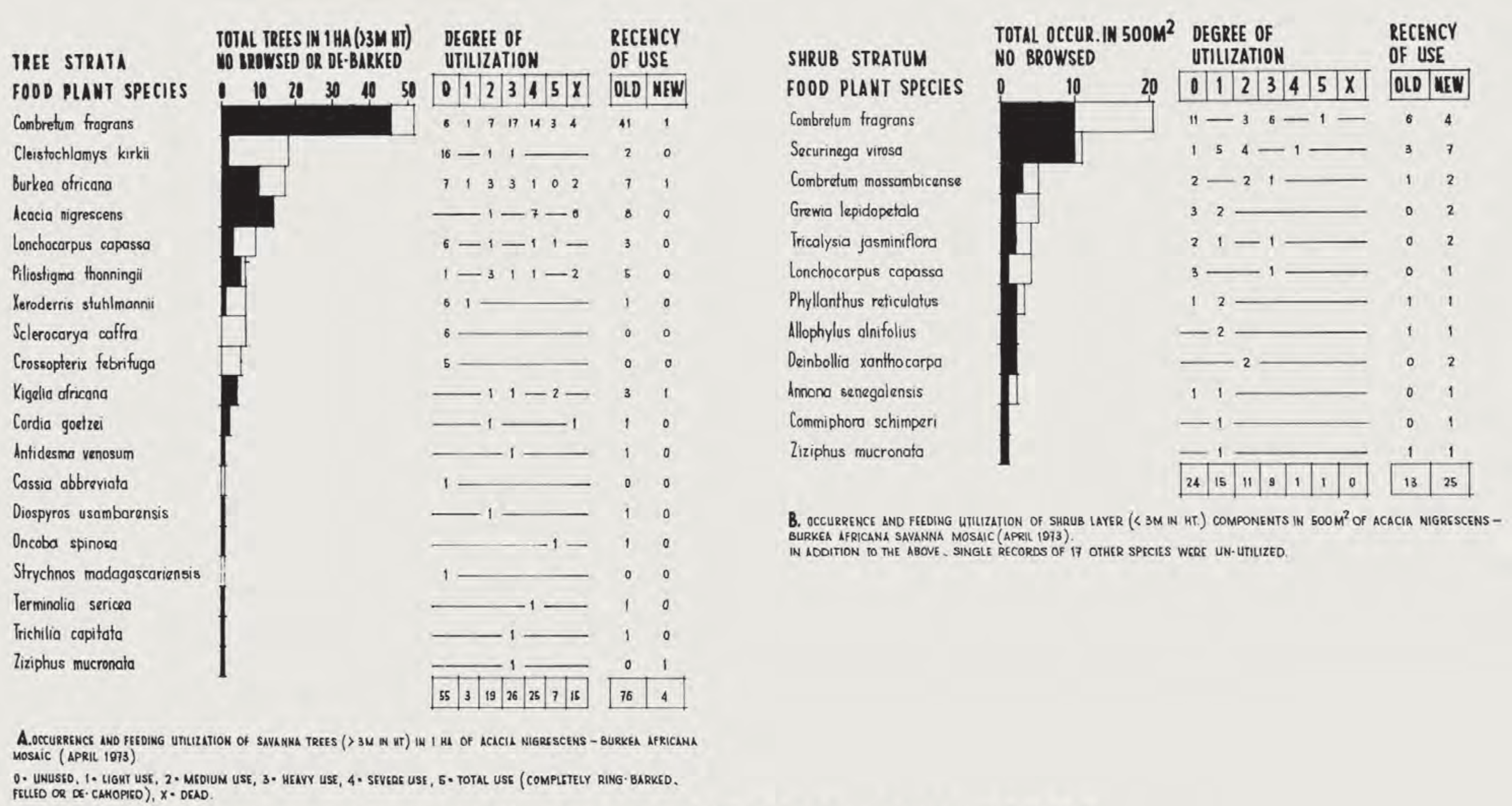
A. OCCURRENCE AND FEEDING UTILIZATION OF HYGROPHILOUS GRASSLAND PLANTS BY A BUFFALO HERD (APRIL 1973)
PERCHED SLACK OF SUNGUE PLAINS WEST OF UREMA

B. OCCURRENCE AND FEEDING UTILIZATION OF SAVANNA GRASSLAND PLANTS BY A BUFFALO HERD (FEBRUARY 1971)
LINE INTERCEPT METHOD (5 X 5M.).

C. OCCURRENCE AND FEEDING UTILIZATION OF GRASS STRATUM IN ACACIA NIGRESCENS (CLAYS) - BURKEA AFRICANA (SANDS) SAVANNA MOSAIC ON RIFT FLOOR (APRIL 1973)

D. OCCURRENCE AND FEEDING UTILIZATION OF GRASSLAND PLANTS ON FEVERTREE - FLOODPLAIN ECOTONE BY IMPALA (FEBRUARY 1971). LINE INTERCEPT METHOD (12 X 5M.)

FIG 9.16 EXAMPLES OF GRASSLAND FEEDING UTILIZATION BY WILD UNGULATES



A. OCCURRENCE AND FEEDING UTILIZATION OF SAVANNA TREES (> 3M IN HT) IN 1 HA OF ACACIA NIGRESCENS – BURKEA AFRICANA MOSAIC (APRIL 1973)

0 = UNUSED, 1 = LIGHT USE, 2 = MEDIUM USE, 3 = HEAVY USE, 4 = SEVERE USE, 5 = TOTAL USE (COMPLETELY RING-BARKED, FELLED OR DE-CANOPIED), X = DEAD.

B. OCCURRENCE AND FEEDING UTILIZATION OF SHRUB LAYER (< 3M IN HT.) COMPONENTS IN 500M² OF ACACIA NIGRESCENS – BURKEA AFRICANA SAVANNA MOSAIC (APRIL 1973).
IN ADDITION TO THE ABOVE, SINGLE RECORDS OF 17 OTHER SPECIES WERE UN-UTILIZED.

FIG 9.17

FEEDING UTILIZATION OF WOODY STRATA
IN ACACIA-BURKEA TREE SAVANNA
ON THE RIFT VALLEY FLOOR

LEFT: Figure 9.17

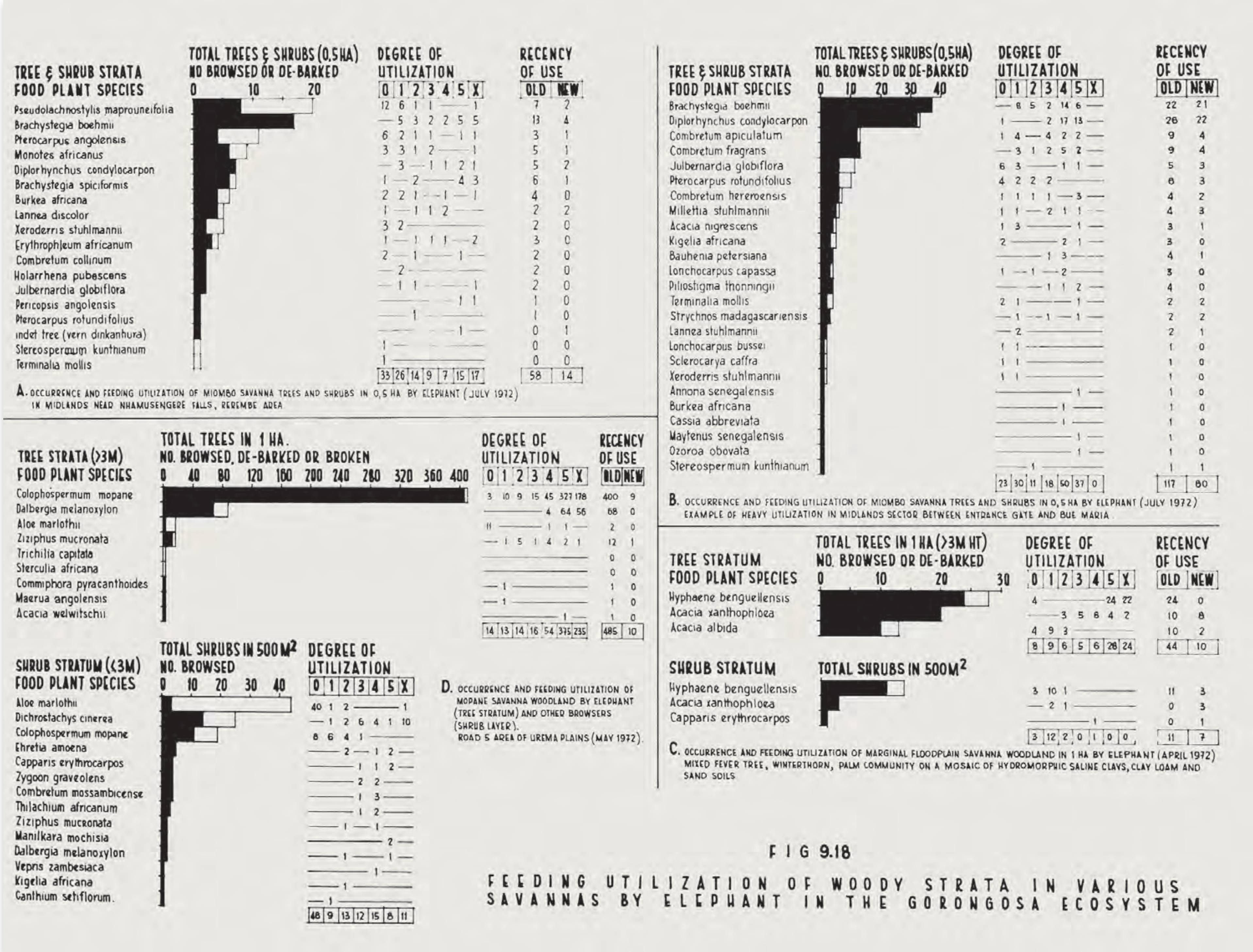
Feeding utilization of woody strata in *Acacia-Burkea* tree savanna on the Rift floor.

Pasture Conditions

Two contrasting grassland types occur in the ecosystem, those on leached acid sandy soils and those on heavy base saturated soils. The former are characteristic of the higher rainfall miombo savannas and dambos on either side of the Rift, and the latter of the Rift Valley. However the Rift Valley soils were laid down by alluvial fan sequences separated by slacks or shallow water lacustrine deposits. Thus, despite a lower, more seasonal, rainfall regime than the adjacent miombo, the alluvial catenas support a mosaic of both sourveld herbage of tall rank grasses, alternating with sweet, medium to short grasslands (chiefly *Urochloa, Heteropogon* and *Cynodon)*. Due to excessive hydromorphism in large areas of fertile bottomland soils in the Rift Valley, rapid growth responses are exhibited resulting in coarse rank growth similar to the miombo grasses, and apparently of very low food value as they are shunned by all grazers. As a corresponding

RIGHT: Figure 9.18

Feeding utilization of woody strata in various savannas by elephant in the Gorongosa ecosystem.



A. OCCURRENCE AND FEEDING UTILIZATION OF MIOMBO SAVANNA TREES AND SHRUBS IN 0,5 HA BY ELEPHANT (JULY 1972) IN MIDLANDS NEAR NHAMUSENGERE FALLS, REREMBE AREA

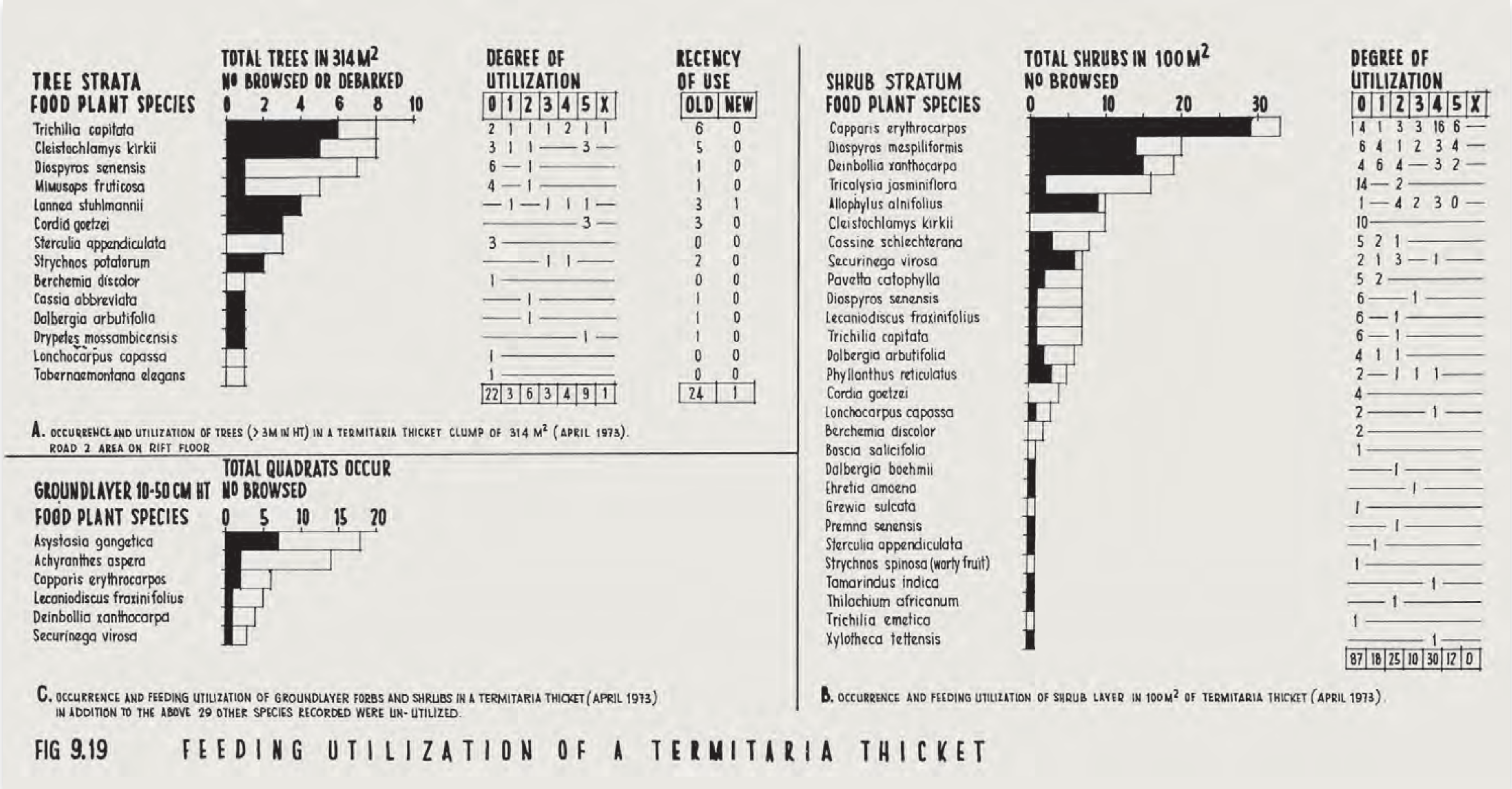
B. OCCURRENCE AND FEEDING UTILIZATION OF MIOMBO SAVANNA TREES AND SHRUBS IN 0,5 HA BY ELEPHANT (JULY 1972) EXAMPLE OF HEAVY UTILIZATION IN MIDLANDS SECTOR BETWEEN ENTRANCE GATE AND BUE MARIA.

D. OCCURRENCE AND FEEDING UTILIZATION OF MOPANE SAVANNA WOODLAND BY ELEPHANT (TREE STRATUM) AND OTHER BROWSERS (SHRUB LAYER).
ROAD 5 AREA OF UREMA PLAINS (MAY 1972).

C. OCCURRENCE AND FEEDING UTILIZATION OF MARGINAL FLOODPLAIN SAVANNA WOODLAND IN 1 HA BY ELEPHANT (APRIL 1972) MIXED FEVER TREE, WINTERTHORN, PALM COMMUNITY ON A MOSAIC OF HYDROMORPHIC SALINE CLAYS, CLAY LOAM AND SAND SOILS

FIG 9.18

FEEDING UTILIZATION OF WOODY STRATA IN VARIOUS SAVANNAS BY ELEPHANT IN THE GORONGOSA ECOSYSTEM



LEFT: Figure 9.19

Feeding utilization of a termitaria thicket.

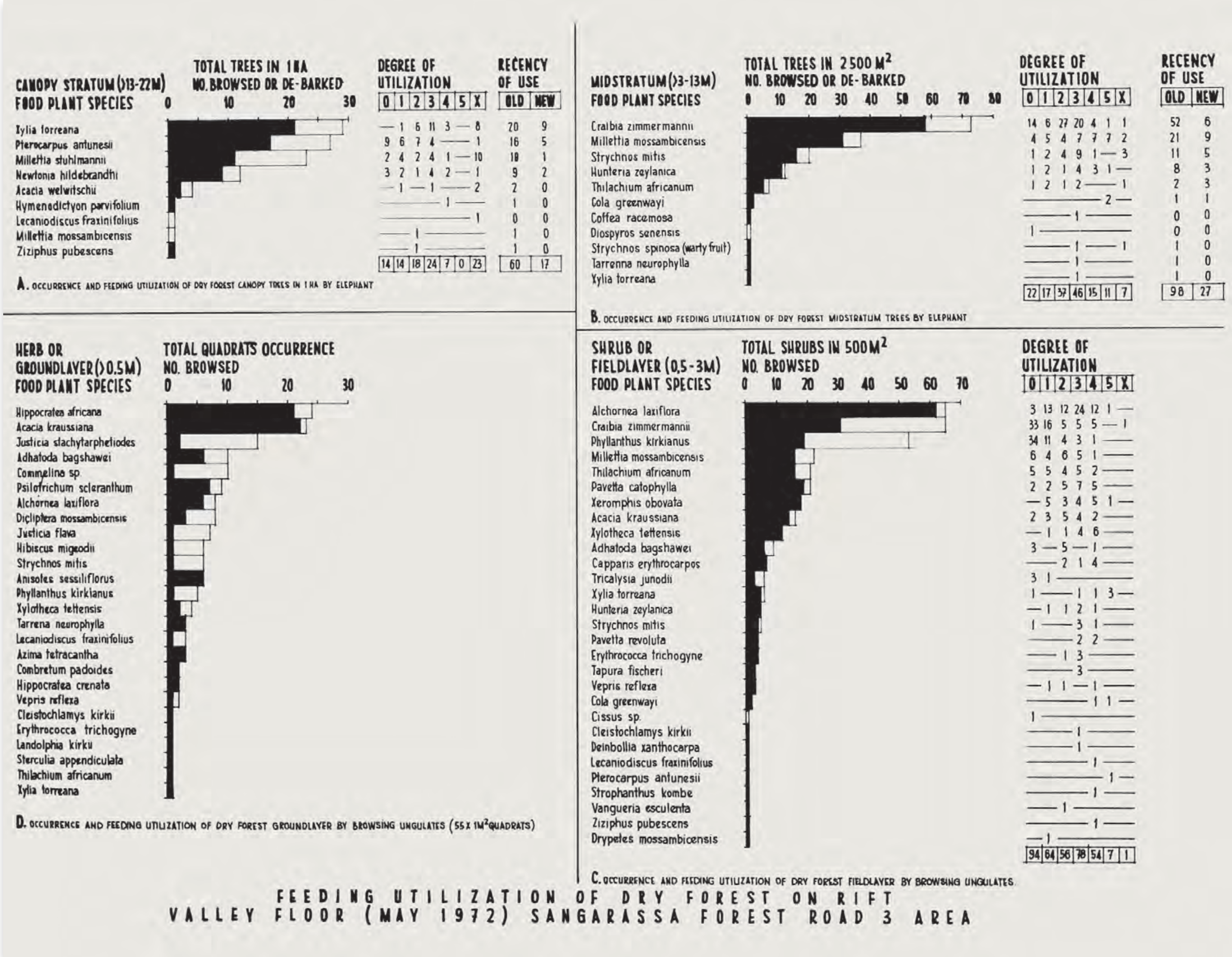
decrease in protein content of grass leaves occurs with advancing maturity, a rapidly maturing pasture is of little nutritional value for grazing ungulates soon after commencement of the growing season (Henrici 1928a, 1928b; Plowes 1957). Yet, when the same grass species are kept short by grazing or cutting, the imposed high vegetative production results in a correspondingly higher protein content (Plowes 1957, p. 45).

Comparative analysis of lower rainfall sweet grasslands on black clays at Matopos Hills in Rhodesia, with sour miombo grasslands near Salisbury, showed markedly contrasting differences in crude protein content. Whilst the sweet pastures contained a crude protein content of 20% in December, the sourveld values were 5.5% attaining a maximum of only 7.4% in the first week in January (Plowes 1957). A 6% crude protein intake was determined as the maintenance level for cattle in Rhodesia, however mass loss was incurred as soon as crude protein levels dropped below 12% (Plowes 1957).

In the Matopos Hills area, a drop from 20% to about 5% occurred over six weeks in response to drought (Plowes 1957). The detailed studies of Henrici (1928a, 1928b) in the Northern Cape–Botswana border area showed that phosphorus and starch content diminish simultaneously in grasses as soon as wilting or incipient drying occurs. Maxima of assimilation products occurred in early spring and during rains.

RIGHT: Figure 9.20

Feeding utilization of dry forest on Rift Valley floor.



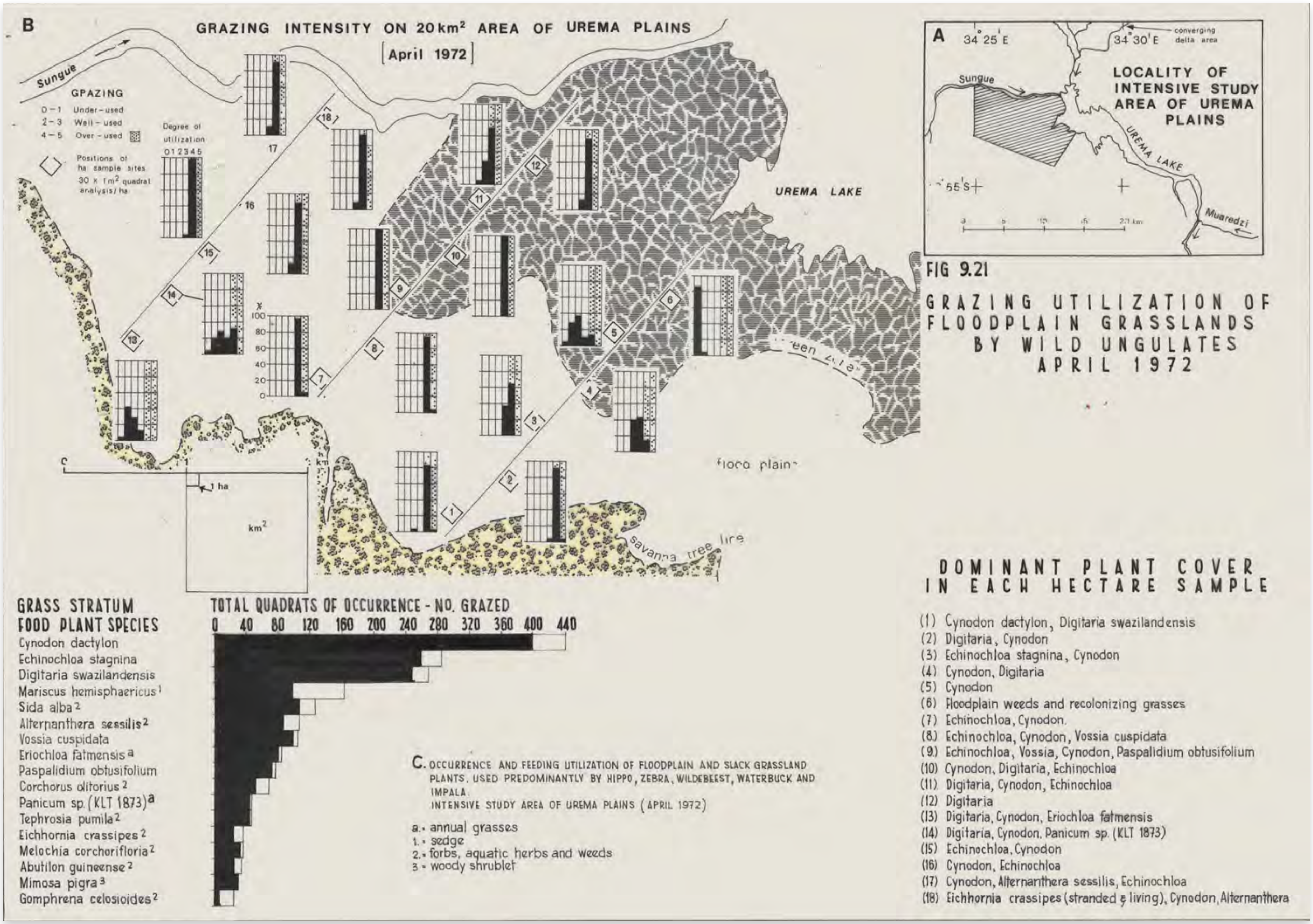


FIG 9.21

GRAZING UTILIZATION OF FLOODPLAIN GRASSLANDS BY WILD UNGULATES APRIL 1972

C. OCCURRENCE AND FEEDING UTILIZATION OF FLOODPLAIN AND SLACK GRASSLAND PLANTS, USED PREDOMINANTLY BY HIPPO, ZEBRA, WILDEBEEST, WATERBUCK AND IMPALA.
INTENSIVE STUDY AREA OF UREMA PLAINS (APRIL 1972)

a. = annual grasses
1. = sedge
2. = forbs, aquatic herbs and weeds
3 = woody shrublet

DOMINANT PLANT COVER IN EACH HECTARE SAMPLE

(1) Cynodon dactylon, Digitaria swazilandensis
(2) Digitaria, Cynodon
(3) Echinochloa stagnina, Cynodon
(4) Cynodon, Digitaria
(5) Cynodon
(6) Floodplain weeds and recolonizing grasses
(7) Echinochloa, Cynodon.
(8.) Echinochloa, Cynodon, Vossia cuspidata
(9.) Echinochloa, Vossia, Cynodon, Paspalidium obtusifolium
(10) Cynodon, Digitaria, Echinochloa
(11) Digitaria, Cynodon, Echinochloa
(12) Digitaria
(13) Digitaria, Cynodon, Eriochloa fatmensis
(14) Digitaria, Cynodon, Panicum sp. (KLT 1873)
(15) Echinochloa, Cynodon
(16) Cynodon, Echinochloa
(17) Cynodon, Alternanthera sessilis, Echinochloa
(18) Eichhornia crassipes (stranded & living), Cynodon, Alternanthera

LEFT: Figure 9.21

Grazing utilization of floodplain grasslands by wild ungulates.

In southern (Myre 1971) and central (Myre and Antao 1972) Mozambique, analyses of pastures showed quite different responses of the same species in different climo-edaphic situations. *Themeda triandra* on heavy latosols in an arid savanna climate was biologically active from September until April, and only until February on the coast in higher rainfall on leached sands (Myre 1971). Acid miombo grasses such as *Andropogon gayanus* and *A. schirensis* were found to be of feeding value for only four to six weeks in the spring, and thereafter are useless as pasture (Myre and Antao 1972).

These miombo and duplex soil dambo grasslands thus have a low carrying capacity (15 ha/SU), and an extremely short nutritive period as a food resource, with a high fibre content for the remainder of the growing season.

The analyses of Henrici (1928a, p. 1,054) further showed that a phosphorus minimum occurred in times of drought with coincident minima of starches and sugars. As a general rule the reverse situation was indicated by a phosphorus maximum. A phosphorus minimum also occurs in midsummer when assimilates are relocated to the stems and root crown for major development of the culms (Henrici 1928b, p. 1,055). Hence bimodal maxima in assimilates are exhibited by many grasses with the major peak in spring (Sept.–Oct.) and a second lesser peak in the autumn (Henrici loc. sit.). Other grasses follow a unimodal strategy with a single phosphorus peak in spring only, whilst yet others maintain a low content of assimilates with no decrease as their culms are developing year-round. Monthly variations in the nutritive value of sour Bankenveld grasses in South Africa showed three crude protein peaks; over the equinoxes and at the summer solstice (Joubert 1954, Table 7).

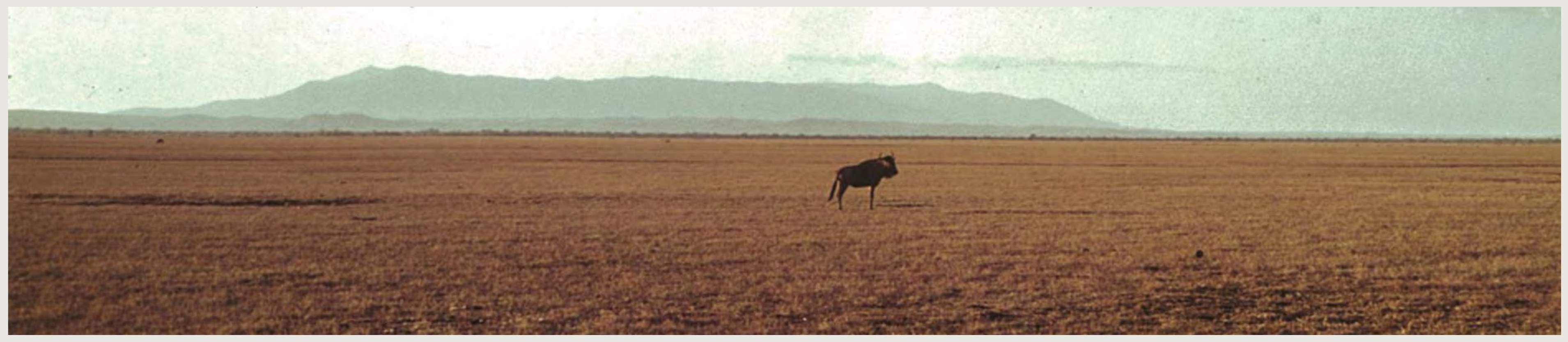
In his treatment of the Serengeti grazing ecosystem, Bell (1971, p. 91) remarks on the reduction of protein content in grasses during culm development. Thus a phenologically induced bimodality in nutritional status of many pastures may be a prime factor underlying bimodal mating and/or calving of many ungulates, including cattle (Bonsma 1939, 1940), at the time of the equinoxes.

The nutritive phenology of vlei or floodplain grasses on heavy soils is the crux to an appreciation of their high biomass supporting qualities. No local data are available, however Plowes (1957) showed that crude protein content in the dry season was highest in grasses on the bottomland black clays, and rain after drought resulted in the highest temporary rise of crude protein content in these grasses. In his study area, *Cynodon* (kweek) was at all times higher in crude protein content than other species.

The vlei grasses in the arid savannas of the northern Cape contain much higher phosphorus in both their leaves and roots than adjacent dryland species (Henrici 1928b, p. 1,104). The nutriment maxima and minima of the vlei grasses were not as uniform as those in the savanna, as different phases are followed by the different species. The main minima were however in March. Many of the vlei grasses showed a higher phosphorus content in the stalks than in the leaves during flooding, indicating that translocation was still in progress

TOP RIGHT:

Urema Plains in the wet season. Unflooded aspect of the short *Cynodon* - *Digitaria* grasslands with a microcosm of the massed concentrations of ungulates.



BOTTOM RIGHT:

Urema Plains in the dry season—the empty quarter. The same area as above four to five months later with golden-brown pastures typical of dried out saline grasslands.

FAR LEFT:

Seasonal rain-filled savanna pan at the height of the wet season (March).

LEFT:

Contrasting dry season aspect of the same pan shown far left four to five months later.

(Henrici op. cit). A second maximum resulted in the stalks when remigration of phosphorus occurred, followed by extremely low values in the culms and a higher phosphorus content in the roots.

Supporting the evidence presented by Plowes (1957), the vlei grasses in the northern Cape were characterised by high phosphorous content indicating high nutrient levels (Henrici op. cit.). Thus similar peaks and lows occur in the nutrient content of floodplain grasses but with a greater variation amongst the different species in response to environmental changes. As with the savanna grasses, wetting and drying affects their growth and nutritive status, but the better moisture and base status of vlei soils result in rapid maturation and a concomitant decrease in protein. Grazing sequences causing repeated growth flushes would maintain a high protein level.

The differential effects of dry and wet years on the nutritional status of flood plain grasslands do not seem to be recorded. It is not known, for example, whether high flood years in the Urema Trough would result in a predominance of pasture of low nutritional status due to the denitrifying effects of anaerobic reducing conditions of protracted inundation. It is considered that loss of nitrate in the gaseous form is enhanced by anaerobic conditions (Brady 1974, p.431) which would in turn effect protein levels in the grasses. Heady (1975, p. 195) points out that under most conditions in the early part of the growing seasons 'the water content of young forage may be so high that an animal cannot consume enough dry matter to be properly nourished'. Possibly therefore, in dry years when floodplain grasslands are reliant on direct rainfall, predominantly sweet conditions result.

The detrimental effects on pasture quality of the high salt content characteristic of floodplain and slack vertisols in the Urema Trough is the other unknown factor. Brady (1974, p. 399) notes three adverse features of sodic soils on the plant cover, the most important of which in the present context is the effect of 'active sodium ions on plant metabolism and nutrition'. Thus the two seasonal extremes of flooding and aridity possibly result in pasture of low nutritional value in the Urema Trough.

Judging solely from recorded observations, loss in animal condition on the Rift floor was directly related to too rapid drying out of pastures (salinisation? see Section 9.5), which implies that any adverse effects from excessive flooding are offset by heavy grazing pressure and maintenance of high nutritional levels of the preferred floodplain pastures.

The feeding behaviour of species such as baboon, elephant, warthog and oribi on the floodplains appear to be outward manifestations of the rise and fall in nutrient status of different parts of hygrophilous grasses such as *Echinochloa stagnina* and *Vossia cuspidata.* During the first rains leaves are grazed. In the period January to March, related either to maximal culm development or to midsummer drought, oribi feed almost exclusively on the culms of these grasses, returning to feed on the leaves in April if rains recur. In autumn and the early dry season the basal parts of these grasses are preferred by baboon, elephant and warthog, and baboon and warthog eat the ripe seeds by stripping the inflorescences through their mouths.

Ecotones, slacks and migration.

TOP RIGHT:

Baboon (*Papio ursinus*) in shallow waters of slack in autumn, feeding exclusively on basal parts of the aquatic grass *Vossia cuspidata*.

TOP CENTRE:

Part of a series of long lines of wildebeest and zebra migrating away from the nothern tandos (Nhamisangu, Macoreia) to the southern ‘green zone’ margins of the Urema Lake.

TOP FAR RIGHT:

Wildebeest and zebra grazing the last ‘green zone’ pastures of slack floors in the dry season when the surrounding savanna grasslands are dry and /or burnt out.

BOTTOM:

Ecotones, a preferred feeding station of Lichtenstein’s hartebeest. In the above example, grazing the sweet grasses on the termite hill pediment.

In the Save Valley in central Mozambique, seasonally flooded alluvial grasslands similar to those of the Urema are estimated to have a carrying capacity of 3–4 ha/SU (Myre and Antão 1972). In addition to the high protein content reported for *Cynodon dactylon* (e.g Plowes 1957; Dougall and Glover 1964) which together with *Digitaria swazilandensis* is the major short grass pasture in Gorongosa, Myre and Antão (1972) record the highest percentages of protein, calcium and phosphorous in the savanna grass *Urochloa mosambicensis* followed by *Panicum maximum* and *Heteropogon contortus*. In Table 9.3, *Urochloa* leads in the dietary preferences of 13 wild ungulates in Gorongosa, and *Urochloa* savanna grasslands occur on soils of high phosphorous content. Grassland dominated by *Urochloa* is classed at 6–8 ha/SU pasture (Myre and Antão 1972).

Relatively little is reported in the literature regarding the nutritive status of browse foods through the annual cycle. Analyses of Karoo bushes in South Africa indicated a tendency for bimodal equinoctial peaks in protein content (Du Toit et al. 1940) which may be related to the bimodal rainfall regime experienced in the Bushmanland region.

Five preferred browse foods in the bushveld of northeastern South

Africa, analysed on a monthly basis, showed crude protein peaks in spring or early summer and again in late summer or autumn. (Tables in Bonsma 1942). Of the five, mopane showed August, November and January/February, *Combretum apiculatum,* October and January peaks, *Boscia albitrunca*, October, December and April peaks, and two *Grewia* species, October/November and January/February peaks. These species exhibited several phosphorous and calcium peaks through the year related to the solstices and equinoxes (Tables in Bonsma 1942).

In Mozambique, two browse foods, mopane and *Combretum apiculatum* were analysed during different phenophases (Myre and Antao 1972). Both trees showed highest crude protein content in the spring (vegetative phase), and then again in the fruiting phase. Calcium content in both species was lowest in spring and highest in the fruiting phase, while phosphorous content remained the same through the growing season.

The tendency of two nutrient peaks in spring and autumn interspersed with two lows, appears to be related to the spring flush of new growth followed by a second high with the reproductive phases and a major low during the dormant period. The incidence of rain, droughts, soil moisture balance and thermal changes must all affect fluctuations in nutrient levels indicated by the woody species noted above.

The widespread occurrence of double flowering and fruiting in some trees at the time of the equinoxes, gives support to the possibility of bimodal nutritive peaks in many other woody plants. Bimodality in mating and/or calving in mixed feeders and browsing wild ungulates is reported by several authors e.g. Bigalke (1970) for springbok, Simpson (1973) for Zambezi bushbuck, and Anderson (1975) for impala. Whether fluctuations in nutritive levels of browse foods show parallel patterns to the grasses related to both phenophase activity and seasonal changes in the African savannas apparently still awaits analysis.

Physical Condition of the Wild Ungulates

During the 1971/1972 intensive study of a sector of the Urema Plains, a monthly record was kept of physical condition of the wild ungulates (Fig 9.22). Animal condition was determined by the visual assessment method of Riney (1960). Individuals and the proportions of herds were assigned to one of three condition classes (a) good—characterised by rounded contours of the posterior, (b) poor—characterised by extreme angularity of the posterior due to protruding skeletal processes, including the ribcage. (c) intermediate—between (a) and (b).

With the exception of zebra, those ungulate species most frequently encountered were recorded. Zebra proved to be difficult, probably due to the disruptive effect of their stripe patterns (Child 1968a), and recording of this species was discontinued.

The condition of grasslands was visually assessed by three features: (a) wilting, (b) discolouration (browning), (c) avoidance by grazers or a change in use of aerial portions to basal parts. These features together indicated the nutritional status of perennial grasses linked to the phases of their seasonal life processes of growth, reproduction and decline (translocation to roots), and interrupted by environmental factors which reset the phenophases.

The physical condition of seven ungulate species is correlated with the environmental condition that pertained between February 1971 and March 1972 on the Rift Valley floor (Fig. 9.22). This period covered the second and beginning of the third, in three consecutive years of low flooding and less than mean annual rainfall (averaging 150 mm below the mean). The most prominent feature recorded is the grave physical condition of the three largest high biomass herbivores. Hippo are in chronically poor condition for the greater part of the year, followed by elephant and buffalo. The third biomass group containing wildebeest, hartebeest, waterbuck and impala show a normal sigmoidal curve related to the seasons, with a rise in condition in the first rains, good condition over the summer to autumn, and decline in mid-winter and torrid period.

As the major portion of the hippo population is confined to the environs of the Urema Lake, which shrinks to an area of about 15 km^2, it is not surprising that they are in poor condition for the greater part of the year. This is particularly so as the hippo biomass is dependent on overgrazed lawns of *Cynodon dactylon* and *Digitaria swazilandensis* which undergo rapid episodic changes related to fluctuations in wetting and drying sequences and the aridifying effect of sodic alluvial clays. Unless a high soils moisture level is maintained, these pastures also undergo daily wilting and nocturnal recovery of turgor until they are completely dried out. As the floodplains are increasingly over-drained, their primary productivity is in rapid decline, and the adjacent savanna grasslands are burnt out every year, which affects elephant and buffalo particularly.

However, another aspect of the hippo situation is illustrated by an isolated herd of about 140 hippo on a cut-off meander of the Pungue River. They are within 10 km distance of two other isolated herds of some 25 animals each, but no others occur for another 30 km (Fig. 9.11). Their site is on the southwest corner of the park and is surrounded by extensive stands of 3–4 m high *Hyparrhenia, Panicum* and *Pennisetum* grasslands in which islands of overgrazed and sheet eroded hippo lawns have been formed by these short grass feeders. Vertical aerial photographs of the large herd showed that every animal in the herd was in poor condition. Thus hippo are dying amidst plenty as the tall pasture around them, un-stimulated by burning or cutting, is structurally unavailable, rank and thus nutritionally poor.

Rapid maturation and decline in food value of the grasslands appear to be the main factor triggering excessive utilisation of trees by elephant, rather than the occurrence of fire, which only occurs two to three months later in the annual cycle (Fig. 9.22). It is not understood why most of the elephant herds are in poor condition when there is abundant browse on the Rift floor, especially of termitaria thickets which are unaffected by fire. The small, male groups and lone tuskers are exceptions, all being in fair to good health throughout the year. By choice, the elephant in Gorongosa are reliant in the dry season on the remaining slack hygrophilous pastures, as shown by their distribution in the air counts and ground records of feeding. These sites are being increasingly over-drained and provide in the dry months only a narrow margin of green contested for by buffalo and most other ungulates especially zebra, wildebeest, and waterbuck.

In sum, the availability and suitability of grasslands and woody strata as food through the annual cycle is governed by the interplay of the following features:

(1) Rain occurrence and amount, and extent of rainless periods between each fall.

(2) Heavy rains and flooding on base saturated soils in a hot climate, resulting in rapid maturation of grasses with a concomitant drop in protein content and excess of rank, fibrous foliage.

(3) The rank grasslands are only utilised if they are physically altered (i.e. restructured, with forced vegetative regrowth of high nutritional value) by trampling, grazing (or cutting) or fire.

(4) The preferred sweet grasslands which cover smaller areas than the sour grasslands, become over-utilised during the summer and autumn grazing sequence and at the height of the dry season when they are fulfilling a life supporting role.

(5) The inadequate narrow dimension of the green zone in the dry season; most of the hygrophilous grasslands are now functionally equivalent to the seasonal savannas due to excessively fast run-off of rain and river floodwaters from floodplains and slacks, causing too rapid drying out and thus loss of primary production.

(6) Influence of the distance of surface water from pastures on whether they can be utilised sufficiently by coarse grass feeders to maintain their productivity.

(7) Matching or dissimilar phenophases in the various ecosystems, in the different strata in each system, and of similar species in different situations (i.e. the influence of mass and staggered food availability).

Animals, therefore, have a wide choice of foods through the annual cycle, resulting from a multiplicity of dissimilar chemo-edaphic influences, gradients, and, responses of superimposed phenophases. However, choice for grazing ungulates in particular, is suddenly reduced by drought and/or the incidence of fire.

The over-riding factor aggravating the rapid decline of the preferred pasture resource is the increasingly rapid drainage of the floodplains and slacks, which enables the base saturated soils to exert a maximal aridifying and saline influence that must adversely affect the nutritional status of pastures. The dense swards of grass extending to beyond the horizon in the miomobo and in the Rift Valley gives an illusion of a super-abundant food resource, however the falsity of this is indicated by the chronically poor condition of the three largest ungulates. Abundant pasture resources could, however, be made a reality by damping run-off and physically altering the grasslands (see Section 10.3).

Lower numbers of elephant and buffalo in the herbivore spectrum would result in even larger areas of useless coarse pasture than occurs at present, however it is these rank grasslands which are particularly used by specialist tall grass grazers such as sable and Lichtenstein's hartebeest, for example, which select the nodal shoots and leaf fascicles.

The areas of rank *Hyparrhenia* and giant *Panicum maximum*, which escape burning, lodge in the late dry season and expose the subordinate layer of preferred soft-leaved grasses and forbs (and/or their own basal shoots)

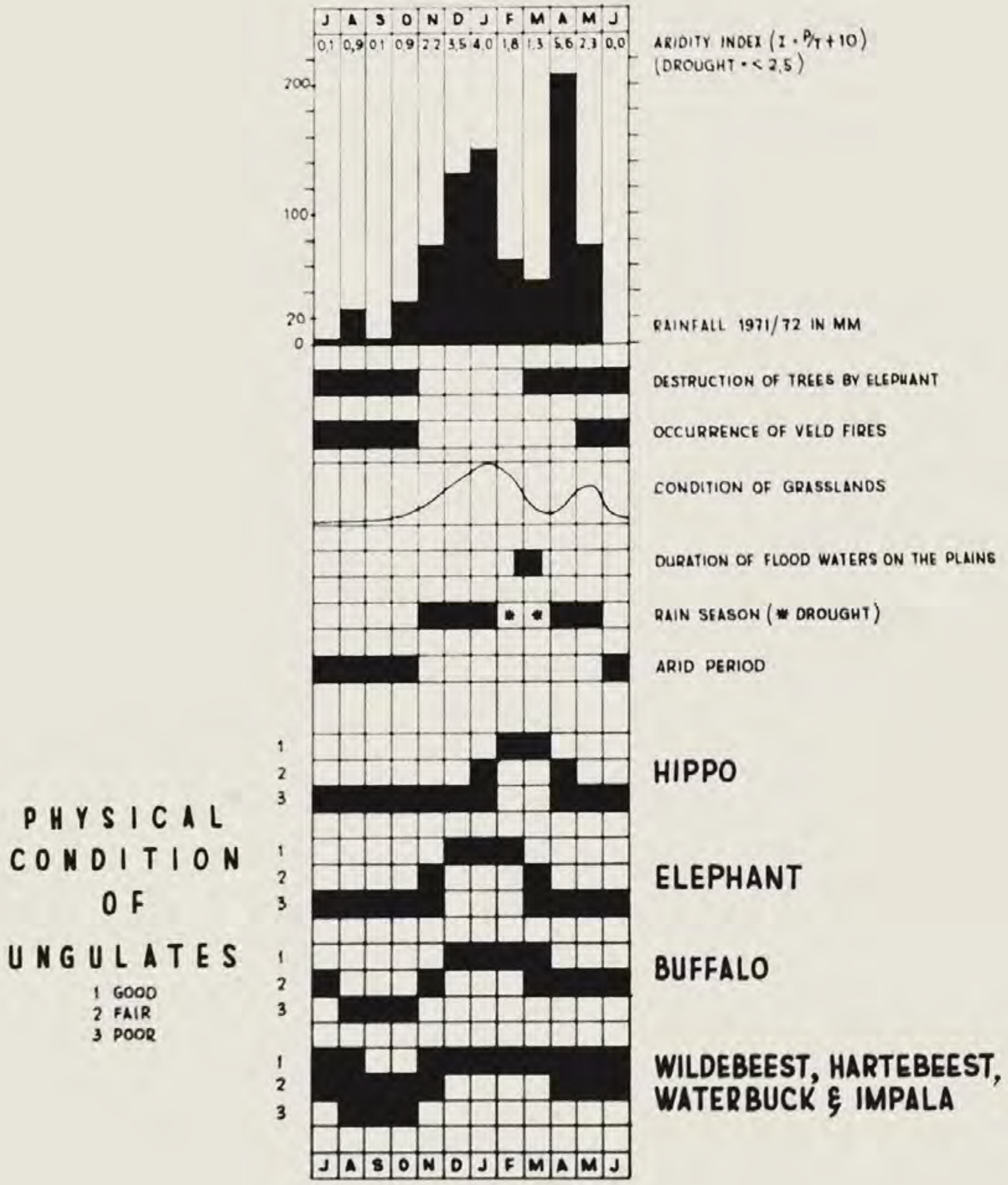


FIG 9.22

DIAGRAMMATIC SUMMARY OF THE RELATIONSHIP BETWEEN PHYSICAL CONDITION OF WILD UNGULATES AND ENVIRONMENTAL FACTORS COVERING THE PERIOD 1971/72

LEFT: Figure 9.22

Physical condition of wild ungulates and its relationship to environmental factors.

although ingress by smaller grazers is still difficult due to the mass of fallen stems.

The evidence from two annual counts shows the highest aggregations of large ungulate herds on the summer pastures, and a general break-up into small herds or groups in the dry season empathetic with the disruption in continuity of pasture quality and quantity. At the same time, a second local high concentration of herds occurs on the slack pastures as they become available, clearly illustrated by the wet and dry season biomass patterns (Fig. 9.13).The most important concentration sites at the height of the dry season are the Dingedinge slacks at the Urema–Pungue confluence and the narrow green zone on the perimeter of Urema Lake.

The high dry season biomass concentration shown in the north of the Park (Fig. 9.13) is anomalous as it was related to an isolated, unseasonal thunderstorm rain which occurred there a week before the air count. This isolated occurrence disrupted the 'typical' dry season pattern but emphasised the fundamental importance of the water factor in pasture utilisation. This area between the Nhandue and Nhamapaza rivers had largely escaped fire, and large herds of elephant, buffalo, zebra and wildebeest had left the environs of the Nhandue River to concentrate on the wetted area. Beyond where the rain has fallen, the landscape was empty of ungulates.

If soil moisture is maintained, a unique pasture feature allowing extended support of high biomass of large ungulates is the predominance and abundance of the preferred grass foods, which occur in association with an extremely low species diversity of forbs and other grasses.

The preferred grasses have a high carrying capacity due to their abundant vegetative reproduction when grazed which probably maintains a maximal nutritional level in the leaves.

The acid grasslands on leached soils, typified by the miombo and sandy high water-table dambos, by contrast

have an extraordinarily high diversity of associated grass species and forbs and an extremely low carrying capacity. This implies the possibility of sustaining a large variety of herbivore species in very small numbers. The low occurrence of soft-leaved plants may, however, be limiting to diversity in the ungulate spectrum. The significance of depauperate animal communities on leached (particularly the white sand podzols) substrates in the tropics is discussed in detail in a notable paper by Janzen (1974).

Amongst many others, he makes an important point, in comparing equatorial and temperate forests, which is clearly applicable to the sour and sweet grassland types in Mozambique. The sea of acid grasslands, as opposed to the more circumscribed and disjunct areas of sweet grassland on fertile soils, may have a far greater primary production or standing crop than the latter, but only a fraction of it is suitable or utilisable from the herbivores point of view.

High herbivore density and biomass on the more homogenous grasslands of fertile soils is enhanced by the grazing succession, which results in the multiplication of primary productivity and diversification of feeding levels where the same predominant grasses are favoured by most species.

9.6 MOVEMENT AND MIGRATION

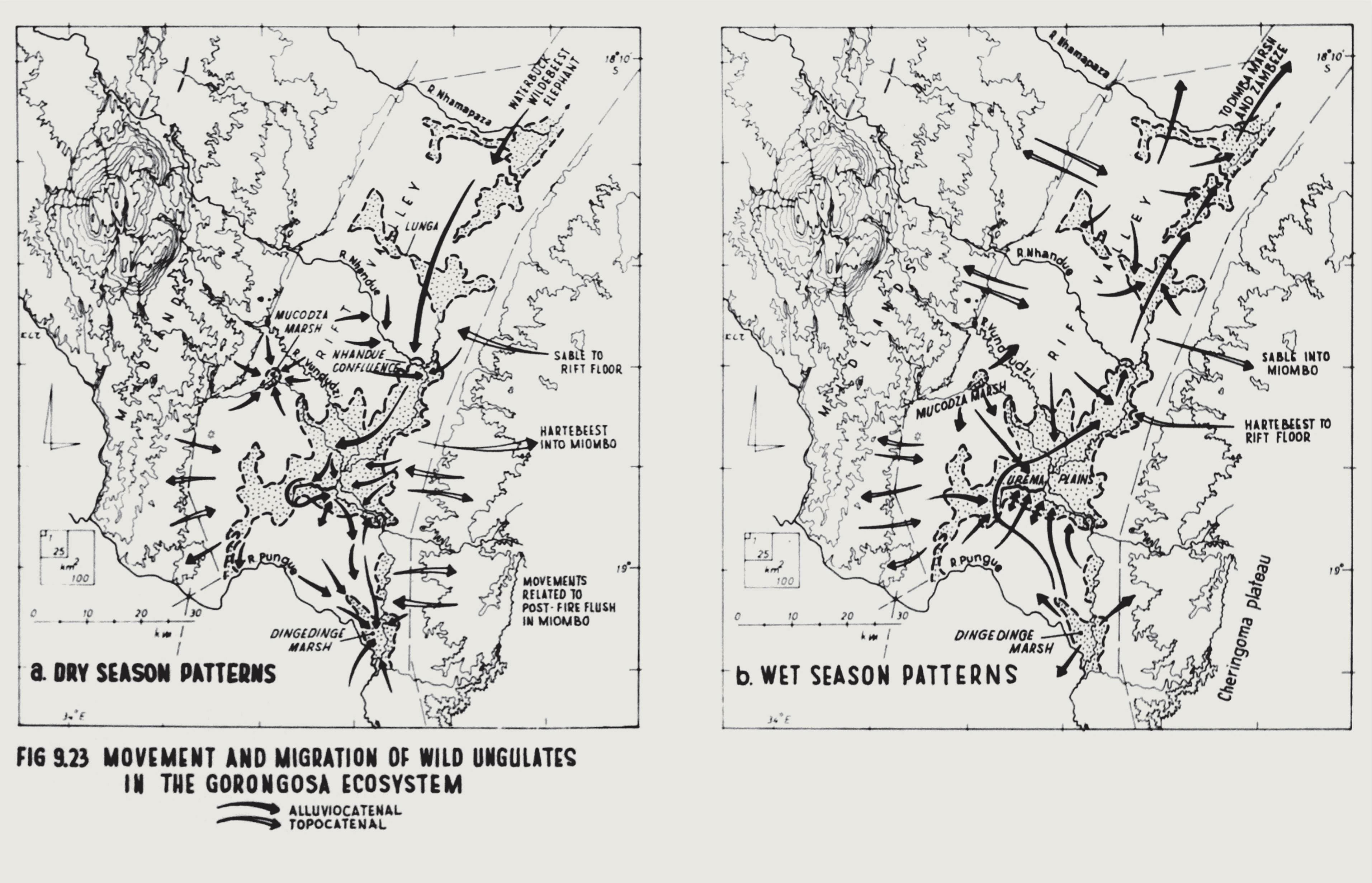
The preceding sections show that both local movement and the seasonal emigration and return of many wild ungulates are governed chiefly by seasonal and episodic changes in the food resources of different ecosystems. Whether the large aggregations of common ungulate species displace or affect the movements and habitat use of shy species such as sable and Lichtenstein's hartebeest is unknown. Nor is it known whether there are adverse effects of crowding at the height of the dry season which influence emigration or dispersal when the rains arrive.

Four main kinds of movement occur in Gorongosa of which the first, and to a lesser degree the second, categories can be termed migrations. The four categories are expressed by the ungulates in various combinations or singly:

(1) Longitudinal within the Rift Valley (migratory responses to phenology of alluvio-catenal systems).

(2) Transverse altitudinal movement between Rift Valley and miombo uplands, (migratory responses to phenology of topocatenal gradients).

(3) Local day and night alternation between open plains



LEFT: Figure 9.23

Movement and migration of wild ungulates in the Gorongosa ecosystem.

and savannas (related to predator avoidance, drinking, feeding and resting behaviour).

(4) Periodic and episodic movements following the change in availability of foods related to the incidence of unseasonal rain, drought and fire; also to staggered fruiting times of the same plant species in different sites (e.g. *Sclerocarya caffra*, *Diospyros mespiliformis*), or gathering of animals to mass fruiting in one sector (e.g. *Acacia albida* pods abundantly available in the dry season chiefly along the southern margin of the Urema Plains).

The lines of the main seasonal migrations and movements are summarised in Fig 9.23. The large ungulates which obtain most of their Iife requirements by moving mainly along the Rift Valley floor are buffalo, wildebeest, waterbuck, zebra, impala, and hippo. The ungulates which require both the Rift floor and hill country on either side are elephant, sable, Lichtenstein's hartebeest, and eland. Of the species which move primarily along the Rift Valley plains, zebra and waterbuck (which share the same habitat, except the shallow water zone) show contrasting population density patterns. The largest number of waterbuck within the park occurs during the dry season when there are the least number of zebra; in the wet season it is the opposite. In the rains small groups of waterbuck have been seen from the air, moving north in lines towards Dimba Marsh.

Of those that use the Rift floor and adjacent hill country, sable and Lichtenstein's hartebeest, which use the same habitat, show an opposing density pattern. The most sable occur on the Rift floor in the dry season, and the most hartebeest in the same area in the wet season. Small groups of zebra, wildebeest and buffalo also move up into the *Brachystegia* savannas periodically, following the new growth after unseasonal rain or post-fire flush of grass. It is suspected that some interchange of zebra groups occurs across the Cheringoma Plateau between the Rift Valley and the southern Zambezi Delta population at Marromeu.

Movement and migration, therefore, largely explores the availability of suitable food resources of uneven distribution and the seasonal changes in habitat structure and physiognomy. As the wild ungulates in Gorongosa are mostly water dependent species, exploration in the dry season is controlled mostly by the occurrence of surface water, and with the advent of the rains the widespread supply of water allows full expression of opportunistic exploration particularly in the Rift Valley where there is generally a minimum of the one rain-filled pan per hectare.

In 1969, with the experienced assistance of José Tello (chief warden at the time), experimental marking of certain ungulates for migratory studies was carried out. A number of buffalo, elephant, wildebeest, and zebra were immobilised with the tranquillizing drug etorphine (M99) using the Palmer Cap-Chur gun and marked using a variety of methods including ear-notching, collars, tags, cold branding, and paints. With the exception of the ear notches, the results were disappointing and further attempts were discontinued as the use of a light aircraft proved quicker and more efficacious for monitoring migratory movements. In addition field staff were relatively few and widely spaced, thus any sightings would have been minimal in the 10,000 km^2 area.

9.7 NATALITY, MORTALITY AND THE SEASONS

Minimal data are presented in this section as natality and predation was planned to be part of the second stage research programme for Gorongosa on population ecology and management.

Natality

The months in which newborn young were recorded in the park are noted in Table 9.5. Inadequate quantitative data allows for only the conspicuous peaks to be marked. The *prima facie* data indicate four kinds of reproductive strategies:

(1) Torrid period birth peak, exemplified by Lichtenstein's hartebeest. Most calves are born in pre-rain scorched period when post-fire grass flush occurs, indicating mating in the first rains.

(2) Births with the first rains, exemplified by impala and wildebeest. Mating in the wildebeest occurs mainly over the autumnal equinox and the month following. Impala were recorded mating over the same time until May and again over the spring equinox.

(3) Bimodal equinoctial peaks. e.g. impala (two breeding peaks are recorded for impala in Zululand by Anderson 1975), and other species e.g. bushbuck (Simpson 1973).

(4) Almost year-round calving with peaks unidentified, e.g. buffalo, elephant, hippo, nyala, waterbuck, and zebra.

Hippo calving peaks 6° north of Gorongosa in the Luangwa Valley occur from January to March (Marshall & Sayer 1976) and 6° south, in the Kruger National Park, peaks are later, in April and May (Pienaar et. al. 1966).

Mortality

Predation

Routine collection of skulls and lower jaws of all definitely identified lion kills was made by ranger and research staff and housed at the Chitengo field laboratory. This, of course, biased the evidence in favour of adult ungulates as predation on young leaves little to no skeletal remains. A preliminary work on the lions of Gorongosa including predation is being prepared by José Tello.

The lion kills recorded from the Urema Plains sector of the park were predominantly old male buffalo, wildebeest, zebra, and waterbuck to a lesser extent. In the dry season adult hippo were killed in abundance around the Urema Lake and its Sungue arm.

Disease

Apart from high parasite infestation rates in some ungulates collected, the resident and visiting veterinarians from the Veterinary Institute in Maputo reported no evidence of diseases which can attain epizootic proportions, such as anthrax, heartwater, and rinderpest. The serious impact that strongylid gastro-intestinal infestations have on the beef economy in Mozambique is reported by Silva and Gonçalves (1972).

Plant poisoning

Accounts of losses in wild ungulates from plant poisoning are rarely reported. Many of the symptoms are easily confused with anthrax (Steyn 1934; Monnig & Veldman 1961). Anthrax outbreaks occur during seasonal extremes, mainly in October in the Kruger National Park (Pienaar 1961), and over the equinoxes in Etosha National Park with a maximum peak in March and April (Ebedes 1974). These outbreak periods are therefore coincident with the most rapid fluctuations in climatic factors, and with growth and wilting of grasslands, plus the pre-rains spring flush of geophytes and suffrutices which are often the only green plants available at the time.

TABLE 9.5
Months in which newborn ungulates were recorded in Urema Trough.
Conspicuous peaks are indicated by boxes. ▣ (Data recorded by JLPL Tello and the author).

SPECIES	J	A	S	O	N	D	J	F	M	A	M	J
Buffalo	●					●	●	▣	●	●	●	
Bushbuck					●	●	●			●	●	
Bushpig							●	●				
Eland		●	●	●	●							
Elephant	●					●	●	●	●	●	●	
Impala					▣	●	●	●	●	●	●	
Kudu	●		●		●		●	●	●			
Lichtenstein's hatrtebeest		●	▣	●	●	●						
Nyala	●		●	●	●			●	●	●	●	●
Oribi					●		●	●		●		
Red duiker					●		●					
Reedbuck	●		●	●					●			
Sable		●	●	●	●	●	●	●	●			
Suni					●	●						
Waterbuck	●	●	●	●	●	●	●	▣	●	●	●	●
Warthog			●	●	●	●	●	●				
Wildebeest					●	▣	●					
Zebra	●	●	●	●	●	●	●	●	●			

In the torrid period in Gorongosa, buffalo in extreme debilitated condition with swaying hindquarters and blood tinged diarrhoea, were encountered where large areas had been burnt out. No reports of anthrax or other disease were made by the resident veterinarian. In October 1972 large numbers of buffalo died with the above symptoms and professional hunters in the north of the ecosystem on the Rift floor reported deaths of eland, nyala (mainly males), reedbuck, warthog, waterbuck and zebra. October 1972 was the second year of less than mean annual rainfall and the greater part of the country had been burnt out. Some of the buffalo deaths were close to watering points.

Two eland encountered by the hunters ran and fell repeatedly, lying on the ground and pawing the air (cycling movements). A similar behaviour was reported for bushpig in the south of the Park at the same time. These latter symptoms are typical of plant poisoning by lilaceous genera (*Ornithogalum, Urginea, Gloriosa*) known collectively as *slangkop* in South Africa, or of tulip poisoning by *Moraea* (*Iridaceae*), all of which occur in the area (Steyn 1934 and pers. com.). Another likely culprit, which is abundant on certain floodplain sectors (e.g. Macoreia), is the horse-tail *Equisetum ramosissimum*. This plant remains green when all grasses are completely dried out, or it re-shoots in October before the grasses. The symptoms caused by its consumption are similar to those noted above, including staggering, falling down, and shivering of the body, but the poisoning is apparently not fatal (Steyn 1934, p. 201).

Apart from the possible sources of poisoning mentioned above, a likely widespread source that I became aware of in Gorongosa, is the natural development of lethal amounts of prussic (hydrocyanic) acid in certain grasses under wilting conditions. There is apparently no published reference to the effect of prussic acid of wilted pastures on wild ungulates, hence this subject is explored briefly here.

In South Africa, where it is known as *geilsiekte*, 'prussic acid poisoning is one of the most common and fatal forms of plant poisoning occurring in animals, especially sheep, goats and cattle. It is responsible for annual losses of thousands of animals…aggravated by... rapid climatic changes as rain followed by drought, heat, frost…' (Monnig and Veldman 1961, p. 223).

In summarising the conditions responsible for producing fatal amounts of prussic acid, Steyn (1934 and pers. com.) lists the following: wilting in hot dry weather (especially in pre-rain spring), post-fire flush in dry weather, bruising, trampling, early frosts in autumn, the rapid flush and wilting of grasses in over-grazed sheet eroded areas. This author also makes the important point that high protein grasses and those occurring on fertile base saturated soils are most liable to produce toxic amounts of prussic acid when wilted. The addition of nitrogen fertilizer for example, stimulates the production of prussic acid when wilting conditions occur.

Of the grasses which produce high concentrations of prussic acid in the Cape–Botswana border area (Henrici 1926) and near Pretoria (Steyn 1929, 1934) the following occur in Gorongosa: *Aristida congesta, Cynodon dactylon, Eustachys paspaloides*, *Pogonarthria squarrosa, Sorghum verticilliflorum* and *Themeda triandra*. Other grasses in Gorongosa with high protein content which may be suspected are *Digitaria swazilandensis, Urochloa mosambicensis* and possibly hygrophilous grasses such as *Echinochloa and Vossia*.

In *Cynodon, Eustachys*, and *Sorghum*, prussic acid content increased from early morning until about 14h00 followed by a slight decline until 18h00 and a rapid decline to zero at sunset (Steyn 1934). Wilted grasses tested several hours after turgidity was regained from rain, showed negative results (Henrici 1926). This author noted that in her study area, the development of a purplish-red colour on drying out was a field diagnostic feature of grasses with little to no cyanogenetic compounds, and those containing these compounds never showed this discolouration.

Monnig and Veldman (1961) note that the symptoms for anthrax, heartwater (rickettsioses) and prussic acid poisoning are similar. Prussic acid is a rapid and fatal poison, 'large amounts causing death almost instantaneously with spasms and respiratory paralysis' (Steyn 1934). Pienaar (1961, p. 8) describes the symptoms for anthrax in wild ungulates during an outbreak in the Kruger National Park '... in the majority of cases it appeared that death occurred suddenly and there were few or no signs of kicking or struggle. A zebra was found dead with a mouthful of green grass on which it had been feeding…' which fits closely the symptoms described for lethal prussic acid poisoning (Steyn 1934 and pers. com.; Monnig and Veldman 1961).

Experiments by Steyn (1933, 1934) showed that sulphur administered to stock during circumstances leading to wilting of pastures was an efficient poisoning preventative treatment. In Etosha National Park a longterm detailed study by Ebedes (1974) showed highest occurrence of anthrax deaths in wild ungulates over the spring and autumn periods. He suggests that animals which recover may build up an immunity in adults, which is then broken by an unknown stress factor.

The summer and autumn grazing in Etosha is concentrated on *Enneapogon desvauxii* grassland, a high protein species which shows rapid flush and wilting responses to environmental changes. This grass can thus be highly suspected of being a major producer of prussic acid in wilting conditions.

Most of the natural springs and borehole waters used by wildlife in Etosha have a high sulphur content. In the same area many gravel pits were made for the removal of road construction material and these bare depressions are filled by the rains in summer and are important nuclei for anthrax (Ebedes 1974). Ebedes has for many years held that the gravel pits were a prime culprit in the explosive increase of anthrax in the summer grazing area of Etosha (op. cit.). It is possible that these gravel pit waters are deficient in sulphur and thus provide no natural preventative to any prussic acid effects which, if it does not kill them, could lower the resistance of wild ungulates to anthrax or any other disease. If prussic acid poisoning turned out to be the unknown stress factor, the use of sulphur in drinking water will have far-reaching application in wildlife areas with endemic anthrax. Henrici (1926) and Steyn (1931, 1933) describe a simple chemical field test for determining cyanogenesis (prussic acid formation).

Drought

Some examples of environmental extremes on wildlife in the Urema Trough are related by hunters from the region. A hunter of the early days in Gorongosa reports that an extreme drought occurred in 1934. This was aggravated by burnt out grasslands and large numbers of buffalo, hippo, waterbuck, and wildebeest died. At that period zebra are said to have been numerically dominant and only a few died in the drought. The Urema Lake dwindled to a narrow water and the Vundudzi River from Gorongosa Mountain only just flowed (Mr J Gamble, Muda Sugar Estates, Beira District, pers. com. 1969).

Another extreme drought period was experienced over the consecutive years 1953 to 1954 when high numbers of hippo, waterbuck, and wildebeest died. A slight flow continued in the Vundudzi River but the lake was again reduced to a narrow strip of water. Coincident with their poor condition, some of the waterbuck and wildebeest may have been infected by disease as many tribespeople died after eating the meat of these two species, (data from old game guards born and bred in the Chitengo area, pers. com. 1969).

Flooding and wet years

Flooding of the Urema slack basin is gentle but along the Pungue, Nhandue and Nhamapaza rivers it is sudden and strong. Mass deaths from flooding are, however, not reported from these rivers. In the Marromeu sector of the Zambezi Delta large numbers of buffalo were killed by Zambezi floods prior to the construction of the Kariba Dam (Tinley and De Sousa Dias 1973, p. 111). The last major flood occurred in December 1958 when many buffalo and waterbuck were said to have been washed out to sea.

In the Kruger National Park (Dr. G.L. Smuts pers. com.) a general relationship has been noted between the increase of buffalo and decrease of wildebeest in high rainfall years and the reverse in low rainfall years. Evidence from a Zululand game ranch showed that wildebeest calves were most affected by tall grass conditions in wet years and highest losses occurred under these circumstances amongst the yearlings (C.L. Tinley pers. com.).

No conclusive data is availabe from Gorongosa on the differential influence of cold snaps associated with frontal polar air incursions, or of dry and wet years on the various ungulate species. Wildebeest alone showed a marked coincident rise in population during the three consecutive dry years 1970–1972 (Table 9.2).

9.8 ANIMAL FEEDING ASSOCIATIONS

In the geoecological evolution of a landscape and its biotic associations the preferential seed dispersal of plant foods favoured by animals forms a major selective pressure or bias. In the Gorongosa ecosystem the predominantly bird and mammal dispersed plant components of all thicket types and forest, which are actively invading savanna and grassland, emphasizes the dimension of this bias.

The enormous, complex, and fascinating field of animal associations in the sea and on land are dealt with in part by Allee et al. (1949, Ch. 23, p. 35), Limbaugh (1961), Moynihan (1968, 1973), Cott (1975) and Wilson (1975) amongst others. A classic symbiotic relationship in the African savannas, involving widely divergent animals with a common interest, is that of the greater honeyguide *Indicator indicator* with the honey badger and man in search of the products of the African honey bee *Apis mellifera,* analysed in detail by Friedman (1955, pp. 25–71).

In the present study, the interspecies associations of birds and/or primates with ungulates in fruit-eating relationships are seen to be one of the most important multiplier effects in system dynamics due to the synchronous combination of seed dispersal activities at both the arboreal and terrestrial levels. What is dropped or dislodged by arboreal species is used directly by the attendant terrestrial species below.

An important component of ecosystem evolution and replacement is therefore any reinforcement of the selective bias, a multiplier effect, by interspecies feeding associations. The multiplier effect is compounded by the centripetal influence of the fruit tree as a perch, resulting in the development of tree-base thickets of animal-preferred fruit species.

Some species which do not, as far as I know, take part in interspecies associations, such as the frugivorous civet cat, can have an inordinate influence on succession by their habitual use of the same dung middens The implications of these preferential selection pressures will be dealt with in the following section on animal succession.

The vertebrate feeding relationships in Gorongosa can be grouped around three main categories of animal or other central factor: (a) 'beaters', (b) 'caterers', and (c) 'socialisers'. Most of the associations are opportunistic responses to food availability and the faunal make-up of a particular circumstance. The above categories can act singly, or in concert, change kaleidoscopically with circumstances, and include a fourth category 'protectors' not dealt with specifically here. The 'protective' role afforded by one or all of several species occurring together relates to the positive advantages of their dIfferent levels of danger perception or awareness in different situations (refer to Moynihan's work quoted below). Another kind of protective role is the nesting association of passerine birds with the nests of 'protectors', e.g. weaver birds nesting in the same tree as a bird of prey, or waxbills nesting next to hornets. In most of the interspecies associations noted in Gorongosa, a symbiotic relationship exists between the animals, which exhibit by their reactions complete understanding of each other's alarm calls, feeding calls and behavioural postures or signals associated with threat, food finding, and danger.

From 250 sight records of higher vertebrate associations on the Rift floor, some examples from each category are given below with emphasis on the yellow baboon–ungulate associations in the savanna–thicket mosaic of the Rift floor, and hornbill – samango monkey-ungulate associations in forest.

Beaters

Embraced by this category is any abiotic or biotic factor which makes a food resource more freely available through physical disturbance. At the simplest level are veld fires, attended by many birds such as kites, marabou storks, black-necked herons, bee-eaters, drongos, flycatchers, bulbuls and shrikes during the day, and replaced at sunset by myriads of bats feeding on the disturbed insects. In the forests of the mountain and Cheringoma coast, the rain of insects disturbed by columns of driver ants (*Dorylus* sp.) is attended by alethes, robins and sheppardias.

Birds and dragonflies follow the passage of large mammals, or even a vehicle, to feed on disturbed insects. In wooded terrain, drongos hawk insects disturbed by feeding elephant, and in aquatic sites, jacanas crowd around elephant or hippo feeding amongst water grasses and lilies.

A more conspicuous and common example of the same relationship is that of cattle egrets with buffalo and elephant, or with domestic stock. A game ranger in Gorongosa once recorded a ground hornbill used simultaneously as a perch and as a beater by carmine bee-eaters. In east Africa this has been recorded for kori bustards as well as for ground hornbills (Cott 1975).

Caterers

'Caterers' are animals which by their method of feeding make food resources easily available for other animals. Lion kills provide food for vulture attendants, and tree-felling by elephant makes browse available to smaller browsers. These are two examples amongst many. In this

RIGHT: Figure 9.24

Animals that associate with baboon on the Rift floor in the Gorongosa ecosystem.

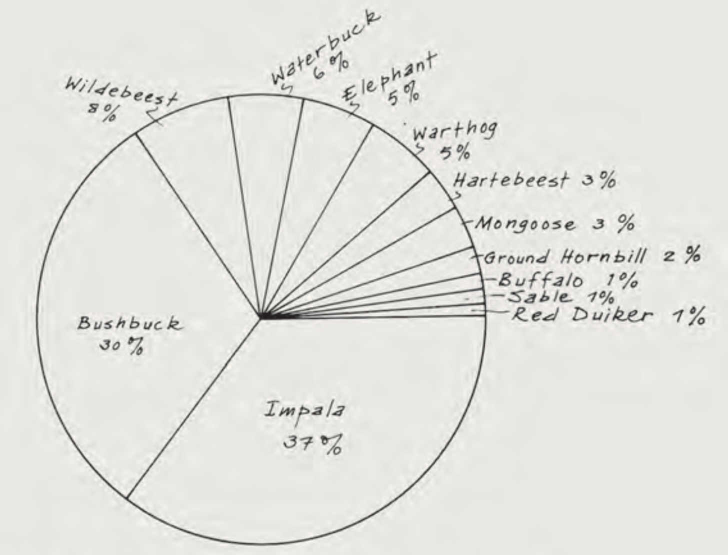


Fig 9.24 ANIMALS THAT ASSOCIATE WITH BABOON ON THE RIFT FLOOR IN THE GORONGOSA ECOSYSTEM.

category the arboreal frugivores play an important role by dropping or knocking fruit onto the ground where it is then available to many other species of animal. Both the caterers and the beaters are nuclear species, in Wilson's (1975) terminology, which other species seek out and follow. Those that seek them out are referred to as attendant species (op. cit.). The nuclear position of yellow baboon in feeding associations in the Rift Valley habitats is illustrated by the preliminary data depicted in Fig. 9.24. This figure only shows the 'tip of the iceberg' in fact, as records are totally biased to those that were easily observed. The association of bushbuck, warthog, dwarf and banded mongoose with baboon is probably very much higher, and there are probably seasonal changes in the predominant attendants.

When the associated sounds of baboon and/or falling fruit from a tree are heard, species such as elephant, bushbuck, impala and red duiker often stop what they are doing and move towards this particular feeding station. Here they feed on the shower of partially bitten, rejected and disturbed fruits which land beneath the tree. An example of this behaviour was provided by a herd of 20 impala grazing on the floodplain-savanna ecotone. One hundred metres away, without attendants, was a large troop of baboon feeding on the ground. A little later at the sound of an *Acacia albida* pod dropping with a rattle onto the ground, the oldest (apparently) female impala looked up immediately to the canopy of the tree, where baboons were now feeding, turned and walked over, followed by another impala, to feed on the falling pods. None of the other impala had looked up but they followed closely behind the old female. When the baboons moved through the canopy to an adjacent tree the impala followed beneath and stayed with the primates for more than five hours. My observations support De Vore and Hall (1964, pp. 58–59) who state that impala and bushbuck '...seem to actively seek out baboon groups and stay with them for all or most of the day'. The period that they remain in association appears to be related to habitat make-up and to baboon feeding strategies. The association of impala and/or bushbuck with baboon is recorded from most areas where they occur together, but there are apparently regional differences in the tendencies of any other species to associate with baboons (Elder & Elder 1970).

In the forests of the Gorongosa transect, silvery-cheeked hornbill (*Bycanistes brevis),* or trumpeter hornbill (*B. buccinator)* and samango monkeys feeding in the canopy act as nuclear species to ungulate attendants including blue duiker, red duiker, suni and bushbuck. Associated at one *Ficus polita* for example, in the forests of the Cheringoma coast, were both species of hornbill with suni and red duiker below them feeding on fallen fruit. In the Rift Valley a pair of red duiker was observed to follow a troop of samango monkeys from the security of a forest into the adjacent savanna–termitaria thicket mosaic. On the way to a termitarium thicket the samango stopped to feed on *Acacia nigrescens* flowers, and those dropped were eaten by the duiker. Inside the island thicket the duiker were feeding on fruit of *Cassine schlechterana* and *Berchemia discolor* dropped from the canopy.

In thicket on the Rift floor, a bush squirrel *Paraxerus cepapi* was noted in attendance to a red duiker that had pawed-up potato-like tubers, the squirrel darted down and collected pieces of the tuber chopped up by the duiker's hooves. In the Cheringoma forests tribal hunters report suni feeding on the fruit flesh being dropped by a red squirrel *Paraxerus palliatus* that was more intent on getting at the kernel.

In the Congo equatorial rain forest, long-tailed hornbill *Tropicranus albocristatus*, monkeys and a large squirrel form feeding associations (Chapin 1939, p. 352). The monkeys, feeding on fruits, act as beaters by putting up insects which are taken by the hornbill, and as caterers by biting off some of the fleshy parts of the fruits exposing the kernel which the squirrel is after.

A coarse feeder such as elephant provides masses of partially digested and broken fruit in its dung. The dung is invaded by insects such as scarabid beetles and termites. Baboons feed on the outer parts of broken up marula *Sclerocarya caffra* fruits, and bush squirrels eat the seed kernels of marula and the termites found in the dung (one stomach sample contained 50% of each). Many other animals such as francolin, guineafowl and mongoose search elephant dung for food. The large communal dung heaps formed by white rhino are also centres of food searching activity for many kinds of animals (Player and Feely 1960).

Socializers

In this group are the associations actively formed by gregarious species with other species, not necessarily with the primary intent of feeding. These associations are over and above the more casual or coincidental associations of, say, a zebra and wildebeest mosaic on the same pasture, although all gradations between the two extremes probably occur. Two examples of active association are given. In the heat of the day whilst a herd of 16 adult and subadult waterbuck males were resting, ruminating, or sparring in the shade of winter thorn trees on the edge of the floodplains, a large herd of impala entered the floodplains just over one kilometre away. One of the older males looked up and watched the dots of the impala intently. This individual then walked off towards the impala herd followed eventually by all the other waterbuck. They traversed the one kilometre to the far edge of the treeline and joined the impala herd without feeding once. After joining up they followed the impala out onto the floodplains for another kilometre before settling and feeding together with them on the green zone of the lake margins.

The other example is provided by lone territorial wildebeest bulls which actively seek out the company of baboon troops and move with them to the limits of their territories. This latter association appears to be a mutualism related to sociality and mutual alertness to danger. Although feeding is not necessarily involved, the lone bull will have more opportunity to feed because of the baboons' alertness. Low attentiveness on the part of ungulates in the company of primates seems to be a common feature of these associations (Struhsaker 1967; Washburn & De Vore 1969). In the Rift savannas, vervet monkey troops have been noted in association with one or other of the following ungulates: bushbuck, impala, oribi, and lone wildebeest bulls. It was not ascertained whether these were feeding associations, or which were the nuclear and attendant species.

No data were obtained in Gorongosa on whether fruit eating associations of canopy and ground level feeders (or other symbioses) were confined solely to daylight hours and whether other associations were formed at night, e.g. between animals such as bushy-tailed galago, fruitbats, civet, side-striped jackal, bushpig and other ungulates.

The occurrence of interspecies gregariousness is a conspicuous feature in the savanna–thicket mosaic of the Rift Valley where high densities of primates and ungulates occur. It also appears to be a common feature in the forest area, but was not recorded from miombo, probably due to the general scarcity of larger mammals in that system. Mixed bird parties are however encountered in miombo as in the other wooded systems.

In analysing the occurrence of mixed bird flocks in the Andes, Moynihan (1973, pp. 17–18) points out some salient features. The members of these mixed bird parties show '… pronounced intraspecific geographic variation in their interspecific behaviour.' In one sector the mixed bird flocks were small with few species which remained as coherent parties for brief periods. In other sectors mixed parties were '...larger, more stable, cohesive, and complex.' In yet other areas mixed flocks were quite absent.

To account for these peculiarities in mixed bird flocks and and the mixed primate associations which occur in Central and South America Moynihan (1973) provides perceptive insight into the factors at play, which seem to be closely applicable to the associations observed in Gorongosa and elsewhere in Africa; 'It is obvious that the development of flocking depends on several factors. There are positive correlations among densities of populations, thickness of vegetation, and frequency and elaboration of interspecific gregariousness within regions. But these cannot account for the whole of the major geographic trends. They do not explain the exceptions. There must be something else involved. This would appear to be an "invasion" or "frontier" effect. Interspecific gregariousness seems to go up with exposure to, or anticipated number of, invasions from or into other regions of the same life zone or an adjacent zone.'

'…What is the functional significance of this apparent connection of interspecific gregariousness with frontiers, strays, and invasions? The advantages of mixed flocking from the point of view of a straying bird in the unfamiliar area are obvious and much the same as in the monkeys cited above. By associating with experienced local individuals, a stray may be able to discover and identify food and/or danger relatively rapidly…It may be difficult for an animal to join and follow strangers without also developing some tendency to allow itself to be joined and followed by strangers. It seems to be characteristic of most animals that they cannot, at least do not, support very great qualitative difference in kind of social responses, a species that is gregarious in some circumstances usually tends to be gregarious in other circumstances.' In reference to the mixed monkey associations Moynihan (1973) also lists feeding habits, territorial behaviour and distribution and abundance of foods as underlying factors.

This subject is also explored in detail by Wilson (1975, e.g. pp. 49–59, 353, 358), who includes examples from insect societies as well. He suggests that insects surpass the vertebrates in the development of social symbiosis due to a far greater dependence on altruism, and that this … 'indiscriminate generosity opens up multiple lines of entry into the energy flow of the colony'. It would not be surprising if in-depth studies of vertebrate associations, in Africa at least, showed far greater symbiotic, if not altruistic relationships than may generally be believed. A literature survey alone would probably prove surprising.

In the examples of feeding symbiosis from Gorongosa, an outstanding feature appears to be the opportunistic use by individuals, or groups, of the changing scene in abundance, and the diversity of circumstances which they can exploit. These conditions comprise an interplay of the feeding, social, and security behaviour of other species—their unconscious role as beaters, caterers, and warners or protectors. Exploitation of these features appears to be derived from learned correlations resulting from high frequency of interspecies encounters. From this exploitation of advantageous and usable features in the behaviour of other species facilitative, if not altruistic, symbiotic relations are developed.

Whether some of the vertebrate feeding associations may be a means of obtaining access to resources falling within the bounds of aggressively territorial species does not seem to have been noted. This feature is shown to be a fundamental adaptive feature of inter-species fish associations on reefs, where schooling is a '…mechanism for circumventing the territoriality of competitors' (Robertson et al. 1976).

Moynihan (1973 p. 18) suggests that the frequency of interspecific gregariousness appears to go up with the diversity of juxtaposed communities and ecotones. The conspicuous difference in occurrence of interspecies associations between the Rift Valley and miombo savannas is probably directly related to the influence of the extraordinary heterogeneity in the Rift as opposed to the homogeneity of unbroken miombo over large areas. These influences are in turn underlain by a heterogeneity of fertile substrates in the Rift, each with different constraints and potentials, as opposed to relatively homogeneous leached soils in the miombo (c.f. Janzen 1974).

In the Rift, the matrix of contrasting (in physiognomy, structure or biotic content) communities in close juxtaposition provides a multiplicity of interfaces which intermesh in mosaic patterns. The plant food resources such as preferred grasses, browse and fruits have a clumped dispersion within each community and many of these and their individual plant components, such as fruit trees, exhibit a staggered series of phenophases or, at the other extreme, mass fruiting over one period.

Thus herbivores of all kinds are induced to move and explore an uneven food resource which brings species into contact with changing plant and animal matrices in space and time. Where unevenness in the food resource is aggravated by rarity, or widely separated occurrence, contacts are likely to be infrequent, as in the miombo for example. Conversely an uneven but closely packed food resource would promote high frequency of contacts, as in the Rift Valley.

As evinced by the differences in degree and kind of biotic succession between and within systems, uneven herbivore selection pressures have far reaching influences in the kinetics of geoecological succession and thus landscape evolution. These aspects are explored in the following section.

9.9 ROLE IN GEOECOLOGICAL SUCCESSION

Ecosystems and their biotic communities are in a kinetic state of multi-directional change as a result of climatic fluctuations, geomorphic processes and the responses and interactions of the living constituents. The life processes of plants and animals in themselves bring about changes in the system due to their individual (e.g. dominants), and compounded (co-evolutionary) effects such as feeding associations. The changes can be advantageous, or inimicable to the plant and animal constituents. In the latter case the constituents will be replaced by others, better adapted or more tolerant of the altered conditions.

The various ways by which communities and the environment are altered by animals include: seed dispersal and thicket encroachment; pan making; hill building by termites; draining of marshland by path-making; physiognomic, structural and floristic change to habitats by large herbivores. In this regard, Fraser Darling (1960, pp. 91–93) provided a first analysis of the stratification and niche structure of African ungulates as noted in Zambia. The widespread invasion of grasslands by scrub due to excessive populations of grazing ungulates is well documented from all parts of the Continent (eg. Mostert et al. 1971; Acocks 1975, for South Africa). In parts of East Africa the opposite

Physical condition and geoecological role of hippo.

RIGHT:

Aerial photo of a hippo herd showing typical poor condition of Gorongosa hippo in the dry season (note conspicuous spinal ridge in most animals).

FAR TOP RIGHT:

Hippo paths in the wet season across soft floodplain clay. Subsequent erosion shows all land facets in miniature of valley cut and fill processes e.g. valley widening by multiple lateral nickpoints, aggraded (fill) donga bed fixed by grass, bare pseudo levee (waxing slope) and gullies invaded by woody plants.

FAR BOTTOM RIGHT:

Borassus palm savanna with 3 m high *Hyparrhenia rufa* grass stratum trampled out and overgrazed by hippo and sheet eroded. The subordinate lawn grass pastures preferred by hippo have extended and even-aged *Acacia sieberiana* invades the new erosion surface at left and right.

situation results from excessive population densities of elephant which destroy forest or wooded savanna and inhibit their expansion, so that with the aid of fire these communities are being reduced and replaced by grasslands (Laws 1970; Laws et al. 1975). Concomitant with increase of grassland is the build up in grazing populations such as buffalo and hippo (e.g. as reported in the Luangwa Valley by Marshall & Sayer 1976, p. 394), and the contraction of tsetse fly, for example, in other areas (Ford 1966). Such changes thus have reciprocal effects throughout all component parts of ecosystems and communities.

In examples of the role of animals in affecting ecosystem change in Gorongosa, emphasis will be on the following aspects:

(1) Geoecological effects.

(2) Utilisation modification of plant communities, and

(3) Woody plant seed dispersal.

Geoecological Effects

The most important agent of change in the Urema Trough is the hippo. Their habitually used footpaths radiate out to grazing areas from riverine day-retreats. These paths also link all marsh and pan areas. Whilst footpaths aid the spread of floodwaters in flat areas, once incised their canalising effects have far reaching repercussions in floodplain ecosystems.

Slacks, marshes, and pans are inundated by direct rainfall and the spread of floodwaters across the convexities separating one depression from another. In the ebb these basins again become isolated and the waters gradually contract and dry up through the dry season. The tempo of drying-up is different in each basin due to their

Physical condition and geoecological role of hippo. *(cont)*

LEFT:

Headward eroding nickpoint incising flood-plain grassland at the head of a hippo path. New phase of savanna invasion above the nickpoint and in the incision. Joaquim Martins in middle ground.

Physical condition and geoecological role of hippo. *(cont.)*

disparate dimensions. As the water dries up a margin of green pasture is provided, which contracts with the water to the lowest part of the depression toward the end of the dry season.

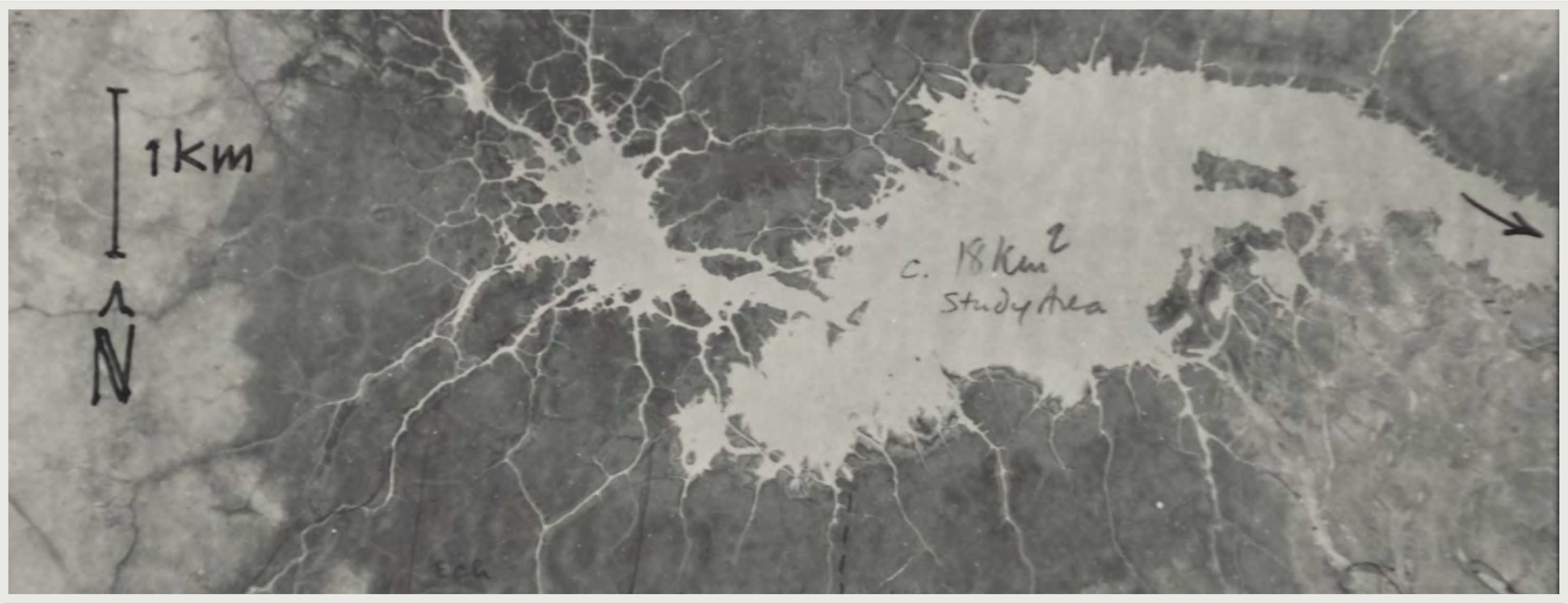
In the wet season and flood period, the hippo paths are canalised by the animals' movement to and from the depressions over the soft ground. The canalising effect changes the entire dynamics of the depressions due to over-drainage, and the hygrophilous grasses dry out nearly as rapidly as the adjacent savannas. Not only is a valuable pasture resource lost, but the excessive waterlogging which kept scrub encroachment at bay is no longer operative. Thus savanna invasion of the depressions occurs causing extinction of hippo habitat. An aquatic marsh grass system characterised by hippo and wildfowl is then replaced by acacia and impala and all other savanna features and components. By this process, path-making by hippo is a cause of their own local extinction. In an external (exoreic) drainage system such as the Urema floodplain, erosion is mainly caused by hippo channels made in the wet season. These link otherwise separate wetlands to the main exit of the Urema's seaward drainage. In contrast, in an internal (endoreic) drainage system, such as the Okavango Swamps, the hippo paths help spread floodwaters and aid access for other herbivores (Tinley 1966).

The geoecological effects of hill building termites have been noted in Section 6.3. Ungulate activity around or on top of the hills wears them down, reversing the microrelief to provide a minimum of one, and maximum of about three, pans per hectare in the Rift Valley. Each of these becomes a seasonal aquatic system with annual fish and perennial hygrophilous grasses.

Each island pan provides green pasture through until the mid dry season and is intimately related with the adjacent termitaria thickets composed of preferred browse and fruit plants.

Utilisation Modification of Plant Comunities

The dry forest patches on the Rift floor are generally small and linear as they are confined to the duplex sands of distributary channels and splays of fossil alluvial fans. Hence many ungulates, such as wildebeest and zebra, which do not normally enter forest, pass through them to the open terrain on the opposite side. Elephant and buffalo utilise the forest for shade and food, the former browsing the field layer and mid-stratum and the buffalo the



RIGHT:

Hippo paths in the wet season across soft floodplain clay. Subsequent erosion shows all land facets in miniature of valley cut and fill processes e.g. valley widening by multiple lateral nickpoints, aggraded (fill) donga bed fixed by grass, bare pseudo levee (waxing slope) and gullies invaded by woody plants.

herbaceous layer. Once opened up by these activities they are then used for shade purposes by other species as well, which bares the understorey further.

Fire impinges little on dry forest as the abrupt soil change at the ecotone results in a relatively short grass cover. In dry forest the upper canopy trees are clumped and a more continuous cover is formed by the mid-stratum trees, and to a lesser extent the shrub layer. In those forest patches where the lower two layers have been opened up, no suni were encountered, only red duiker. Wherever undamaged patches occurred the suni was present. This relationship probably involves a food factor, and cover from one of the suni's main predators, the crowned eagle.

The structural alteration of grasslands by the grazing succession and movement of large herds of buffalo through 4 m high grassland is noted above. Selective grazing by some species results in floristic changes in grasslands and maintenance of short grass conditions exemplified by the hippo lawns adjacent to the Urema Lake. It is probable that these conditions are exploited by the wildebeest population, which on its own could only maintain suitable pasture in patches. An excessive reduction of hippo would result in a rapid change of floodplain grassland structure with opposing effects on many animal constituents, particularly species such as wildebeest and buffalo.

The over-utilisation of many termitaria thickets, resulting in retrogressive succession and microrelief reversal, causes local extinction or occlusion of the island thicket biota (see Section 6.3). Conversely these and other clump thickets are protected from fire by ungulate utilization as this results in a trampled out perimeter which acts as an effective firebreak.

Dispersal of Woody Plant Seeds by Animals

In the Gorongosa system animal dispersed seeds from forest, thicket and savanna are distributed in suitable sites as a result of the behavioural patterns of the various dispersants. These patterns are in response to nuclear sites in the various habitats which have a centripetal attraction to high frequency of use. They include: (1) perch sites, (2) watering sites, (3) bare or sparsely grassed sites. The more important animal dispersants of woody plant seeds, from mainly drupaceous or baccate fruits, are listed in Table 9.6.

As revealed by detailed metre quadrat analyses of the groundlayer in various systems, seedlings and saplings of bird and mammal preferred species were related mainly to the above sites and were absent, or extremely rare, in the intervening grass ground cover between tree crowns.

Perch sites

In the first category of nuclear sites of attraction are biotic and inanimate prominences of all kinds, including trees, termite hills, stumps, rock outcrops, fence posts, and buildings. The most efficacious means of invasion and replacement of savanna by thicket is through development of tree-base thickets composed of bird and mammal dispersed fruit species. The hard, shot-like seeds of euphorbiaceous trees, such as *Androstachys johnsonii* and the succulent tree euphorbias, which are thrown by explosively dehiscing capsules, are picked up off the ground by turtle doves and wood doves. The faeces, dropped from the trees that these birds use for resting or roosting, contain some undamaged seeds, hence the frequency of these plant species in thicket clumps of all types. Classic descriptions of the sequential invasion of thornveld by animal dispersed thicket species whose seeds were dropped beneath individual trees is given by Bews (1917) Natal, and in other parts of the world by Ridley (1896, 1930, pp. 385–386).

In addition to the activities of birds and primates, the habit of caching seeds by both the bush and red squirrels (San Viljoen pers. com.) against objects, such as logs or tree trunks, must play a vital multiplier role in thicket extension. A vivid description of the seed storing habit of the British grey squirrel is given by Ridley (1930, pp. 379–382). In the same account, evidence is quoted from an American study which showed that after forest is destroyed by fire or felling, the seeds stored and forgotten by squirrels germinate and the new forest which develops is composed of 75% of the favoured squirrel foods.

TABLE 9.6
Important animal dispersants of woody plant seeds in the Gorongosa ecosystem

SPECIES		MOUNTAIN	MIDLANDS	RIFT VALLEY	COAST
BIRDS					
Guineafowl	Crested guineafowl	●	🟣	●	●
Doves/pigeons	Rameron pigeon	●			
	Delagorgue’s pigeon	●			
	Red-eyed turtle dove		●	●	●
	Cape turtle dove	●	●	●	●
	Laughing dove	●	●	●	●
	? Tambourine dove		●	●	●
	? Blue-spotted wood dove		●		●
	? Emerald-spotted wood dove			●	
	Cinnamon dove	●			
	Green pigeon	●	🟣	●	●
Turacos	Green-crested turaco	●			●
	Purple-crested turaco		🟣	●	●
	Grey loerie			●	
Mousebirds	Speckled mousebird	●	🟣	●	
	Red-faced mousebird			●	
Hornbills	Trumpeter hornbill	●	●	●	●
	Silvery-cheeked hornbill	●	●		●
	Grey hornbill			●	
	Red-billed hornbill			●	
	Yellow-billed hornbill			●	
	Crowned hornbill	●	●	●	●
Barbets	Black-collared barbet		●	●	●
	White-eared barbet	●	🟣	●	●
	Yellow-fronted tinker barbet		●		
	Golden-rumped tinker barbet		🟣	●	
	Green tinker barbet	●			
	Crested barbet		●	●	

SPECIES		MOUNTAIN	MIDLANDS	RIFT VALLEY	COAST
Orioles	European golden oriole		●	●	●
	African golden oriole		●	●	●
	Black-headed oriole		●	●	●
	Green-headed oriole	●			
Bulbuls	Black-eyed bulbul		●	●	●
	Terrestrial bulbul	●	●	●	●
	Yellow-streaked bulbul	●	●		
	Stripe-cheeked bulbul	●			
	Yellow- breasted bulbul			●	●
	Sombre bulbul	●	●	●	●
Thrushes, chats robins	Olive thrush	●			
	Gurney’s thrush	●			
	Mocking chat	●			
	Natal robin	●	🟣	●	●
	Heuglin’s robin	●	🟣	●	●
	Cape robin	●			
	Bearded scrub robin		🟣	●	●
	White-browed scrub robin			●	
	Starred robin	●			
	Swynnerton’s robin	●			
	Palm thrush			●	●
	White-breasted alethe	●			●
Starlings	Wattled starling			●	
	Plum-coloured starling		●	●	●
	Blue-eared glossy starling		●	●	
	Lesser blue-eared glossy starling		●	●	
	Black-bellied glossy starling	●	🟣	●	●
	Red-winged starling	●	●		
White-eye	Yellow white-eye	●	●	●	●

KEY

🟣 = confined mostly to the riverine strips.

Cont.

SPECIES		MOUNTAIN	MIDLANDS	RIFT VALLEY	COAST
MAMMALS					
Fruit bats	Wahlberg's epauletted fruit bat	●	●	●	●
	Peter's epauletted fruit bat	?	?	●	●
	Giant fruit-bat			?	●
	Egyptian fruit bat		?	?	●
	Bocage's fruit bat		●	?	?
Primates	Bushy-tailed galago	●	🟣	●	●
	Samango monkey	●	🟣	●	●
	Vervet monkey		●	●	●
	Baboon	●	●	●	●
Carnivores	Side-striped jackal		●	●	●
	Civet		●	●	●
	Tree civet	?	●	?	●
Ungulates	Elephant	●	●	●	●
	Blue duiker	●			●
	Red duiker	●		●	●
	Suni			●	●
	Nyala			●	
	Bushbuck	●	🟣	●	●
	Impala			●	
	Kudu		●	●	
	Bushpig	●	🟣	●	●
Rodents	Bush squirrel			●	
	Sun squirrel	●	●		
	Red squirrel	●		●	●

KEY

🟣 = confined mostly to the riverine strips.
? = uncertain

In Gorongosa, beneath the canopy of each baboon-sleeping tree are dense patches of the termitarium and tree-base thicket tree and shrub components (see Appendix 2 for a list of baboon foods). These are heavily browsed by impala and bushbuck. Melton (in press) in his study of animal associations with termitaria in Uganda found that baboons, during the day, preferentially defaecate on termite hills. This implies that preferential use is probably made of other perches as well, such as rock outcrops or trees.

In mango trees around our house at Chitengo Camp on the Rift floor, fruit bats ate figs taken from a neighbouring *Ficus sycamorus* 20 m away, and seedlings germinated from the rejected seeds dropped under the trees and in the tree crotches. The importance of seed dispersal by fruit bats in the floristic composition and growth of thickets and forest is emphasised by Ridley (1930), Van der Pijl (1957, 1972) and Vazques-Yanes et al. (1975).

Watering sites

The second category includes all sites where fresh or brack surface water is used by birds and mammals, that is, streambanks, dongas, ravines, kloofs, fountains, springs, pan and lake margins. On floodplains, and in areas where sheet and rillwash occur, many woody plant seeds are also dispersed by water-flow and are left in recognisable swashline patterns. Examples of these are common in mopane and acacia savannas, and the fever tree woods marginal to floodplains. The superimposed influence of zoochory to perch sites here reinforces the importance of eminences and obstructions as sites of seed deposition.

Bare or sparsely grassed sites

The third category is of bare or sparsely vegetated patches which are attractive to many animals, particularly cats and ungulates, including elephant, eland, impala, black rhino amongst fruit and pod eating ungulates, and wildebeest and zebra amongst grazing species. Elephant are responsible for large-scale dispersal of seeds everywhere, and especially along their paths. This is evinced by the clumped and linear occurrence of many favoured species such as borassus palm *Borassus aethiopum* and marula *Sclerocarya caffra* along paths as well as in riverine and other sites.

On the Rift Valley floor and in the coastward forest-dambo mosaic of the Cheringoma cuesta, the civet is a prime mover in the development and extension of thicket and forest. A list of the fruits eaten, as determined by the seeds from their middens, is given in Appendix 2 for the two areas. Civets are omnivorous with a frugivore bias as shown by quantitative analysis made from miombo of the Salisbury district in Rhodesia (Smithers pers. com.) His results showed 57% fruit followed by 43% murids (rodents) and insects taken in the dry season; in the wet season 65% insects and 35% fruit.

Civet habitually use dung middens, which are related to openings in the herbaceous cover away from perch sites such as termite hills. The middens, however, occasionally occur within the crown area of trees, particularly on forest margins. As shown by the profile transect of *Androstachys* thicket abutted against coast heath *Philippia simii* (Fig. 8.19), seed germination from the middens has resulted in small scrub-thicket islands of forest trees. Where these occur on suitable substrates they develop into larger thickets, and coalesce laterally into extensive patches, mostly from later seeding by birds. In other areas of the Cheringoma, civet middens beneath miombo savanna canopy trees are composed almost entirely of dense scrub-thicket islands formed by several *Rubiaceae*. However, fruits of certain species characteristic of termitaria and riverine sites, such as *Cleistochlamys kirkii*, eaten by civet fail to grow beyond the seedling stage in midden sites as conditions for them are unsuitable. Their dispersal to termitaria and tree-base sites is thus, probably, chiefly by birds.

If conditions are favourable, mass seed germination of single or mixed woody species occurs on the dung middens, and these develop to form dense thicket patches. The midden is continued to the side of the old one, now grown over with young trees and so on, resulting in the formation of different aged thickets. In the Rift Valley, clumps of a favoured fruit tree *Diospyros usambarensis* of various ages, occurring adjacent to current middens, best illustrate this phenomenon. The fruits eaten by civet are from the same species that are eaten by birds (e.g. green pigeon), primates, elephants and others. These fruit species are typical of tree-base thickets, termitaria and stream banks on the Rift floor, and from termitaria, riverine sites and evergreen forest on the Cheringoma Plateau.

From his studies of bird formed thickets in Malaya, Ridley (1930, pp. 385–386) describes the sequence of habitat changes that occur. 'It is in this way that from isolated trees or bushes a thicket may spring up in a very short time around the tree or through the bush, and as the thickets increase in size and become the roosting place of more birds, copses may be formed, then more extensive woods, and finally forests. By this process woody plant invasion is accelerated in a saltatory manner.

Implications and an Appreciation

Floodplain grasslands are maintained by seasonally excessive flooding and waterlogging. As indicated in previous sections (5.8, 6, and 8) this factor alone is responsible for the treeless grasslands on the Rift floor, and in dambos of the miombo system. As a natural process these grasslands will be incised by headward erosion of nickpoints resulting in increasingly rapid runoff. As soon as the soil moisture balance is tipped towards the mesic or xeric, savanna and/or thicket components invade the grasslands on any slight eminence.

As the flora contains herbaceous and woody plants which have wind and water dispersed seeds as well, the entire successional replacement of ecosystems and communities by these species could take place in the absence of animals. Hippo paths, however, can both accelerate the natural processes or initiate a new sequence of erosion in floodplain and slack-basin areas on the Rift floor. The activity of a single animal species, in this case the hippo, has therefore considerably altered the tempo of geoecological change on the Rift floor, which has simultaneously accelerated the reduction of their own habitat, jeopardising the survival of the species in the Urema Trough area. In accelerating or setting in motion the replacement of grassland by savanna and thicket components through the canalising action of their paths, hippo are responsible for not only precluding their own existence but also that of all biotic constituents dependent on the open grassland ecosystem. Canalisation also sets in train developmental changes in soil properties.

The obverse side of the hippos' predominantly geohydrological role in landscape change is that exemplified by selection biases of frugivores within the biotic community, due to their multiplier effect. Dispersal and successful development of favoured fruit trees reinforces their predominance and further use by increasing their density and thus the frequency of centripetally attractive feeding stations. In this manner the number of vertebrate interspecies associations is multiplied by frequency of contact, which allows a flow of kaleidoscopically changing associations as the aggregations move from one feeding station to another. On the one hand mutualistic interrelations between species are reinforced, and on the other the trend or swing in habitat change is exponentially enhanced for frugivores, but physically (physiognomic and structural), it is increasingly altered by the maturation and coalescence of thicket clumps. These changes preclude many of the frugivores originally responsible for the replacement sequences, but others from closed habitats become intermeshed in the changing aggregations of plant and animal constituents.

The separate or combined influences of geomorphic action of hippo, and the community selection pressure of frugivores results in the same sequence, that of grassland replacement by wooded savanna and thicket/forest. These progressive ecosystem sequences continue until a new homeostasis is attained at which time geomorphic surface replacement can result in a retrogressive sequence. In Gorongosa all sequences are occurring and are active under present-day conditions. In East Africa the action of elephant combined with fire is opening up wooded country to grassland dominated systems.

Ross (1962, pp. 231–342) points out that plant and animal components of systems become separated into dominants and subdominants thus '…in biotic communities some species or groups of species produce special ecological conditions which, superimposed over the general climatic and edaphic conditions of the area, have a profound limiting effect on the occurrence of other species in the community. These influential species are known as dominants…'. Hippo and frugivores are reckoned to be first level dominants in the Rift Valley sector of the Gorongosa ecosystem at present, buffalo and elephant forming a second level of dominants. Tomorrow the scene may change, particularly if there is a crash in hippo numbers and a continued increase in elephant. In the precincts of Gorongosa Mountain, and especially on the Cheringoma Plateau, frugivores are a dominant influence in ecosystem dynamics. Their impact is less conspicuous in the closed Midland miombo and in the summit grasslands on the mountain where fire and climo-edaphic constraints may cancel their influence.

In sum, the factors responsible for natural afforestation processes are: aerobic drainage, effective woody seed dispersal, overgrazing, early dry season (autumn) incidence of fire, or protection from fire. Conversely maintenance or expansion of grasslands are influenced by: waterlogging or flooding, rotting of woody plant seeds in the growing season, late dry season fires, over-browsing (e.g. by elephant), and clearing by man for cultivation, timber and firewood. As demonstrated by comparative examples from the Rift Valley and Cheringoma coast, the absence or removal of one animal from a system, for example hippo, would greatly alter the tempo of change allowing natural dampers such as soil cohesive properties and dense grass cover to preserve slack and marsh systems for much longer periods.

Other facets of community evolution are the reciprocal selective influences between plants and animals. For example there is a growing body of evidence that the stimulus for non-overlapping flowering times in many plants is due to competition for pollinators (e.g. Robertson 1924; Mosquin 1971; Pojar 1974; Reader 1975; Heinrich 1975). A parallel but converse selective bias is suggested for the staggered fruiting phases of many rainforest animal-fruit plants due to interspecific competition for dispersants (e.g. Snow 1966, 1971; Smythe 1970; McKey 1975; Howe & Primack 1975).

In this regard it is interesting to speculate whether the abundance of pods produced by riverine winter thorn *Acacia albida* and its flowering and leaf flush at the 'worst' time of the year is more than an evasion of flooded summer conditions. As the pods are avidly consumed by all wild ungulates and primates, the seeds are probably dispersed mainly by zoochorous means as well as by water; the typical dry season concentration of ungulates in riverine zones may have reinforced the climo-edaphic influence or imposed its own selective influence. The fever tree *Acacia xanthophloea,* which occurs on different soils in the same sites as winter thorn, shows a wet season phenophase activity and the distribution of seedlings and saplings indicate that their seeds are more conspicuously dispersed in swashlines by the flood and ebb of inundations or by rains.

By reciprocating opportunism of the circumstances presented to them in a kaleidoscopically changing mixture of plant and animal species, the living constituents selectively multiply, and thus bias, physical (geohydrological) and biotic (preferred fruits, over-grazing etc.) processes in various directions. These co-actions affect the tempo and content of geoecological succession, directed by the deeper climo-edaphic constraints or opportunities presented by different substrates of various geomorphic surfaces. These physical changes in a plant's and animal's habitat themselves produce a re-orientation of dominant and subdominant or prime mover species relationships, which affects the kinds of community selective pressures operative in space and time.

REFERENCES / CORRELATION
WILDLIFE

Acocks, J.P.H. 1975. *Veld types of South Africa.* 2nd ed., Bot. Surv. S. Afr. Mem. No. 40.

Allee, W.C., Emerson, A.E., Park, 0., Park, T. and Schmidt, K.P. 1949. *Principles of animal ecology.* B. Saunders Co., Philadelphia & London.

Anderson, G.D. & Herlocker, D.J. 1973. *Soil factors affecting the distribution of the vegetative types and their utilization by wild animals in Ngorongoro Crater, Tanzania*. J. Ecology, Vol. 6 (3), pp. 627–652.

Anderson, J.L. 1975. *The occurrence of a secondary breeding peak in the southern impala.* E. Afr. Wildl. J. Vol. 13, pp. 149–151.

Ansell, W.F.H. 1960. *Mammals of Northern Rhodesia.* Govt. Printer, Lusaka.

Attwell, R.I.G. 1970. *Some effects of Lake Kariba on the ecology of a floodplain in the mid-Zambezi Valley of Rhodesia.* Vol. 2 (3), pp. 189–196.

Attwell, R.I.G. 1963. Annual Report, Zambezi Valley Research Station, Records of the Department of National Parks and Wildlife Management, Rhodesia (1968).

Bell, R.H.V. 1971. *A grazing ecosystem in the Serengeti.* Scientific American, iss. 225 (1), pp. 86–93.

Bews, J.W. 1917. *The plant succession in the thornveld.* S. Afr. J. Sci., Vol. 14, pp. 153–172.

Bigalke, R.C. 1970. *Observations on springbok populations.* Zoologica Africana, Vol. 5 (1), pp. 59–70.

Bonsma, J.C. 1939. *Breeding seasons on cattle ranches.* Farming in S. Afr., Vol. 14, p. 230.
—1940. *The influence of climatological factors on cattle.* Farming in S. Afr. Vol., 15, pp. 373–385.
—1942. *Useful bushveld trees and shrubs.* Farming in S. Afr., Vol. 17, pp. 226–239.

Brady, N.C. 1974. *The nature and properties of soils.* 8th ed., MacMillan, NY, London.

Chapin, J.P. 1939. *The birds of the Belgian Congo, Part 2.* Bull. Amer. Mus. Nat. Hist., Vol. 75.

Child, G. 1968a, *Behaviour of large mammals during the formation of Lake Kariba.* National Museum of Rhodesia.
—1968b. *An ecological survey of northeastern Botswana.* United Nations Development Programme, FAO No. TA 2563.

Clancey P.A. 1971. *A handlist of the birds of southern Mozambique.* Mems. Inst. Invest. Cient. Moçamb. 10, 11, Series A.

Cott, H.B. 1975. *Looking at animals.* Collins, London.

Darling, F. Fraser 1937. *A herd of red deer.* Oxford University Press, London.
—1960. *Wildlife in an African territory.* Oxford Univesity Press, London.

De Vore, I. & Hall, K.R.L. 1975. ‘Baboon ecology’ in *Primate Behaviour: Field Studies of Monkeys and Apes.* De Vore, I. (ed.), Holt, Rinehart and Winston, NY, pp. 20–52.

Dodds, D.G. & Patton, D.R. 1968. *Wildlife and landuse surveys of the Luangwa Valley.* FAO/UN, Rome.

Dorst, J. & Dandelot, P. 1970. *A field guide to the larger mammals of Africa.* Collins, London.

Dougall H.W. & Glover, P.E. 1964. *On the chemical composition of* Themeda triandra *and* Cynodon dactylon. E. Afr. Wildl. J., Vol. 2, pp. 67–70.

Du Plessis, S.F. 1969. *The past and present distribution of the Perissodactyla and Artiodactyla in southern Africa.* M.Sc. Thesis, University of Pretoria.

Du Toit, P.J., Louw, J.G. & Malan, A.I. 1940. *A study of the mineral content and feeding value of natural pastures in the Union of South Africa.* Onderstepoort J. Vet. Sci. Anim. Ind., No.14 (182), pp. 123–127.

Ebedes, H. 1974. *Anthrax epizootics in Etosha National Park and an historical note on anthrax in northern South West Africa*. SWA Nature Conservation Division, cyclostyled MS.

Elder W.H. & Elder, Nina L. 1970. *Social groupings and primate associations of the bushbuck* (Tragelaphus scriptus). Mammalia, Vol. 34 (33), pp. 356–362.

Eloff, F.C. 1966. *Range extension of the blue wildebeest.* Koedoe, no. 9, pp. 34–36.

Estes, R.D. 1968. *Territorial behaviour of the wildebeest* (Connochates taurinus *Burchell, 1823*). Ph.D. thesis, Cornell University, USA.

Ford, J. 1966. *The role of elephants in controlling the distribution of tsetse.* IUCN Bulletin New Series, No. 1, p. 6.

Fosbrooke, H.A. 1963.*The* Stomoxys *plague in Ngorongoro. 1962.* E. Afr. Wildl. J., Vol. 1, pp. 124–126.

Friedmann, H. 1955.*The honey guides.* Smithsonian Inst. U.S. Nat. Mus. Bull., No. 208, pp. 25–71.

Galpin, E.E. 1926. *Botanical survey of the Springbok Flats.* Bot. Surv. S. Afr. Mem, No. 12.

Glasgow, J.P. 1963. *The distribution and abundance of tsetse.* Pergamon Press, London, NY.

Gwynne, M.D. & Bell, R.H.V. 1968. *Selection of vegetation components by grazing ungulates in the Serengeti National Park.* Nature Vol. 220, pp. 290–393.

Heady, H.F. 1975. *Rangeland management.* McGraw Hill, NY.

Heinrich, B. 1975. *Bee flowers; a hypothesis of flower variety and blooming times.* Evolution, No. 29, pp. 325–334. Bechuanaland. 11th and 12th Reports Dir. Vet Educ and Res., Part 1, pp. 494–498.

Henrici, M. 1926. *Preliminary report upon the occurrence of hydrocyanic acid in grasses of Bechuanaland.* 11–12th Rep. Wet. Res. Onderstepoort, pp. 494–498.
—1928a. *The relations between the amount of carbohydrates in the leaves of armoedsvlakte grasses and the meteorological factors.* 13th and 14th Reports Dir. Vet. Educ. and Res., Part 1, pp. 1041–1074.

—1928b. *The phosphorous content of the grasses of Bechuanaland in the course of their development.* 13th and 14th Reports Dir. Vet. Educ. and Res., Part 2, pp. 1077-1208.

Howe, H.F. & Primack, R.B. 1975. *Differential seed dispersal by birds of the tree* Casearia nitida *(Flacourtiaceae).* Biotropica, Vol. 7 (4), pp. 278–283.

Janzen, D.H. 1974.*Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae.* Biotropica, Vol. 6 (2), pp. 69–103.

Jarman, P.J. 1972. *Seasonal distribution of large mammal populations in the unflooded middle Zambezi Valley.* J. Applied Ecol. Vol. 9 (1), pp. 283–299.

Joubert, D.M. 1954. *The influence of winter nutritional depressions on the growth, reproduction and production of cattle.* J. Agric. Sc., Vol. 44 (1), pp. 5–65.

Laws, R.M. 1970. *Elephants as agents of habitat and landscape change in East Africa.* Oikos, Vol. 21, pp. 1–15.

Laws R.M., Parker, I.S.C. & Johnstone, R.C.B. 1975. *Elephants and their habitats.* Clarendon Press, Oxford.

Limbaugh, C. 1961. *Cleaning symbiosis.* Scient. Amer., iss. 205 (2), pp. 42–49.

Marshall, P.J. & Sayer, J.A. 1976. *Population ecology and response to cropping of hippopotamus populations in eastern Zambia*. J. Ecology, Vol. 13 (2), pp. 391–403.

McKey, D. 1975. ‘The ecology of coevolved seed dispersal systems’ in *Coevolution of animals and plants.* Gilbert, L.E. & Raven, P.H. (ed.), University of Texas Press, Austin.

Melton, D.A. 1972. *Environmental heterogeneity produced by termitaria in western Uganda with special reference to mound usage by vertebrates.* M.Sc. thesis, University of British Columbia.

Monnig, H.O. & Veldman, F.J. 1961. *Handbook of stock diseases.* Nasionale Boekhandel Bpk., CT., Jhb. (revised ed.).

Moynihan, M. 1968.*The ‘coeribini’. A group of marginal areas, habitats and habits.* Amer. Natur., Vol. 102, pp. 573-581.
—1973. *The evolution of behaviour and the role of behaviour in evolution.* Breviora, No. 415.

Mosquin, T. 1971. *Competition for pollinators as a stimulus for the evolution of flowering time.* Oikos, Vol. 22, pp. 398–402.

Mostert, J.W.C., Roberts, B.R., Heslinga, C.F. & Coetzee, P.G.F. 1971. *Veld management in the O.F.S. Region.* Dept. Agric. Serv. Bulletin, No. 391.

Myre, M. 1971. *As pastagens da região do Maputo.* I.I.A.M. Communicações, No. 75.

Myre, M. & Antão, L.R. 1972. *Reconhecimento pascicola ao Vale do Save.* I.I.A.M. Communicações, No. 75.

Petrides, G.A. 1975. *Principal foods versus preferred foods and their relation to stocking and range condition.* Biol. Cons., Vol. 7, pp. 161–169.

Pienaar, U. DeV. 1961. *A second outbreak of anthrax amongst game animals in the Kruger National Park.* Koedoe, No. 4, pp. 4–17.

Pienaar, U. DeV., Van Wyk, P. & Fairall, N. 1966. *An experimental cropping scheme of hippopotami in the Letaba River of the Kruger National Park.* Koedoe, No. 9, pp. 1–33.

Pijl, L. van der 1975. *The dispersal of plants by bats (chiropterochory)*. Acta Bot. Neerl., Vol. 6, pp. 291–315.
—1972. *Principles of dispersal in higher plants.* Springer-Verlag, 2nd ed.

Pinto, A.A. DaRosa 1959. *Um esboço da avifauna sedentária da região da Gorongosa, Mozambique.* Proc. First Pan-Afr. Congr., Ostrich Suppl. No. 3, pp. 98-125.
—1968. *Lista sistematica das aves do Parque Naçional da Gorongosa.*

Player, I.C. & Feely, J.M. 1960. *A preliminary report on the square-lipped rhinoceros* Ceratotherium simum simum *(Burchell).* Lammergeyer, Vol. 1 (1), pp. 3–24.

Plowes, D.C.H. 1957. *The seasonal variation of crude protein in twenty common veld grasses at Matopos, Southern Rhodesia and related observations.* Rhod. Agric. J., Vol. 54 (1), pp. 33–55.

Pojar, J. 1974. *Reproductive dynamics of four plant communities of southwestern British Colombia.* Can. J. Bot. Vol. 52, pp. 1819–1834.

Reader, R.J. 1975. *Competitive relationships of some bog ericads for major insect pollinators.* Can. J. Bot., Vol. 53, pp. 1300–1305.

Ridley, H.N. 1896. Natural Science, No. 8, p. 180.
—1930.*The dispersal of plants throughout the world.* Reeve and Co., Ashford, England.

Riney, T. 1960. *A field technique for assessing physical condition of some ungulates.* J. Wildl. Mgmnt., Vol. 24 (1), pp. 92–94.

Robertson, C. 1924. *Phenology of entomophilous flowers.* J. Ecology, Vol. 5, pp. 393–402.

Robertson, D.R., Sweatman, H.P.A., Fletcher, E.A. & Cleland, M.G. 1976. *Schooling as a mechanism for circumventing the territoriality of competitors*. Ecology, Vol. 57, pp. 1208–1220.

Ross, H.H. 1962. *A synthesis of evolutionary theory.* Prentice Hall Inc., New Jersey.

Sheppe, W. & Osborne, T. 1971. *Patterns of use of a floodplain by Zambian mammals.* Ecological Monographs, No. 41 (3), pp. 179–205.

Sheppe, W. & Haas, P. 1976. *Large mammal populations of the lower Chobe River, Botswana.* Mammalia 40 (2), pp. 223-243.

Shortridge, G.C. 1934. *The mammals of South West Africa.* Vol. II, Heinemann, London.

Silva, J.A., Cruz, E. & Gonçalves, A. Castelo Branco 1972. *A estrongilidose gastrintestinal dos ruminants em Mozambique—resultados de um ensaio para conbate à helminotse no núcleo bovino do posto zootéctnico de Angónia.* Veterin. Moçamb., Vol. 5 (2), pp. 69–75.

Simon, N. 1962. *Between the sunlight and the thunder.* Collins, London.

Simpson, C.D. 1973. *Tooth replacement, growth and ageing criteria for the Zambezi bushbuck*—Tragelaphus s. ornatus *(Pocock).* Arnoldia, Rhod., no. 6 (6), pp 1–25.

Smithers, R.H.N. & Tello, J.P.L. 1976. *Checklist and atlas of the mammals of Mozambique.* Museum Memoir No. 8, Trustees of the National Museums, Salisbury, Rhodesia.

Smythe, N. 1970. *Relationships between fruiting seasons and seed dispersal methods in a tropical forest.* Amer. Nat., Vol. 104, pp. 25–35.

Snow, D.W. 1966. *A possible selective factor in the evolution of fruiting seasons in tropical forest.* Oikos, Vol. 15, pp. 274–281.
—1971. *Evolutionary aspects of fruit-eating by birds.* Ibis, Vol. 113, pp. 194–202.

Spinage, C.A. 1962. *Rinderpest and faunal distribution patterns.* Afr. Wildl., Vol. 161 (1), pp. 55–60.

Steyn, D.G. 1929. *Recent investigations into the toxicity of known and unknown poisonous plants in the Union of South Africa.* 15th Rept. Dir. Vet. Serv., pp. 777–803.
—1931. *Geilsiekte and its detection in the field.* Jour. S. Afr. Vet. Med. Assoc., Vol. 2, pp. 23– 26.
—1933. *The diagnosis, treatment and prevention of vegetable poisoning.* J. S. Afr. Vet. Med. Assoc., Vol. 4 (2), pp. 193–201.
—1934. T*he toxicology of plants in South Africa.* CNA, pp. 118–138.

Struhsaker, T.T. 1967. *Ecology of vervet monkeys* (Cercopithecus aethiops*) in the Masai-Amboseli Game Reserve, Kenya.* Ecology, Vol. 48 (6), pp. 891–904.

Sydney, Jasmine 1965. *The past and present distribution of some African ungulates.* Trans. Zoo. Soc. Lond., Vol. 30.

Tello, J.L.P.L. & Van Gelder, R.G. 1975. *The natural history of nyala,* Tragelaphus angasi *(Mammalia, Bovidae) in Mozambique.* Bull. Amer. Mus. Nat. Hist., Vol. 155 (4), pp. 321–386.

Tinley, K.L. 1964. *Some observations on certain tabanid flies in north-eastern Zululand (Diptera, Tabanidae).* Proc. R. Ent. Soc. Lon. (A), Vol. 39 (4-6), pp. 73–75.
—1966. *An ecological reconnaissance of the Moremi Wildlife Reserve, Botswana.* Okovango Wildlife Society, Johannesburg, Gothic, CT.
—1969a. *Dikdik* Madoqua kirkii *in South West Africa: notes on distribution, ecology and behaviour.* Madoqua, No.1, pp. 7–33.
—1969b. *First air count of the buffalo of Marrameu*. Veterin. Moçamb., Vol. 1 (2), pp. 155–170.
—1969c. *The ecological limits of Gorongosa National Park, Mozambique: and the maintenance of wilderness.* Report to the Mozambique Govt. Fauna Branch of the Veterinary Services of Mozambique, Mim.
—1975. 'Habitat physiognomy, structure and relationships'. In *Die Soogdiernavorsingsinstituut 1966–1975, Symposium proceedings*. Publication of the University of Pretoria, New Series no. 97, pp. 69–77.

Tinley, K.L. & Sousa Dias, A.H.G. De 1973.*Wildlife reconnaissance of the mid-Zambezi Valley in Mozambique before formation of the Cabora Bassa Dam*. Veterin. Moçamb., Vol. 6 (2), pp. 103–131.

Vasse, W. 1909. *Three years' sport in Mozambique.* Pitman & Sons, London (translated from the French by R. and H. M. Lydekker).

Vaughan-Kirby, F.V. 1899. *Sport in east central Africa,* Rowland Ward, London.

Vazquez-Yanes, C., Orozco, A., Francois, G. & Trejo, L. 1975. *Observations on seed dispersal by bats in a tropical humid region in Veracruz, Mexico.* Biotropica, Vol. 7 (2), pp. 73–76.

Vedder, H. 1966. *South West Africa in early times.* Cass, London.

Vesey-Fitzgerald, D.F. 1960. *Grazing succession among East African game animals.* J. Mammalogy, Vol. 41 (2), pp. 161–172.
—1965. *The utilization of natural pastures by wild animals in the Rukwa Valley, Tanganyika.* E. Afr. Wildl. J., Vol. 3, pp. 38–48.

Washburn, S.L. & DeVore, I. 1969. *Baboon ecology and human evolution.* Howell, F.C. & Bourliere F. (Eds.) Harper & Row, New York.

Weir, J.S. & Davison, E. 1965. *Daily occurrence of African game animals at water holes during dry weather.* Zoologica Africana, Vol. 1 (1), pp. 267–273.

Wellington, J.H. 1955. *Southern Africa: a geographical study.* Vol. 1, Cambridge University Press, London.

Wilson, E.O. 1975. *Sociobiology: the new synthesis.* Harvard University Press.

Wilson, V.J. 1966. *Observations on Lichtenstein's hartebeest,* Alcelaphus lichtensteini, *over a three-year period, and their response to various tsetse control measures in eastern Zambia.* (Rhod.), Vol. 2 (15).

PART 2

CORRELATION

Chapter 10

Conservation

RIGHT:

José, Martin and Ken — darting of buffalo.

Conservation

10.1 INTRODUCTION

The present and future survival of wildlife and natural areas in Africa depends almost exclusively on the favour of the rural human populations in everyday contact with them. All conservation measures will be fruitless until these populations are made to realise the value of these areas by obtaining immediate tangible benefit from them, and until they are involved in their protection and utilisation as part of the regional economy in the widest sense. Simultaneously, there must be modification of traditional land-use to intensive practices, and of practical education for promoting sound husbandry of their habitats. These three facets are the crux to changing the deteriorating conservation trend on the continent.

In large parts of Africa, national parks, forest reserves, and other specially protected sites were given total preservation status without thought of further consequences. Such status was necessary in the initial stage to ensure that they were not encroached on by human activities. But after this critical point had been overcome, there has not been reassessment of the protected resources in the light of the natural processes of the landscape. Many of these resources, specially protected for their unique features, are now threatened internally by natural processes of succession.

In the larger national parks, protection has resulted in population explosions of the large herbivores with attendant damage to the habitats. Culling programmes have been initiated in some to balance the herbivore populations with the pasture resource. The products of these culling programmes, typically, are never tasted by the surrounding human populations. Either private enterprise, or the central government, are the sole receivers of any financial advantage from such programmes. The same consequences result from tourism in national parks—the surrounding human populations, apart from those who are employed in the park itself, obtain no material advantages from it. In this way natural reserves of all kinds have existed as islands and have not contributed directly to the regional economy.

In Africa there is a total of 91 species of wild ungulates, as compared to only 20 in South America for example (determined from Dorst & Dandelot 1970, and Keast 1972, Ch. 8 respectively). This unique assemblage of herbivores was, and still is in parts, the protein basis of the peoples of Africa, with the exception of certain groups such as the Masai pastoralists. But decimation over vast areas in the name of development, tsetse control and unbridled hunting has reduced this resource, the remnants of which are protected today in national parks. But in many parks these wildlife populations are now threatened by their own overpopulation due to sanctuary effect, and the damage of this on their habitats.

Fraser Darling (1960) has given the most lucid exposition of the potential of the indigenous African ungulates as a bountiful resource. He makes the point (p. 133) that the necessity of cropping overpopulations of ungulates in most national parks, and the example of efficient utilisation of the meat, in some '...exposes the inadequacy of the notion that national parks should be absolute sanctuaries.' Ledger (1964), Talbot et al. (1965), and Laws et al. (1975), amongst others, corroborate this thesis.

National parks and nature reserves protect in available form many types of information and resources (for example, plant and animal protein) for direct or future use, either to increase the productivity of the adjacent human habitats, or as living laboratories for research on the dynamics of natural systems. These dynamics include geomorphic and biotic succession, interrelationships, and interdependence. This information is fundamental for distinguishing natural changes in the environment from those induced by man. In sum, they are sites protecting the diversity and dynamism of mankind's environment for our continuing survival and stability, socially, spiritually and biologically.

10.2 PROTECTION AND UTILISATION

The natural areas of the African continent must be seen in their geographical, ecological and cultural context, Their diversity in each region or locality should be used in accordance with their intrinsic properties for a variety of criteria —from near total protection (e.g. for endemics) to rural hunting areas. In this way natural areas and wildlife will be integrated as part of the whole man–land relationship, well expressed by Dasmann's (1975) 'Conservation Alternative'. In 1968 a plan was put forward for involvement of rural people with the management and protection of Gorongosa National Park. Surrounding Gorongosa are more than 30,000 peasant cultivators, part of whom are fully occupied with beekeeping, which depends on undamaged *Brachystegia* (miombo) woodlands. As the area is occupied by tsetse fly, nagana precludes the use of domestic stock; hence the people are mostly dependent for their protein on the wildlife resource. On the one hand, the plan included total utilisation of a sustained yield culling programme for reducing the hippo and buffalo populations, and on the other, encouragement of the use of the miombo system within the park by the beekeepers. In this way a mutualism would be drawn from the people's dependence on protein supply and undamaged miombo, and the dependence of all on rural vigilance against commercial poachers, unrestrained firing and hunting, and damage to forests and catchments by shifting and cash crop cultivation. In short, creative cooperation with the rural inhabitants was planned to the benefit of all aspects. Unfortunately political changes have left this plan (Tinley 1969) in limbo. However, present interest and enthusiasm in the cultural and resource values of natural areas in Mozambique engenders optimism for rational land use and the maintenance of wilderness areas there (Paul Dutton pers. com.).

The dimension of any economic advantage to the surrounding human populations depends on the size of the natural area and its turn-over of products. A large national park with alluvial grasslands capable of producing more than 500 tonnes of meat a year from wildlife will have a far greater sphere of influence than a small natural area, especially if the latter is only capable of providing forest products. But the two resources are incomparable, because they are quite different. The sphere of influence of small natural areas would be far greater if there were many of them. The crux of any possible future increase in wildland rests on the success of the present natural areas in taking part in the regional economy.

Over the last 5 years an extremely successful red-meat production scheme, coupled with hunting, was initiated and built up by my brother, Charles Tinley, on Bester's Game Ranch of 6,000 ha in the Zululand thornveld. In the first year (1972), 100 animals were culled for hunting only, fetching R7,500. In the second year, 350 animals for hunting only, fetched R25,000. In the third year 1,800 were culled for red-meat production plus hunting, providing R90,000 (of which 20% was from hunting).

In the fourth year (projected) 2,800 would be cropped, fetching R140,000 (Arnott 1974). A small, meat processing factory was built locally at a cost of R90,000 which was repaid in less than a year by the game resource. Hunting was not confined to trophy animals, thus a much larger clientele could be supported by the local ranch populations.

This unique venture has proved the value of game as a capital-less resource which can grow on its own turnover. In Arnott's (1974) words '…there's meat for Africa, if you're game'. Vital now is for this expertise and experience to be spread across the continent.

In addition to the wild ungulate resource, many other natural products from the savannas and forests are heavily relied on by rural people. An idea of the importance and multiplicity of veld products is shown by the following list: animal foods (including fish), drought foods, honey, wax, bark tubes for hives, timber, thatch, firewood, twine, fruit, seeds, medicines, oils, dyes, gums and resins, spices, spinaches (wild greens), tuber foods, tannins, weaving materials, scents, hunting materials including poisons used in fishing.

It is clear that under high population demands, only some of these products, for example thatch, can be reaped on a rational basis without harm to natural communities in parks. Whilst others, for example timber for construction purposes, should be stopped as soon as possible and be replaced by timber from plantations. It is vital, however, that each reserve is seen as a natural resource belonging to the regional community. In this way the people will get out as much as they put into the resources in the way of rational use and protection.

Rational use implies two fundamental requirements—practical knowledge of the productivity and availability of the product and an authority which ensures that management methods are in accordance with these determinants. Thus practical studies are required to determine allowable take-off of certain products in addition to the maintenance of the various systems in each reserve.

A tree producing a special medicine, or high protein seed, requires study to ascertain what its life requirements and conservation status are; its method of dispersal, whether its productivity is associated with certain soils, slope aspects, other plant species, fire or climatic factors, etc. Can it be propagated most easily by cuttings or from seed? Without this data it is possible to starve amidst plenty, or to eliminate the resources that are rare or localised. The strategy used for assessing the conservation status of communities or their components in Mozambique is summarised in Table 10.1.

As the destiny of natural areas and rural development, based on human and environmental values, are bound inextricably together, it is unacceptable to have wild ungulate populations confined to parks where their future is in jeopardy by over-population whilst most of Africa suffers from chronic protein deficiency. What is required is replenishment of wildlife populations over the vast, relatively empty areas, and their sustained utilisation as a food resource, thus expanding the size of productive natural areas to continental proportions.

Only by the development of an altruistic symbiosis (mutualism) between the surrounding rural people and the natural area (park, reserve, wilderness area etc.) by means of their benefitting from park products, will it be possible to obtain cooperation to regulate where people live or cultivate. In this way it will be possible to lessen the impact on resources, such as water, on which all are dependent. Concurrently, conservation organizations and others involved in the stewardship of parks require to be involved in demonstrating labour-saving and intensive cultivation methods, permaculture for example. Such aid should be wholly empathetic with the life-ways, cultures and religion of the tribes-people; as clear on the why as on the how. Table 10.2 notes the aspects in which conservation organizations should become involved if they are to realize meaningful, outward, creative conservation.

TABLE 10.1

Strategy used for assessing the conservation status of ecosystems and communities of Mozambique.

FEATURE	PARAMETERS	QUALITIES/VALUES
Principal feature	Endemism and rarity	(a) Plants and/or animals endemic to a particular site. (b) Non-endemic components occurring in small numbers or confined to a few sites. Determined as locally (i) abundant (ii) common (iii) scarce
	Limits	Extreme limits of biogeographic or ecosystem outliers, remnants or initials (including centres of speciation), barriers and filter bridges.
	Natural processes: dynamics and vulnerability	Successional status (trends, contraction, expansion), environmental dynamics and limiting factors (including geomorphic succession, storms, drought, fire, temperature changes particularly in shallow coastal waters, size and shape of community).
	Landscape diversity	The number of systems within a region or area. Control: (a) Topography, aspect, substrate and resultant climatic influences (interdigitation, overlap and confluence of ecosystems or their components). (b) Continuum sequence (variation of essentially similar ecosystem/s due to environmental gradients).
	Quality	Intact/disturbance rating 1-5* 1 Intact (undisturbed) 2 Minor disturbance 3 Medium disturbance 4 Major disturbance 5 Destroyed or altered beyond repair (* including invasion or dominance by alien plants and/or animals).
	Danger from human activities	Examples include communications (roads, railways, powerlines, pipelines and canals etc.); Urbanisation (e.g. spread in coastal areas, tourist impact through recreation facilities etc.); lack of responsible land use planning, human settlement schemes, dams et al.
	Priority	Priority conservation for threatened species and/or natural systems including scenery. Priority action/urgency rating 1–5 1 Immediate 2 Within 1 year 3 Within 5 years 4 Within 10 years 5 Within 20 years
Other features	Archaeological sites	
	Geological sites (unique outcrops and fossils)	
	Historical and cultural sites	
	Type localities of plants and animals	
	Sufficient representative examples of plant or animal populations (gene banks) on various environmental gradients (latitudinal, altitudinal etc.)	
	Breeding, nesting, roosting and resting sites (e.g. seabirds).	

TABLE 10.2

Seven spheres of conservation involvement.

SPHERES	CONSERVATION INVOLVEMENT
1 Rural education	• Change of content and emphasis to human and environmental values based on local or regional characteristics. • Technological aids as the tools of man.
2 Rural land use	• Intensive agricultural methods introduced by way of their traditional systems (e.g. VALLEY TRUST experiment in Natal using trench cultivation, permaculture). • Capital-less resource production (e.g. protein from wildlife). • Replacement of scarce resources e.g. firewood by establishment of plantations to save indigenous forests. • Self-sufficiency in food production.
3 Regional co-relations	• Relation of the natural area to its region (a) Physical—ecosystem diversity, and the role of natural or accelerated landscape changes in the region on the dynamics of the natural area. (b) Economic—in its complete sense, the maintenance and exchange of rural resources.
4 Involvement of rural people	• Involvement with the protection and management of natural areas (a mutualism drawn from co-active benefits [3b]).
5 Statewide involvement	• Statewide involvement in establishment of full spectrum of natural areas. • Their relation on a state and local level.
6 Management of natural areas	• Internal management of natural areas based on geomorphic, hydrologic and ecological processes and trends determined by sallient factor analysis (management based on causes not effects, using the visible reponses as indicators). • The internal dynamics must be correlated with the wider framework of changes occurring in the catchment basin or region in which the natural area occurs.
7 Expertise diversification	• Employment (and/or hire) of staff from the following fields unrepresented in southern African conservation organisations: agriculture, economics, education, engineering, geography, geomorphology, forestry, human ecology (anthropology), hydrology, landscape planning, pasture science, soil science. • Representatives from rural communities adjacent to natural areas of all kinds as local field propagandists and demonstrators (including herbalists, beekeepers, hunters, fishermen, teachers).

10.3 MANAGEMENT

Habitats

This entire thesis has focused down to a single point—the fundamental role of soil moisture balance in all ecological relations. In addition it has traced the evolution of the ecosystem to the present and these data have provided a template from which it is relatively easy to predict future changes. The areas undergoing the most rapid flux are where the canalisation of floodplains is changing the soil moisture balance, permitting active invasion by woody plant communities. Whilst hippo and frugivores are the prime movers accelerating these processes, they would occur inexorably over the longer term anyway due to erosional lowering of land surfaces to various base levels under the force of gravity.

Since its origin the Rift floor has been gradually drying out; aridification of a floodplain system and its replacement by a dry to mesic savanna–thicket–dry forest mosaic. The near extinction of the floodplain ecosystem as a natural process is destined in the near future (within several decades) unless remedial measures are taken. The final phases of woody predominance of the entire Rift floor are depicted in Fig 6.4. This stage will undergo further change but the processes are likely to be slow. Floodplain conditions will not return unless local, secondary or primary base levels are raised to cause renewed flooding and die-back of woody cover.

There is thus a management dilemma—do we accept the elimination of a floodplain grassland ecosystem and its replacement by wooded cover ecosystem (i.e. exchanging hippo habitat for impala, and then bushbuck habitat) or do we 'stick our finger in the breached dyke' and damp down the inexorable process? Evidence presented in Ch. 6 (Process and Response) shows that in Gorongosa the greatest diversity of habitats and life occurs under present circumstances, but from now on the area will become more homogenous physiognomically and structurally (Fig. 6.4).

In order to maintain this diversity a two-pronged strategy is required in mangement; habitat modification and maintenance, concomitantly with reduction, on a sustained yield basis (park product), of ungulate overpopulations. To cull one animal species is dangerous as the demise of one may change the pasture structure with far-reaching results on the population trends of other animals. That culling alone is pointless is easily demonstrated by trying to save Lichtenstein's hartebeest, for example, by culling any other ungulate species which may be competing with it for food, or by drastically reducing its predators. The preferred dambo ecotone habitat of this species may, however, be on the verge of extinction by natural geoecological successional processes, and this, not reduction of the other herbivores or predators, is what is required to be established, if the process is not already gone too far. Occlusion of habitats is a normal landscape process and where this occurs mobile animal species can move further afield except in fenced-off areas. In the latter situation therefore, certain species are liable to extinction under the inexorable landscape changes, whilst others opportunistically take advantage of them and a buildup in their populations results.

The control of a floodplain system is relatively easy compared to hill country, as the smallest blockage can restore the flood and ebb regime (Fig 10.1). The key sites are the local base level sills or 'critical heights' which earlier formed the convexities enclosing each slack basin, until they were breached (had the plug pulled out) releasing the water and thus resulting in the loss of inundations. Several kinds of practical problems require careful attention as otherwise they would nullify any attempt to save the floodplains and slacks.

(1) Where possible dykes should be built across the top of nickpoints, with an overflow sluice course for floodwaters to pass around the weir and enter the incised stream course from a lateral position.

(2) In places where the nickpoint has already eroded a gully into a slack, for example the Mucodza Marsh (Fig 10.2) and Chizunguzungu tando, it is useless putting the weir at its head as the point is to restore the entire slack basin. Thus the weir must be constructed at the old local base level sill on the rim of the depression. Most important is that the section of gully cut off above the weir must be filled with water or levelled with sand brought in from elsewhere, and packed in. Unless the nickpoint sites are smothered, active headward erosion will continue. If filled by water or soil, the nickpoint is effectively drowned and stopped.

(3) In slack-basin areas where floodwaters enter at one end and exit at the opposite side (e.g. the Pungue new course through the Dingedinge slack Fig. 10.3), it is wasted effort to close off the entrance as this will naturally seal itself off in flood periods if the exit is closed downstream, which will pond the waters in the slack basin. The entrance becomes a site of splay deposition, aggrades, and is fixed by reedbeds. Hence, the effective course of action is to close the exit by massive infill from adjacent banks using a buIIdozer.

(4) A special case is the restoration of the plug action of alluvial deposits from the Muaredzi stream at the exit of the lake (Fig 10.3). Here a weir is required to completely close off the present Urema course to force the water level up sufficiently to flow out along an adjacent flood channel (a natural spillway). In this site a low slotted weir should be built into the ground so that its crest is close to the present spillway surface. The weir should be slotted in such a way that sufficiently high floods result followed by a gradual lowering of the lake—a slow ebb through the autumn and dry season. The maintenance of a flood-ebb sequence is essential. Immediately west of the present Muaredzi confluence is another much deeper channel which requires total sealing off.

(5) Finally, the erosive power of the smallest drainage lines in flat country is usually grossly underestimated, resulting in washaways of all constructions. Where possible these constructions should be built in such a manner that they emulate, as closely as possible, the appearance of natural splay or bar deposits. Straight lines should be avoided.

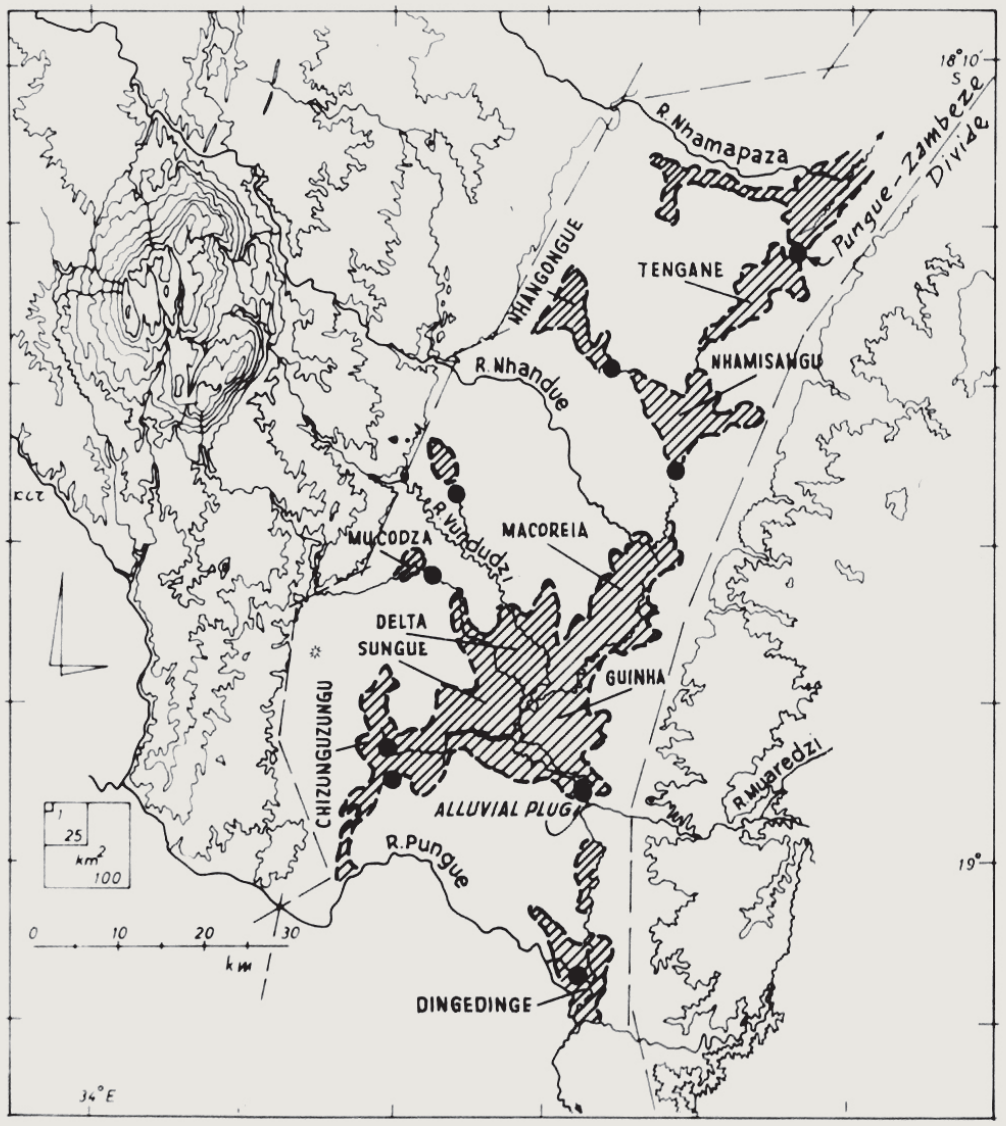


FIG 10.1 MANAGEMENT OF FLOODPLAIN GRASSLANDS BY REINSTATING THE CONVEXITES RESPONSIBLE FOR THEIR EXISTENCE

▨ FLOODPLAIN GRASSLAND AND SLACKS (TANDOS)

● CONVEXITIES FORMING CRITICAL HEIGHTS OR BASE LEVELS. SOME INCISED OTHERS THREATENED BY HEADWARD EROSION OF NICKPOINTS. THESE SITES TO BE RESTORED BY PERMANENT WEIRS.

LEFT: Figure 10.1

Management of floodplain grassland by reinstating the convexities responsible for their existence.

A first result of a restored higher flood level will be the die-off of areas of marginal floodplain woodland and expansion of the aquatic pasture grasses *Echinochloa stagnina* and *Vossia cuspidata*. Chemical analysis of these grasses should help determine the length of inundation permissible in order to maintain pasture quality (vide Section 9.5).

These are some of the factors to be taken into account when a longer lasting flood and ebb sequence is required, and in this, an ideal management tool would be a weir with a simple vertically adjustable notch.

Ungulates and Prime Movers

The present management approaches in national parks either ignore the habitat problems and concentrate on culling over-populations of particular species, or attempt random bush clearing programmes although there is no hope of restoring grassland because of changed soil moisture balance. Effort has to be directed at restoring a high soil moisture as well, if cutting, fire or other methods are used in bush clearing. Unless this is done, deep rooted savanna trees must, as a natural process, become the dominant cover.

Restoring the soil moisture balance in many sites, particularly in plainsland and old vlei or dambo areas, will by itself kill the scrub encroachment. Thus scrub clearing must be selectively applied in the field to land facets and soil profiles where effective hydromorphism can be restored. A valuable quick aid in delineating such sites is the use of air photos from twenty or thirty years ago in which natural distribution patterns of grassland, forest and savanna can be seen, as it was then as yet little changed by poor land use practices,

Other management approaches such as culling the top of the food pyramid, predators for example, is possibly justifiable to protect rare or endangered species. However, it is impossible to predict what subsequent chain of events

RIGHT: Figure 10.2

Urema Lake outlet (alluvial plug site) and Mucodza Marsh.

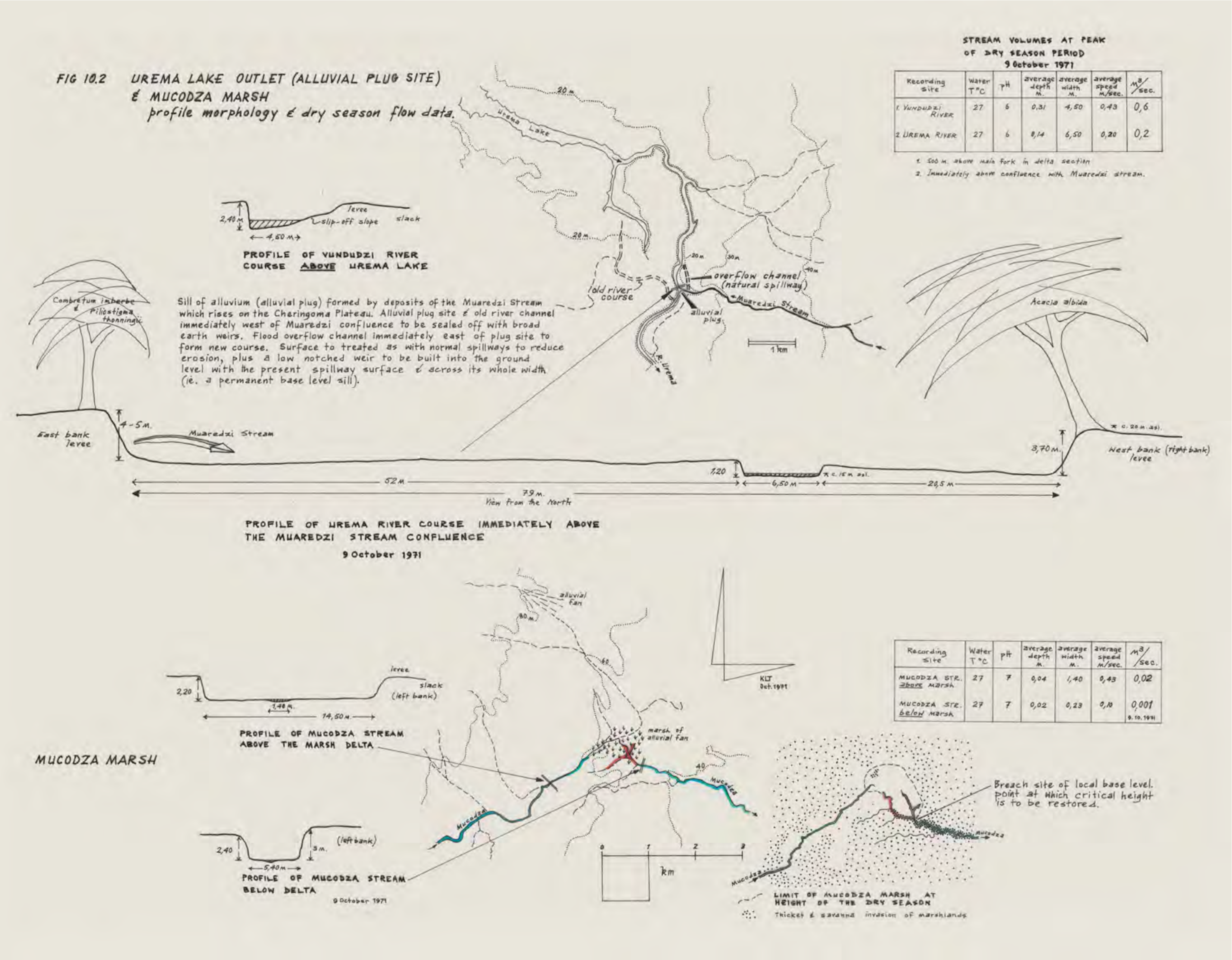


FIG 10.2 URÉMA LAKE OUTLET (ALLUVIAL PLUG SITE) & MUCODZA MARSH
profile morphology & dry season flow data.

Sill of alluvium (alluvial plug) formed by deposits of the Muaredzi Stream which rises on the Cheringoma Plateau. Alluvial plug site & old river channel immediately west of Muaredzi confluence to be sealed off with broad earth weirs. Flood overflow channel immediately east of plug site to form new course. Surface to treated as with normal spillways to reduce erosion, plus a low notched weir to be built into the ground level with the present spillway surface & across its whole width (ie. a permanent base level sill).

STREAM VOLUMES AT PEAK OF DRY SEASON PERIOD
9 October 1971

Recording site	Water T°C	pH	average depth m.	average width m.	average speed m/sec.	m³/sec.
1. VUNDUDZI RIVER	27	6	0,31	4,50	0,43	0,6
2. UREMA RIVER	27	6	0,14	6,50	0,20	0,2

1. 500 m. above main fork in delta section
2. Immediately above confluence with Muaredzi stream.

Recording site	Water T°C	pH	average depth m.	average width m.	average speed m/sec.	m³/sec.
MUCODZA STR. above marsh	27	7	0,04	1,40	0,43	0,02
MUCODZA STR. below marsh	27	7	0,02	0,23	0,10	0,001 9.10.1971

may follow such a move as new interactions are superimposed over the natural processes and responses at play, and habitat restoration may well be all that is required in any case.

If culling is to be taken to its ludicrous conclusion, it would be to mount a campaign against all frugivores as they are the prime movers in afforestation and thus in the extinction of grasslands!

As distasteful as mowers or cutter machines may be to the wilderness atmosphere of a national park, cutting is far preferable to burning, which depresses valuable soft leaved, sensitive grasses, such as *Urochloa mosambicensis* in favour of coarse thatch grasses, and it compounds encroachment of scrub. Ideally tribal people en masse should be employed to cut thatch grass and encouraged to use, sell or barter this product for other requirements (another park product).

The only manner in which fire can be used effectively to open up heavily wooded savanna, or to maintain an existing grassland, is where ungulate populations are sparse, so that there is adequate rank regrowth and thus adequate fuel for another, late season, fire. The selection for rank fibrous pastures will, however, further militate against most grazers.

In the final count, meaningful habitat management can only be effectively carried out where ungulate populations are low. Thus diversity, not quantity, is a primary requirement in areas where no buffer systems, such as floodplains or slack pastures are available. Where this habitat, or its equivalents on a small scale such as pans, are present in abundance, large numbers of single species such as buffalo may be maintained, according however to the capabilities of the dry season riverine conditions.

All wild ungulate stocks must be balanced with the riverine zones available in the dry season, i.e. stocking rates related to dry season riverine carrying capacity, which does not result in undue destruction of these zones. What is required then is for a pan system in the hinterland to be restored (where breached), or deepened to hold water for the duration of the rains and autumn until mid-year (June), and then dry out, forcing the herds back to the riverine zones. The provision of permanent water points away from the riverine zones effectively spreads the 'riverine zone', allowing for greater build up of species which are forced back to the natural riverine areas anyway, due to lack of suitable pasture, where they multiply the

LEFT:

Ecological interdependence and dynamics of the Gorongosa ecosystem. Mountain rains shed to Rift Valley (water in foreground). Floodplain grassland dependent on seasonal flooding, ungulates dependent on grassland and water, incision, drying out and savanna invasion along levees and other convexities (foreground).

RIGHT:

Mucodza Marsh showing headward eroding donga which has incised the local base level sill responsible for the genesis and maintenance of the marsh.

BOTTOM RIGHT:

Northern wooded sector of the Urema Plains depicting savanna invasion of drained slack basins, their original outlines still discernable, (i.e. later stage of process shown above.. View to the southwest of the Bunga Inselbergs and Gorongosa Mountain.

FAR RIGHT:

Miombo ambient *Brachystegia* savanna woodland; pre-rain spring aspect with post-fire flush of grass stratum and mosaic red leaf flush of canopy trees.

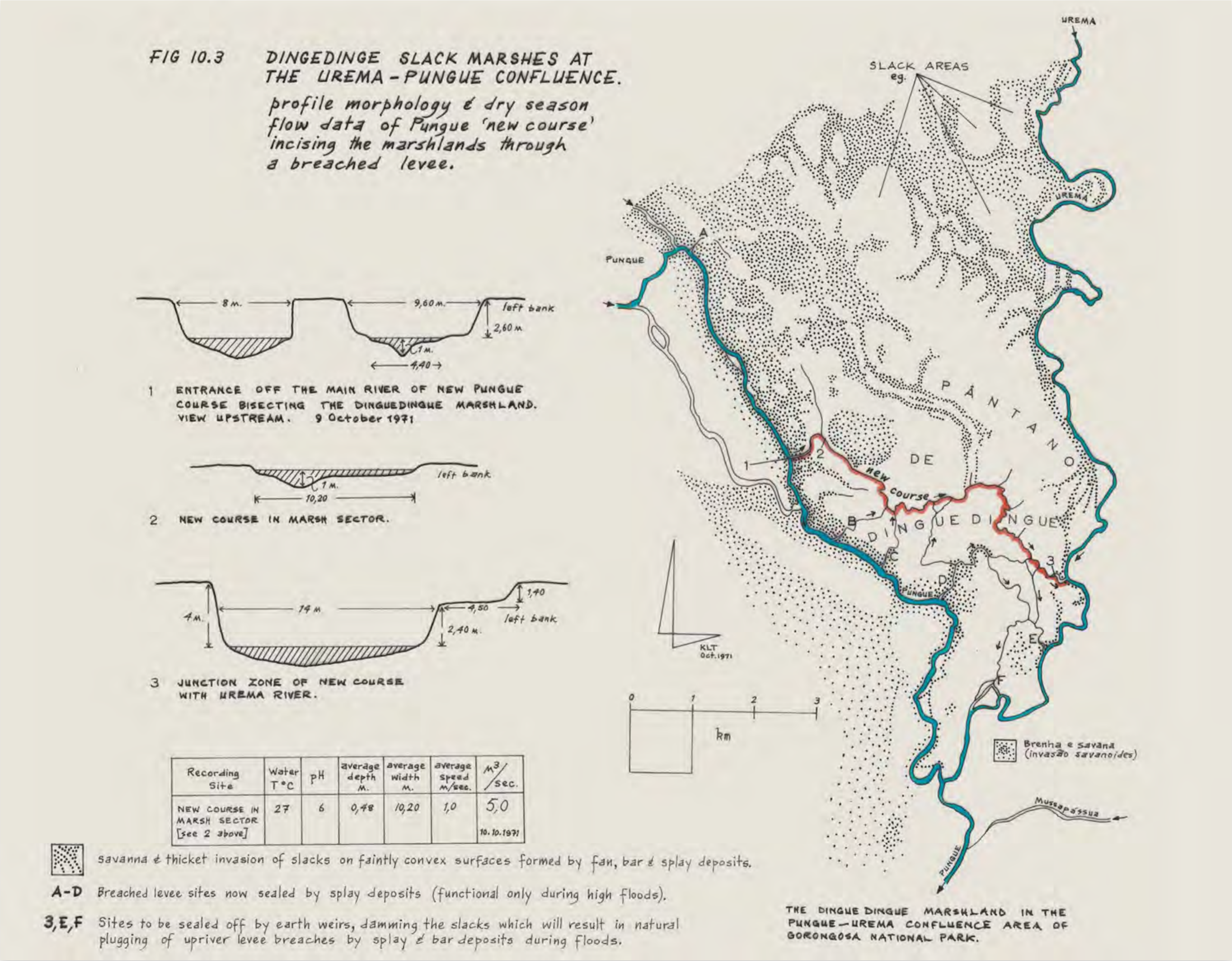
impact by adding to the populations already dependent there.

Hence, in any landscape, ungulate populations must be kept at the level at which natural riverine zones can support them in the dry season without massive destruction of these sites. This requires geohydrological analysis of the drainage in slack pastures on either side of the actual stream or river beds. If slacks are connected at the lower end by drainage channels, then these pastures are on their way to becoming (if not already) only seasonally productive in the rains instead of through the 'worst' time of year. The crux of all management therefore rests on an appreciation of geomorphic processes, in particular the fluvial aspects which provide (slacks) or eliminate (by nickpoint breaching) high primarily productivity in the dry season.

Carrying Capacities

Biomass figures of the principal large ungulates are given in Table 10.3. Using a standard stock unit (SSU) of 454 kg mass, the stocking rate at the time of study was of the order 1 SSU/6-8 ha on the 3,650 km^2 area of Rift Valley floor. If the dry season carrying capacity is as much as half of this, then the Rift floor is grossly overstocked.

As should be clearly evident from the plexus of pasture responses and influences explored in Section 9.5, this aspect remains the most glaring gap in the necessary knowledge for the formulation of a meaningful management programme, as pasture



Recording Site	Water T°C	pH	average depth m.	average width m.	average speed m/sec.	m^3/sec.
NEW COURSE IN MARSH SECTOR [see 2 above]	27	6	0,48	10,20	1,0	5,0 10.10.1971

LEFT: Figure 10.3

Management of Dingedinge slack marshes at the Urema–Pungue confluence.

OPPOSITE:

Marking young elephants for tracking their movements.

quality at various times of the year and under different circumstances is totally unknown. The prevalence of poor physical condition in the three largest biomass species, elephant, buffalo and hippo, is indicative of the inadequacy of suitable pastures in the dry season, despite its super-abundant cover. The restoration of hygrophilous pastures, which are the primary food base throughout the year, over extensive areas would greatly alter the picture from the present situation where only some 40 km^2 of green pasture is left at the height of the dry season. Another unknown factor is the total area occupied by the tall thatch grasses that are prevalent in many sectors. Together with the dried out (salinised) floodplain pasture, these too, would have to be subtracted from the effective total carrying capacity of the dry season.

Myre and Antão (1972) estimate that the carrying capacity of grasslands on floodplain alluvium is between 3 ha and 5 ha/SSU. Reference to Table 10.2 shows that elephant are already close to 1/km^2 on the entire Rift floor, without taking into consideration the dry season riverine carrying capacity. The elephant population is thus probably beyond the safe carrying capacity, as emphasized by the poor physical condition of most of the matriarch herds. Restoration of green slack pastures would probably tide the present elephant population, in better condition, through the dry season.

Hippo are obviously overpopulated, as the greater part of the population is confined to the grazing around the Urema Lake, and the majority of animals are in chronically poor physical condition for three-quarters of the year (Fig 9.22). A reduction of at least half the population is indicated. However, monitoring of changes in grass structure and possible differential impact on the wildebeest and buffalo populations in particular would have to be recorded.

Buffalo is the third species which shows extremely decimated physical condtion, accompanied by die-offs during the torrid pre-rains period between August and October. Though elephant are mixed feeders, utilising a large proportion of browse in the Gorongosa ecosystem, they and buffalo are heavily reliant on the last green zones of slacks and riverine strips during the dry season. From large scale maps it is estimated that a maximum of 40 km^2 of green pasture is left at the height of the dry season in the entire Rift floor area within the ecosystem limits (i.e. only 1%, due to canalisation of slack pastures). The major grazing population is confined largely to this 1% base at the height of the dry season. If unseasonal rain or fire brings a flush of regrowth to other pastures, the herds move out to these and return to the green zone base once withering occurs.

TABLE 10.3
Biomass of principal large wild ungulates in the Gorongosa ecosystem.
(derived from air counts)

SPECIES	TOTAL NO.	MEAN BODY MASS kg.	BIOMASS kg.	% OF TOTAL BIOMASS	BIOMASS kg/km^2	DENSITY/ km^2 IN RIFT VALLEY (3,659 km^2)*
Elephant	2,200	3,182	7,000,400	34.6	1,918	0.6
Buffalo	14,000	500	7,000,000	34.6	1,918	4.0
Hippo	3,000	1,136	3,408,000	17.3	934	1.0
Wildebeest	5,500	182	1,001,000	4.9	274	1.5
Waterbuck	3,500	205	717,500	3.5	197	1.0
Zebra	3,000	216	648,000	3.2	178	1.0
Eland	500	455	227,500	1.1	62	0.1
Sable	700	159	111,300	0.5	30	0.2
Hartebeest	800	92	73,600	0.3	20	0.2
Totals	33,200	6,127	20,187,300	100	5,531	10.6

KEY
(not included: Kudu, nyala, bushbuck, reedbuck, impala, klipspringer, red duiker, grey duiker, blue duiker, Sharpe's grysbok, suni, oribi, warthog, bushpig, black rhino, white rhino)
* Rift valley floor the main concentration area

Until the hygrophilous pastures have been restored by blocking off the breach sites, and a through-the-year chemical analysis is made of the browse foods and the important pasture grasses listed in Table 9.3 under different conditions, it is vital that reduction of hippo and buffalo numbers is commenced and their products utilised before crashes in their populations result in a large scale waste of animal protein. It would be in vain to make recommendations on carrying capacities of these and other ungulates without a periodic monitoring programme of the response in condition of the animals and pasture to the effects of culling and habitat manipulation, as well as their influences on other species. In this, the use of a helicopter for accurate air coverage of animal populations and habitats is fundamental.

REFERENCES / CORRELATION CONSERVATION

Arnott, B. 1974. *There's meat for Africa if you're game.* Farmer's Weekly, Sept. 4th, pp. 16–19.

Darling, F. Fraser 1960. *Wildlife husbandry in Africa.* Scientific American, vol. 203 (5), pp. 123–134.

Dasman, R.F. 1975. Dasman, R.F., The Conservation Alternative. New York.

Laws, R.M., Parker, I.C.S. & Johnstone, R.C.B. 1975. *Elephants and their habitats.* Clarendon Press, Oxford.

Ledger, H.P. 1964. *The role of wildlife in African agriculture.* E. Afr. Agric. For. J., vol. 30, pp.137–141.

Myre, M. & Antão, L.R. 1972. *Reconhecimento pascicola ao Vale do Save.* I.I.A.M. Communicãçoes, no.75.

Schumacher, R.E.F. 1973. *Small is beautiful: a study of economics as if people mattered.* Blond and Briggs, London.

Talbot, L.M., Payne, W.J.A., Ledger, H.P., Verdcourt, L.D. & Talbot, Martha H. 1965. *The meat production potential of wild animals in Africa.* Commonwealth Agric. Bureaux Techn. Com. No. 16.

Tinley, K.L. 1969. *The ecological limits of Gorongosa National Park, Moçambique: and the maintenance of wilderness.* Report to the Moçambique Govt. Mim.

PART 3

GORONGOSA PATTERNS

Chapter 11

Kaleidoscope

Kaleidoscope

11.1 INTRODUCTION

The essence of the Gorongosa ecosystem is the constantly changing kaleidoscope of the physical and living components in different rhythms directed from below by the constraints or opportunities presented by changing edaphic properties.

Kaleidoscope, used here in an ecosystem context, is made up totally of moving parts: the two rotatable pieces of the tube comprising (a) climatic controls (particularly of precipitation in the tropics), and (b) the edaphic or substrate control. Each is subject to a different rate of movement due to lag effects, relative quiescence or rapid change in counter or empathetic responses, the two parts of the tube thus show reciprocal interactions (e.g. the influence of changes in relief, or precipitation and rain inhibiting effect of bare, or denuded, land surfaces due to their high albedo).

Within this tube are the coloured chips which represent the living components that form different patterns of recombination with every movement of either one or both the tube parts, as well as adjustments from their own interactions. Amongst the chips are some brighter than others, which represent the prime mover components or dominants, their brightness altering in each adjustment where others become dominant.

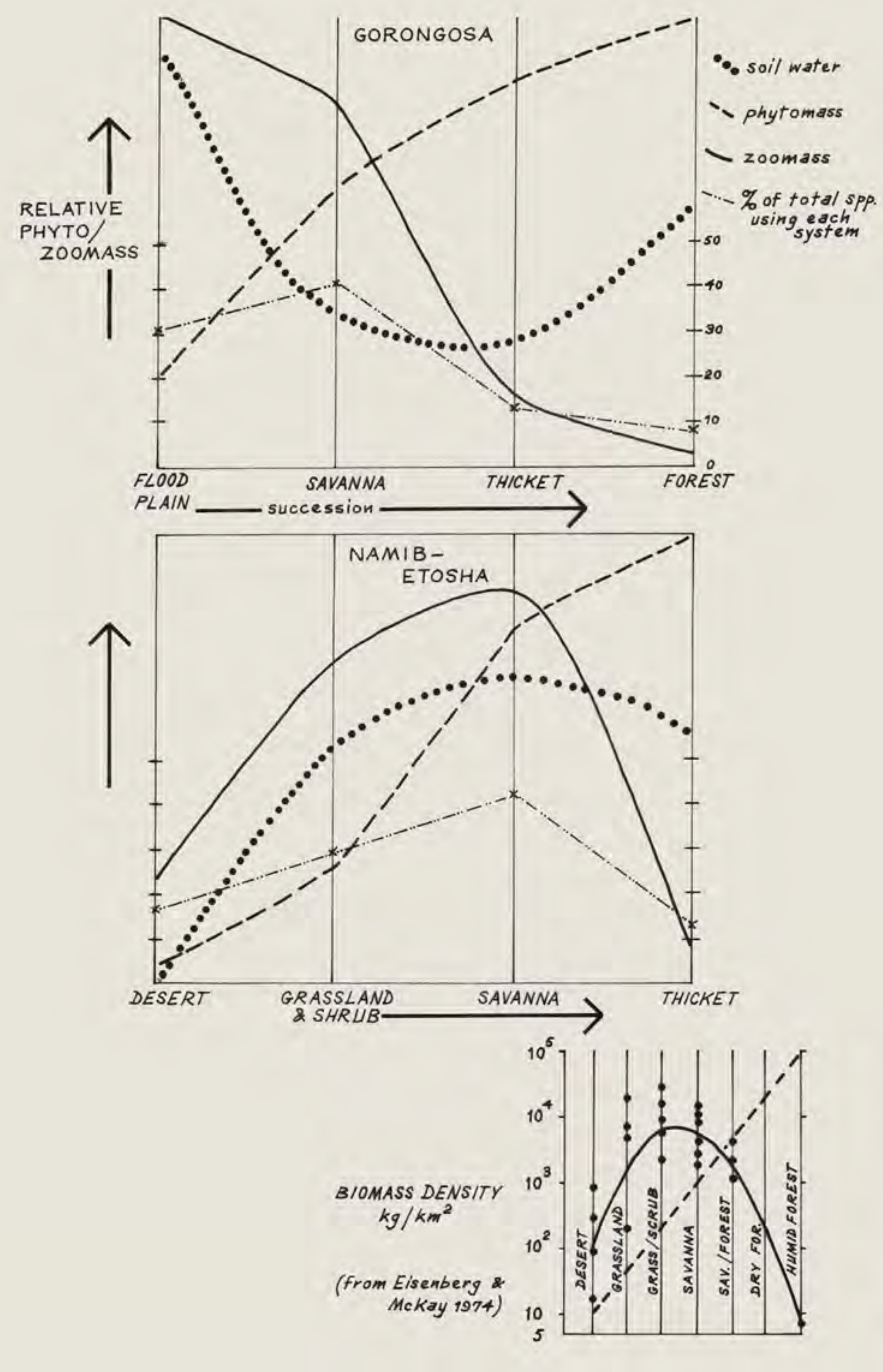
Of all the environmental factors at play in the southern tropics between the west coast Namib Desert and the east coast Mozambique Plain, the master factor is edaphic—soil moisture balance, which even over-rules frost effect where trees occur in frost hollows on moist soils. Climatic influences are thus in high measure expressed through the properties peculiar to each substrate. This has a parallel in a unique property of the Earth which acts as a black-body radiator of the Sun's radiant energy, without which no weather as we know it could be generated. Thus the solar radiation, or climate in the ecosystem context, is expressed through its translation via the Earth or edaphic medium.

The differential edaphic properties orchestrate the ecological dynamics and influence the sociobiological expression possible in different circumstances, and thus the evolutionary consequences by determining the spatial and temporal make-up of ecosystems or communities. This in turn affects the ecological interdependence exhibited by a particular situation including prey-predator and social relationships.

In landscape evolution the most important geomorphic dynamic is scarp retreat (King 1962); in ecology the key geomorphic process, as highlighted by this thesis, is the development of nickpoints. The formation of a nickpoint alone alters the soil moisture balance of landscapes of all dimensions, from the microscale to continental proportions, determining the kinetics of ecological succession.

Under an unchanging local or regional climate, large changes in habitat structure, relative plant and animal biomass, species composition and complete community replacement are wrought over contemporary time (3–50 years) by normal geomorphic succession. This succession is either a spatial replacement of land surfaces by erosion (sheet, donga, slumping or pipe erosion) and deposition, i.e. older landsurfaces being replaced by younger, or in situ change due to increased runoff from either a reduction in plant cover, incised local base levels and headward migration of nickpoints, or a combination of these altering the soil moisture content.

These changes in the landscape are inexorable processes, damped or slowed down by the presence of resistant rock, highly cohesive clay soils or dense plant cover. Any factors altering the efficacy of these controls act essentially as accelerator factors, increasing the velocity of the successional sequences often long since initiated. In many sites, poor land use practices can in fact initiate a trail of new geomorphic changes. In the biological field,



(from Eisenberg & McKay 1974)

LEFT: Figure 11.1

Generalised mass relationships of plant and animal (wild ungulates) communities and ungulate diversity to climo-edaphic (soil moisture balance) regimes on the same latitude in the southern tropics of Africa.

succession is usually thought to be a dynamic feature of plant communities only. There are In fact three principal kinds of kinetic multi-directional successions with feedbacks between each:

(1) Substrate succession
  (a) Geomorphic surface replacement
  (b) Edaphic changes in situ
(2) Biotic succession and opportunism
  (a) Spatial, on new surfaces
  (b) In situ succession within a community or a system. (responding to physical changes and the influence of biotic dominants and prime mover components).
(3) Evolutionary succession
  On a longer time scale and as result of the preceding features including diastrophic changes, climatic change, systems and species changes resulting in dispersal, contraction, kaleidoscopic recombinations, speciation and extinction.

Unless the intrinsic dynamics of ecosystems, and the successional stage and tendencies of processes, are taken into account, most management activities to save rare or endemic species and ecosystems are pointless in the face of the inexorable natural or accelerated changes or fluctuations over the short-term, outlined above. Indeed we may only disrupt the species succession best adapted to the new changes of, say, scrub encroachment for example. A refreshing example of a geoecological holistic approach to management problems is provided by a unique paper on cyclical ecosystem changes in the Amboseli endorheic basin related to climatic fluctuations on Mount Kilimanjaro nearby (Western & Van Praet 1973), in many ways analogous to the relationship between the Urema basin and Gorongosa Mountain.

Some fundamental questions need to be asked so that we can maintain or reinstate the natural controls or dampers in the system:
(a) which geomorphic processes are active in a system? (b) what are the successional stages of these surfaces? (e) which are the key factors controlling the velocity of these changes? (d) which factors influence soil moisture content? (e.g. if local base level sills are the controlling features, are they durable or friable and if the latter, can they be reinforced or reinstated?) (f) which biotic components are dominants or prime movers in ecological dynamics in a particular area? (g) are the prime mover components responsible for damping or accelerating geoecological succession? (h) what are the successional status, trends or tendencies in various communities or ecosystems?

The far reaching implications of these natural or accelerated successional changes, which do not require any regional change in climate, require a re-evaluation and re-interpretation of the following:

(1) Complete revision of many ecological principles.
(2) The time factor in geomorphic succession (erroneously thought to be purely of geologic time scale).
(3) The age of ecosystems or major plant formations and their evolutionary status (e.g. 'oldest' forest formations on youngest geomorphic surfaces, and 'derived' grassland and savanna formations on the oldest planation surfaces).
(4) Biogeographic dynamics.
(5) Palaeo studies.
(6) Edaphic and pedological change.
(7) Management and planning.
(8) Relative ratio changes between phyto and zoomass.
(9) Exclusion of certain animal components by habitat occlusion and the spread of others.
(10) Dynamics, structure, diversity and richness of ecosystems.

The successional relationships of plant and animal communities (wild ungulates in this example) to contrasting climo-edaphic (soil moisture balance) controls in the Gorongosa ecosystems, and that of the desert and arid savannas at the same latitude on the west coast, are depicted in simplistic and generalised form in the accompanying figure. In each case the greatest diversity of coincident parameters is associated with the duplex savanna ecosystems, which is a superimposed combination of grassland and woodland. As the systems on either side of it have a relatively homogenous structure and physiognomy, are savannas therefore not the true 'climax' ecosystem or community in the kinetic sequence?

REFERENCES / CORRELATION KALEIDOSCOPE

Eisenberg, J.F. & McKay, G.M. 1974. 'Comparison of ungulate adaptations in the New World and Old World tropical forests with special reference to Ceylon and the rain forests of Central America'. In *The behaviour of ungulates and its relation to management*. IUCN Publ. New Series No.24, Vol. 2, pp. 585–602.

King, L.C. 1962. *Morphology of the Earth.* Oliver & Boyd, Edinburgh and London.

Western, D. & Van Praet, C. 1973. *Cyclical changes in the habitat and climate of an East African eco-system.* Nature, Vol. 41 (5385), pp. 104–106.

◆

APPENDIX 1

SOIL PROPERTIES

Analytical data for representative soil profiles from the Gorongosa-Cheringoma area

GORONGOSA MOUNTAIN & MIDLANDS

	Vb		Lb			
Depth cm	0 – 30	30 – 100	0 – 40	>>40		
Texture	Sa	CILm	SaCI	CI		
Stru/Cons	Bloc/H	Pris/H	Wk/s	Bloc/H		
Mottling	none	none	none	none		
Permeability	good	good	poor	res		
pH (H_2O)	5.8	5.7	5.1	5.4		
Salinity (C)	0.2	0.1	0.3	0.1		
$CaCO_3$ (HCl)	0	0	0	0		
P (Etr ppm)	11.0	10.0	9.0	8.0		
Colour	Brownish black	Dark red brown	Brownish black	Reddish brown		

	Cvb		Cpg			
Depth cm	0 – 20	20 – 120	0 – 25	25 – 100	100 - 140	
Texture	CILm	CI	SaLm	SaLm	stony	
Stru/Cons	Mod/S	St/H	None/S	None/S	compact	
Mottling	none	none	none	none	none	
Permeability	good	g - p	rapid	rapid	rapid	
pH (H_2O)	6.0	5.5	6.3	6.1	6.3	
Salinity (C)	0.3	0.1	0.4	0.2	0.2	
$CaCO_3$ (HCI)	0	0	0	0	0	
P (Etr ppm)	62.5	10.5	5.5	1.4	1.0	
Colour	v Dark reddish brown	Dark reddish brown	Dark brown	Dull yellow brown	Brown	

	Cpv			Vtc		
Depth cm	0 – 20	20 – 60	60 – 100	0 – 10	10 – 40	40 – 80
Texture	SaCILm	SaCILm	stony	CILm	CI	
Stru/Cons	Mod/S	Mod/S	compact	Mod/H	Pris/vH	
Mottling	none	none	none	none	none	
Permeability	good	good	good	good	poor	
pH (H_2O)	7.0	6.8	6.2	6.4	6.9	8.9
Salinity (C)	0.4	0.2	0.1	2.8	2.6	5.7
$CaCO_3$ (HCI)	0	0	0	0	5%	10%
P (Etr ppm)	10.4	3.3	3.6	36.0	25.0	1.4
Colour	Brownish Black	Dark reddish brown	Reddish brown	Brownish black	Dark reddish brown	Brownish red

GORONGOSA MOUNTAIN & MIDLANDS *(cont.)*

	Pg		Pgh			
Depth cm	0 – 25	>40	0 – 25	25 – 60	>60	
Texture	Sa	stony Sa	Sa	Sa-SaCI	Sa-SaCI	
Stru/Cons	Non/S	Non/S	Non/S	Non/S	St/vH (Fe concs)	
Mottling	none	none	none	mod	strong	
Permeability	rapid	rapid	rapid	res	sev res (G)	
pH (H_2O)	5.9	5.8	6.2	5.8	5.4	
Salinity (C)	0.3	1.8	0.3	0.2	0.2	
$CaCO_3$ (HCI)	0	0	0	0	0	
P (Etr ppm)	2.64	2.12	7.0	3.4	4.3	
Colour	Brownish grey	Dull yellow brown	Brownish black	Greyish yellow brown	Brownish grey	

RIFT VALLEY

	Ah		A			
Depth cm	0 – 90	90 – 120	0 – 40	40 – 70	70 – 120	
Texture	CI	SaCI	SaCI	SaCI-Sa	SaCI-Sa	
Stru/Cons	Bloc/H	Pris/H	Wk/S	Mod/H – S	Mod/H – S	
Mottling	none	strong	none	none	dist wk	
Permeability	poor	res (G)	res	p-g	p-g	
pH (H_2O)	5.7	6.8	6.4	6.5	6.6	
Salinity (C)	4.2	13.1	0.4	0.1	0.1	
$CaCO_3$ (HCI)	0	0-concs	0	0	0	
P (Etr ppm)	15.4	3.4	16.3	3.8	2.9	
Colour	Black	Grey	Greyish Brown	Brown	Brownish orange	

	Cd			Chd		
Depth cm	0 – 20	20 – 40	40 – 100	0 – 20	20 – 50	50 - 120
Texture	SaLm	SaCI	SaCILm	SaCI	SaCI-CI	SaCI
Stru/Cons	Mod/S	Mod/H	Cem/vH	Mod/S	Pris/H	Cem/H (Fe cons)
Mottling	none	none	none	none	strong	strong
Permeability	good	poor	good	poor	p - g	p - g
pH (H_2O)	6.6	6.9	7.0	6.1	6.0	6.6
Salinity (C)	0.4	0.1	0.4	0.4	0.2	0.2
$CaCO_3$ (HCI)	0	0	0	0	0	0
P (Etr ppm)	26.6	14.8	17.7	19.7	16.8	15.1
Colour	Black	Greyish yellow brown	Dark brown	Black	Brownish black	Dark brown

RIFT VALLEY CONT.

	Cp			Chp		
Depth cm	0 – 20	20 – 50	50 – 120	0 – 20	20 – 40	40 – 60
Texture	Sa-SaLm	Sa-SaLm	Sa	SaLm	SaLm	SaCILm
Stru/Cons	Wk/S	Non/S	Non/L	wk/S	Non/S	Pris/sH
Mottling	none	none	none	none	strong	strong
Permeability	good	rapid	rapid	good	good	S7.0ev res (G)
pH (H_2O)	6.4	5.3	6.1	6.1	7.1	8.6
Salinity (C)	0.4	0.1	0.1	0.5	0.2	1.3
$CaCO_3$ (HCI)	0	0	0	0	0	0
P (Etr ppm)	3.1	0.3	0.0	6.1	5.0	2.9
Colour	Brownish black	Greyish yellow	Brownish grey	Brownish black	Greyish	Greyish yellow brown
	Chc					
Depth cm	0 – 30	30 – 60	60 - 120			
Texture	Sa-SaCI	SaCI	SaCI			
Stru/Cons	Mod/S	Pris/vH	Pris/vH			
Mottling	none	strong	strong			
Permeability	g-p	sev res	sev res			
pH (H_2O)	6.1	6.9	8.3			
Salinity (C)	0.4	0.4	1.5 – 5.0			
$CaCO_3$ (HCI)	0	5 – 10%	>10%			
P (Etr ppm)	5.8	3.2	6.2			
Colour	Black	Brownish black	Yellowish brown			

CHERINGOMA PLATEAU

	Vp			Vcd		
Depth cm	0 – 20	20 – 80	80 – 140	0 – 30	30 – 70	
Texture	Sa	Sa	SaLm	SaCILm	SaCI	
Stru/Cons	Non/L	Non/L	Wk/sH	Mod/S	Mod/S	
Mottling	none	none	none	none	none	
Permeability	rapid	rapid	good	good	good	
pH (H_2O)	6.1	5.7	5.3	6.3	5.9	
Salinity (C)	0.3	0.1	0.1	0.4	0.1 (C)	
$CaCO_3$ (HCI)	0	0	0	0	0	
P (Etr ppm)	2.5	0.5	2.0	3.7	3.2	
Colour	Dark red brown	Dull redbrown	Red	Brownish black	Dark red brown	
	Bp			Pd		
Depth cm	0 – 30	30 – 100	120	0 – 15	15 – 40	40 – 120
Texture	Sa	Sa	SaCI	Sa	Sa	SaCI
Stru/Cons	Non/L	Non/L	Non/S	Mom/S	Non/S	Pris/vH
Mottling	none	none	strong	none	none	strong
Permeability	rapid	rapid	sev res.	rapid	rapid	sev res. (G)
pH (H_2O)	6.0	5.7	5.4	6.4	5.7	5.4
Salinity (C)	0.2	0.1		0.3	0.1	0.2 (C)
$CaCO_3$ (HCI)	0	0	0	0	0	0
P (Etr ppm)	3.6	1.2		4.0	0.5	0.3
Colour	Brownish grey	Dull yellow orange		Brownish grey	Brown	Brownish grey
	Pcm			Nd		
Depth cm	0 – 25	25 – 75	75 – 120	0 – 50	50 – 90	90 – 120
Texture	SaCILm	SaCI	CI	SaCI	SaCI	SaCI
Stru/Cons	Bloc/S	St/sH	St/H	St/sH	Pris/vH	St/vH
Mottling	none	none	none	none	none	strong
Permeability	rapid	good	poor	g – p	poor	res.
pH (H_2O)	6.6	6.2	8.1	6.4	5.4	5.8
Salinity (C)	0.4	0.2	0.3	0.4	0.2	0.2 (C)
$CaCO_3$ (HCI)	0	5%	10%	0	0	0
P (Etr ppm)	3.3	3.4	0.5	2.7	3.1	0.3
Colour	Black	Brown		Black	Brownish grey	v. Dark red brown

CHERINGOMA COAST*

	Dambo Grassland				Heath (Fynbos) Scrub-thicket			
Depth cm	0 – 25	25 – 45	45 – 70	70 – 120	0 – 7	7 – 45	45 – 60	60 – 80
Texture	Sa	Sa	SaLm	SaLm (Ort)	Org Qrtz	Sa	Ort	Org. Sa
Stru/Cons	Non/L	Non/L	Non/S	St/Fe pan	Non/L	Non/L	St/v H ind	Non/S
Mottling	none	none	mod	strong	none	none	strong	strong
Permeability	rapid	rapid	good	res	good	rapid	red	good
pH (H_2O)	5.6	5.7	5.4	5.6	5.0	5.8	5.4	5.4
Salinity (C)	6200 (R)	9600	9300	12400	3150	15600	12200	1100
$CaCO_3$ (HCI)	0	0	0	0	0	0	0	0
Colour	Black	Dark red brown	Greyish brown	Dark grey yellow	Black	Brownish grey	Reddish black	V Dark brown
	Androstachys Thicket on termite hill pediment				Mesic Evergreen Forest (*Hirtella, Pseudobersama, Pachystela, Manilkara, Olea*)			
Depth cm	0 – 5	5 – 40	40 – 50	50 – 60	0 – 12	12 – 35	35 – 135	135 – 180
Texture	Org. Qrtz	Org. Sa	Sa	Sa	Sa	Sa	Sa	SaCI
Stru/Cons	Non/L	Non/L	Non/Comp.	Non/S	Non/L	Non/L	Non/L	Non/comp.
Mottling	none	none	strong	strong	none	none	none	strong
Permeability	good	rapid	poor	good	rapid	rapid	rapid	res.
pH (H_2O)	4.4	5.1	4.8	5.1	6.4	6.7	6.8	5.4
Salinity (C)	1060 (R)	2080	1300	2500	1200	5200	8300	2850
$CaCO_3$ (HCI)	0	0	0	0	0	0	0	0
Colour	Reddish black	Brownish black	Reddish black	v Dark reddish brown	Black	Brownish black	Brown	Dull red brown
	Diheteropogon Alluvial Grassland				*Brachiaria* Alluvial Grassland			
Depth cm	0 – 5	5 – 10	10 – 25	> 25	0 – 10	10 – 25	> 25	
Texture	CILm	CILm	CILm	SALm	SALm	CILm	CI	
Stru/Cons	Mod/sH	Mod/sH	Pris/S	Mod/S	Non/S	Pris/S	Pris/sH	
Mottling	none	none	none	none	none	weak	strong	
Permeability	good	good	good	good	good	res.	sev.res. (G)	
pH (H_2O)	5.6	5.4	5.5	5.0	4.7	4.5	4.4	
Salinity (C)	1540 (R)	1180	1200	500	920	350	160	
$CaCO_3$ (HCI)	0	0	0	0	0	0	0	

KEY TO ABBREVIATIONS

Texture	Sa – Sand; Lm – Loam; CI – Clay; Org – organic matter; Ort – ortstein (cemented iron and organic matter in subsoil of podzols); Qrtz – pure quartz.
Structure (Stru)	Bloc – blocky, Pris – prismatic; St – strong; Mod – moderate; Wk – weak; Non - none
Consistence (Cons)	vH – very hard; H – hard; sH – slightly hard; S – soft; L – loose; ind – indurated; Cem – cemented. conc – concretions, pan – subsurface impermeable horizon compacted and/or indurated.
Permeability	rapid, good (g), poor (p), res – restricted, sev. Res. – Severely restricted, g-p = good to poor. (G) – gley horizon, (terminology from Loxton 1962)
Salinity (C)	Conductivity (mmhos/cm at 25^{0}C) 4,0 saline, 4,0 non-saline
**Salinity (R)*	Resistance (ohms) 250 saline, 250 non-saline (only Cheringoma Coast)
P (Extr ppm)	Extractable phosphorus (P in mg/kg). Colorimetric method using molybdenum blue, Extracted in alkaline medium with sodium hydroxide (Fernandes 1968b: 33)
Colour	Terms derived from *Revised Standard Soil Colour Charts* by M.O.H Takehara 1967. For original Munsell colour notations for Gorongosa see Fernandes (1968 a, 1968b)

APPENDIX 2

FOOD PLANTS

Food plants of larger mammals recorded in the Gorongosa ecosystem by direct observation of feeding and from dung (1968–1973).
Except where specifically noted all feeding records refer to grazing or browsing utilization. Species are listed alphabetically.

BABOON

PLANTS	WET SEASON (Nov.–Apr.)	
Grasses	*Echinochloa* sp. nr. *haploclada* fr	*Paspalidium obtusifolium* cu
	E. stagnina fr	*Paspalum scrobiculatum* fr
	Eriochloa stapfiana fr	*Urochloa mosambicensis* fr
	Panicum coloratum fr	*Vossia cuspidata* cu, ro
	P. maximum fr	
Sedges	*Cyperus esculentus* ro	
Forbs	*Abutilon* spp. fl	*Ludwigia stolonifera*
Woody plants	*Acacia sieberana* gu, fr	*Ficus sycamorus* fr
	A. robusta gu, fr	*Kigelia africana* fr
	A. xanthophloea gu	*Manilkara mochisa* fr
	Annona senegalensis fr	*Mimosa pigra* fr
	Artabotrys monteiroae fr	*Strychnos potatorum* fr
	Berchemia discolor fr	*Thilachium africanum* fr
	Borassus aethiopum fr	*Vangueria infausta* fr
	Capparis erythrocarpos fr	*Xeroderris stuhlmannii* fr
	Cleistochlamys kirkii fr	*Ximenia americana* fr
	Diospyros mespiliformis fr	*Xylotheca tettensis* fr
	D. usambarensis fr	*Ziziphus mucronate* fr
	Drypetes mossambicensis fr	*Z. pubescens* fr
	Ehretia amoena fr	

PLANTS	DRY SEASON (May.–Oct.)	
Grasses	*Vetiveria nigritana* ro	*Vossia cuspidata* ro
Forbs	*Eichhornia crassipes* ro	*Pistia stratioites*
	Ludwigia stolonifera ro	
Woody plants	*Acacia albida* fr	*Kigelia africana* fr
	A. sieberana fr	*Mimosa pigra*
	A. robusta fr	*Mimusops fruticose* fr
	Albizzia harveyi fr	*Piliostigma thonningii* fr
	Boscia salicifolia fr	*Salvadora persica* fr
	Brachystegia glaucescens fr	*Sterculia appendiculata* fr
	Capparis erythrocarpos fr	*Tamarindus indica* fr
	Diospyros mespiliformis fr	*Thilachium africanum* fr
	Ficus sycamorus fr	*Trichilia capitata* fr
	F. zambesiaca fr	*Xanthocercis zambesiaca* fr
	Friesodielsia obovata fr	*Ximenia americana* fr
	Hyphaene benguellensis fr	*Ziziphus mucronata* fr

KEY TO ABBREVIATIONS
ba = bark, cu = culms, gu = gum, fl = flowers,
fr = fruit and seeds, ro = roots and tubers.
\+ = in addition to browse.

BUFFALO

PLANTS	WET SEASON (Nov.–Apr.)	
Grasses	*Brachiaria deflexa*	*Heteropogon contortus*
	Cymbopogon excavatus	*Leptochloa panicea*
	Dactyloctenium geminatum	*Panicum coloratum*
	Digitaria milanjiana	*P. maximum*
	D. swazilandensis	*Setaria eylesii*
	Eragrostis atrovirens	*Sporobolus pyramidalis*
	E. superba	*Urochloa mosambicensis*
	Echinochloa nr. *haploclada*	*U. pullulans*
	E. stagnina	*Vossia cuspidata*
	Eriochloa stapfiana	
Sedges	*Cyperus digitatus*	*Cyperus tenuispica*
	C. esculentus	*Mariscus hemisphaericus*
	C. sphacelatus	
Forbs and Suffrutices	*Aeschynomene indica*	*Sesbania mossambicensis*
	Ageratum conyzoides	*Sesbania sesban*
	Corchorus olitorius	*Solanum panduriforme*
	Enicostema hyssopifolium	*Tephrosia pumila*
	Melochia corchorifolia	*Vernonia kirkii*

PLANTS	DRY SEASON (May.–Oct.)	
Grasses	*Brachiaria deflexa*	*Paspalidium obtusifolium*
	Digitaria milanjiana	*Phragmites mauritianus*
	Echinochloa stagnina	*Setaria eylesii*
	Eriochloa stapfiana	*Urochloa mosambicensis*
	Hemarthria altissima	*Vossia cuspidata*
	Panicum coloratum	*Vetiveria nigritana*
	P. maximum	
Woody plants	*Acacia albida* fr	*Tamarindus indica* fr
	Hyphaene benguellensis fr	

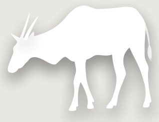
BUSHBUCK

PLANTS	WET SEASON (Nov.–Apr.)	
Grasses	*Urochloa mosambicensis*	
Sedges	*Mariscus hemisphaericus*	
Forbs and Suffrutices	*Abrus precatorius*	*Cissempelos mucronata*
	Abutilon spp.	*Cleome gynandra*
	Acalypha senensis	*Commelina* spp.
	Achyranthes aspera	*Corchorus trilocularis*
	Aerva leucura	*C. olitorius*
	Ageratum conyzoides	*Crotalaria poysperma*
	Amaranthus graecizans	*Hoslundia opposita*
	Anisotes spp.	*Ipomoea coptica*
	Astripomea malvacea	*Lippia javanica*
	Barleria spinulosa	*Poedaria foetans*
	Boerhaavia diffusa	*Solanum panduriforme*
	Capsicum frutescens	*Vernonia cinerea*
	Ceratotheca sesamoides	*Vigna unguiculate*
	Ceropegia sp.	
Woody plants	*Antidesma venosum*	*Grewia sulcata* + fr
	Combretum microphyllum	*Kigelia africana* fl
	C. mossambicense	*Tricalysia jasminiflora*
	Deinbollia xanthocarpa	*Ziziphus mucronata* + fr
PLANTS	**DRY SEASON (May–Oct.)**	
Forbs and Suffrutices	*Ceropegia* sp.	*Indigofera spicata*
	Cissempolos mucronata	
Woody plants cont.	*Acacia robusta*	*Markhamia acuminata*
	Allophylus alnifolius	*Mimosa pigra* + fr.
	Capparis erythrocarpos + fr	*Phyllanthus reticulatus* + fr
	Commiphora schimperi	*Poederia foetans*
	Deinbollia xanthocarpa	*Securinega virosa* + fr
	Diospyros mespiliformis + fr	*Steganotaenia araliacea*
	D. usambarensis + fr	*Trichilia capitata*
	Hyphaene benguellensis fr	*T. emetica*
	Kigelia africana fl	*Vangueria infausta* + fr
	Landolphia kirkii	*Ziziphus mucronata* + fr

KEY TO ABBREVIATIONS
ba = bark, cu = culms, gu = gum, fl = flowers,
fr = fruit and seeds, ro = roots and tubers.
\+ = in addition to browse.

CIVET
(fruits eaten as determined from seeds in dung)

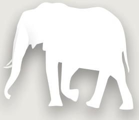
PLANTS	RIFT VALLEY	CHERINGOMA CUESTA
Fruit	*Acacia albida*	*Z. mucronata*
	A. nilotica	*Cleistochlamys kirkii*
	Cassia spp.	*Diospyros natalensis*
	Cordia goetzei	*Erythroxylum emarginatum*
	Cassine schlechterana	*E. gerrardii*
	Cissus spp.	*Ficus* spp.
	Cleistochlamys kirkii	*Friesodielsia obovata*
	Diospyros mespiliformis	*Hirtella zanguebarica*
	D. usambarensis	*Manilkara discolor*
	Ficus spp.	*Olea capensis*
	Grewia spp.	*Pachystela brevipes*
	Manilkara mochisia	*Parinari curatellifolia*
	Mimusops fruticosa	*Pseudolachnosylis maprouneifolia*
	Securinega virosa	*Rhus* spp.
	Strychnos potatorum	*Syzygium guineense*
	Tamarindus indica	*Uapaca* spp.
	Ximenia americana	*Vitex doniana*
	Ziziphus mauritiana	*Ximenia caffra*



ELAND

PLANTS	WET SEASON (Nov.–Apr.)	
Grasses	*Urochloa mosambicensis*	
Forbs	*Tephrosia pumila*	
Woody Plants	*Mimosa pigra*	
PLANTS	**DRY SEASON (May–Oct.)**	
Grasses	*Heteropogon contortus*	*Sporobolus pyramidalis*
	Panicum maximum	
Woody Plants	*Acacia albida* fr	*Kigelia africana* fr
	Combretum fragrans	*Lonchocarpus capassa*

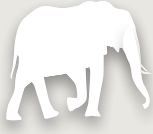
ELEPHANT



PLANTS	WET SEASON (Nov.–Apr.)	
Grasses	*Brachiaria deflexa*	*Eriochloa fatmensis*
	B. sp. nr. *glauca*	*Panicum coloratum*
	Chloris virgata	*P. maximum*
	Cymbopogon excavatus	*Setaria eylesii*
	Cynondon dactylon	*Sorghum verticilliflorum*
	Dactyloctenium aegyptium	*Sporobolus pyramidalis*
	Digitaria swazilandensis	*Urochloa mosambicensis*
	Echinochloa sp. nr. *haploclada*	*U. pullulans*
	E. stagnina	*Vossia cuspidata*
Sedges	*Cyperus esculentus*	
Forbs	*Blepharis caloneura*	*Sesbania sesban*
	Commelina spp.	*Solanum panduriforme*
	Heliotropium ovalifolium	*Tephrosia pumila*
	Indigophera astragalina	*Tiliacora funifera*
	Nymphaea spp.	
Woody Plants	*Acacia borleae* ba	*Ficus sycamorus* + fr
	A. galpinii ba	*Grewia sulcata*
	A. nigrescens + ba	*Holarrhena pubescens*
	A. polyacantha	*Hyphaene benguellensis* + fr
	A. robusta + ba	*Kigelia africana*
	A. xanthophloea + ba	*Lecaniodiscus fraxinifolius*
	Afzelia quanzensis	*Maerua angolensis*
	Albizia harveyi + ba	*Markhamia acuminata*
	Allophylus alnifolius + ro	*Newtonia hildebrandtii* ba
	Brachystegia spiciformis + ba	*Oncoba spinosa*
	Capparis erythrocarpos	*Piliostigma thonningii* + fr
	Cissus integrifolia + fr	*Salvadora persica* + fr
	Cola greenwayi	*Sclerocarya caffra* + ba, fr
	Colophospermum mopane + ba	*Trichilia capitata*
	Combretum imberbe	*Vitex doniana* + fr
	Craibia zimmermannii + ro, ba	*Xylia torreana* + ba
	Dalbergia arbutifolia	*Ziziphus mucronata* + fr
	Drypetes mossambicensis	

PLANTS	DRY SEASON (May–Oct.)	
Grasses	*Cynodon dactylon*	*Panicum maximum*
	Digitaria milanjiana	*Setaria eylesii*
	Heteropogon contorus	*Urochloa mosambicensis*
	Hyparrhenia rufa	*Vetiveria nigritana*
	Ischaemum afrum	*Vossia cuspidata*
	Panicum coloratum	
Sedges	*Cyperus esculentus*	
Forbs	*Abutilon* spp.	*Abutilon* spp.
	Achyranthes aspera	*Achyranthes aspera*
	Ctenolepsis sp.	*Ctenolepsis* sp.
	Sida acuta	*Sida acuta*
	Sida alba	*Sida alba*
Woody Plants	*Acacia albida* + fr, ba	*Erythrina livingstoniana* ba
	A. galpinii + ba	*Erythrophleum africanum* ba
	A. gerrardii	*Ficus sansibarica* + fr
	A. nigrescens ba	*F. stuhlmanii* + fr
	A. polyacantha	*F. sycamorus* ba, fr
	A. nilotica + fr	*F. zambesiaca* + fr
	A. robusta + fr, ba	*Hunteria zeylanica*
	A. sieberana fr	*Hymenodictyon parvifolium*
	A. welwitschii ba	*Hyphaene benguellensis* + fr
	A. xanthophloea + ba, ro	*Julbernadia globiflora* ba
	Adansonia digitata fr	*Khaya nyassica* ba
	Afzelia quanzensis	*Kigelia africana*
	Albizia anthelmintica ba	*Lannea stuhlmannii* ba
	A. glaberrima ba	*Lonchocarpus bussei* + ba
	A. versicolor ba	*L. capassa* + ba
	Ambligonocarpus andongensis ba, fr	*Manilkara mochisia*
	Annona amoena	*Markhamia acuminata*
	Antidesma venosum + ba	*Maytenus senegalensis*
	Balanites maughamii fr	*Milletia mossambicensis*
	Bauhinia petersiana	*M. stuhlmannii*
	B. tomentosa	*Mimosa pigra* + fr
	Berchemia discolor	*Mimusops fruticosa*

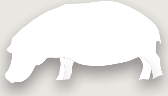
(cont.)



ELEPHANT CONT.

PLANTS	DRY SEASON (May–Oct.)	
Woody Plants Cont.	*Borassus aethiopum* fr	*Monotes africanus*
	Brachystegia boehmii + fr	*Ozoroa* sp.
	B. spiciformis ba	*Piliostigma thonningii* + ba, fr
	Burkea africana ba	*Pseudolachnostylis maprouneifolia* ba
	Capparis erythrocarpos + fr	*Pterocarpus angolensis* ba
	C. sepiaria	*P. antunesii*
	Cardiogyne africana (Maclura a.)	*P. brenanii*
	Cassia abbreviata ba	*P. rotundifolia* ba
	Cissampelos mucronata	*Ricinodendron rautanenii* fr
	Cleistochlamys kirkii + fr	*Sclerocarya caffra* + ba
	Colophospermum mopane + ba	*Sterculia africana* + ba
	Combretum apiculatum ba	*S. appendiculata* ba
	C. fragrans + ba	*Stereospermum kunthianum* ba
	C. hereroensis + ba	*Strychnos madagascariensis* + ba, fr
	C. imberbe ba	*S. mitis*
	Commiphora pyracanthoides	*S. potatorum* + fr
	C. schimperi	*S. spinosa* + fr
	Cordia goetzii	*Swartzia madagascariensis* fr
	Cordyla africana ba, fr	*Tabernaemontana elegans* ba
	Crossopterix febrifuga	*Tamarindus indica* + fr, ba
	Dalbergia arbutifolia ba	*Tarenna neurophylla*
	D. melanoxylon + ba	*Terminalia mollis* ba
	Deinbollia xanthocarpa	*T. sericea* ba
	Dichrostachys cinerea + fr	*Thilachium africanum*
	Diospyros mespiliformis fr	*Trichilia capitata* + ba, fr
	D. mossambicensis	*Turrea nilotica*
	D. senesis	*Xanthocercis zambesiaca* + fr
	D. quiloensis	*Xeroderris stuhlmanii* ba
	Diplorhynchus condylocarpon + ba	*Ximenia americana* + fr
	Euphorbia halipedicola	*Ziziphus mucronata* + ba, fr

KEY TO ABBREVIATIONS
ba = bark, cu = culms, gu = gum, fl = flowers,
fr = fruit and seeds, ro = roots and tubers.
+ = in addition to browse.



HIPPO

PLANTS	WET SEASON (Nov.–Apr.)	
Grasses	*Cynodon dactylon*	*Panicum coloratum*
	Digitaria swazilandensis	*Paspalidium obtusifolium*
	Echinochloa stagnina	*Urochloa mosambicensis*
	Eragrostic atrovirens	*U. pullulans*
	Heteropogon contortus	*Vossia cuspidata*
Sedges	*Cyperus esculentus*	
Forbes	*Commelina* sp.	*Ipomoea aquatica*
PLANTS	DRY SEASON (May–Oct.)	
Grasses	*Cynodon dactylon*	*Panicum maximum*
	Digitaria swazilandensis	*Paspalidium obtusifolium*
	Echinochloa stagnina	*Setaria eylesii*
	Eriochloa fatmensis	*S. sphacelate*
	Haemarthria altissima	*Urochloa mosambicensis*
	Hyparrhenia dichroa	*Vetiveria nigritana*
	Ischaemum afrum	*Vossia cuspidata*
	Panicum coloratum	
Sedges	*Cyperus esculentus*	*Mariscus hemisphaericus*
Forbes	*Alternanthera sessilis*	*Heliotropium indicum*
	Amaranthus graecizans	*H. ovalifolium*
	Bergia mossabicensis	*Ludwigia stolonifera*
	Coldenia procumbens	*Polygonum plebium*
	Euphorbia minutiflora	*Rorippa micrantha*
	Glinus lotoides	*Sida alba*
	Glinus oppositifolius	
Woody Plants	*Acacia albida* fr	

IMPALA

PLANTS	WET SEASON (Nov – Apr)	
Grasses	*Chloris gayana*	*Panicum coloratum*
	Cynodon dactylon	*P. maximum*
	Digitaria milanjiana	*P.* sp. (KLT)
	D. swazilandensis	*Sporobolus ioclados*
	Eragrostis aethiopica	*S. kentrophyllus*
	E. atrovirens	*S. pyramidalis*
	Echinochloa sp. nr. *haploclada*	*Urochloa mosambicensis*
	E. stagnina	*Tragus berteronianus*
	Eriochloa fatmensis	*Vossia cuspidata*
Sedges	*Cyperus esculentus*	*Mariscus hemisphaericus*
Forbs and Suffrutices	*Abutilon* spp.	*H. ovalifolium*
	Acalypha senensis	*Ipomoea aquatica*
	Achyranthes aspera	*I. coptica*
	Aeschynomene indica	*Ludwigia stolonifera*
	Ageratum conyzoides	*Melochia corchorifolia*
	Amaranthus graecizans	*Monechma tettensis*
	Ceropegia sp.	*Neptunia oleracea*
	Cleome gynandra	*Sida acuta*
	Commelina sp.	*S. alba*
	Corchorus olitorius	*Tephrosia pumila*
	C. trilocularis	*Trianthema portulacastrum*
	Ctenolepis cerasiformis	*Vernonia cinerea*
	Heliotropium indicum	
Woody Plants	*Acacia albida*	*Mimosa pigra*
	A. xanthophloea	*Phyllanthus recticulatus*
	Capparis erythrocarpos	*P. niruri*
	Cleistochlamys kirkii	*Securinega virosa*
	Commiphora pyracanthoides	*Ximenia americana*
	Grewia sulcata	*Ziziphus mucronata*

PLANTS	DRY SEASON (May – Oct)	
Grasses	*Brachiaria deflexa*	*Panicum coloratum*
	Digitaria milanjiana	*P. maximum*
	D. swazilandensis	*P.* sp. (KL 1760)
	Echinochloa stagnina	*Setaria nigrirostris*
	Eragrostis atrovirens	*Urochloa mosambicensis*
	Eriochloa fatmensis	*Vossia cuspidata*
	Hyperthelia dissoluta	
Sedges	*Cyperus esculentus*	*Mariscus hemisphaericus*
Forbs and Suffrutices	*Abutilon* spp.	*Sida alba*
	Alternanthera sessilis	*Tephrosia pumila*
	Gomphrena celosioides	*Tricalysia jasminiflora*
	Oldenlandia corymbosa	*Vernonia cinerea*
	Sida acuta	
Woody Plants	*Acacia albida* + fr	*Deinbollia xanthocarpa* + fr
	A. nigrescens fl	*Lecaniodiscus fraxinifolius*
	A. robusta fr	*Lonchocarpus capassa* fl
	A. sieberana fr	*Mimosa pigra* + fr
	A. xanthophloea + fl	*Salvadora persica* + fl, fr
	Asparagus spp.	*Tamarindus indica* + fr
	Capparis erythrocarpos + fl	*Xanthocercis zambesiaca* fr
	Cleistochlamys kirkii	*Ximenia americana* + fr
	Combretum mossambicense + fl	*Ziziphus mucronata* + fr

LICHTENSTEIN’S HARTEBEEST

PLANTS	WET SEASON (Nov.–Apr.)	
Grasses	*Cymbopogon excavatus*	*Themeda triandra*
	Heteropogon contortus	*Urochloa mosambicensis*
PLANTS	DRY SEASON (May–Oct.)	
Grasses	*Chloris gayana*	*Panicum coloratum*
	Digitaria milanjiana	*P. maximum*
	Echinochloa sp. nr. *haploclada*	*Paspalum scrobiculatum*
	E. stagnina	*Setaria eylesii*
	Enteropogon macrostachyus	*Sporobolus pyramidalis*
	Heteropogon contortus	*S. ioclados*
	Hyparrhenia dichroa	*Themeda triandra*
	H. dissoluta	*Urochloa mosambicensis*
	H. rufa	
Sedges	*Mariscus hemisphaericus*	
Woody Plants	*Maerua brunnescens*	

KEY TO ABBREVIATIONS
ba = bark, cu = culms, gu = gum, fl = flowers,
fr = fruit and seeds, ro = roots and tubers.
\+ = in addition to browse.

ORIBI

PLANTS	WET SEASON (Nov.–Apr.)	
Grasses	*Cynodon dactylon*	*Panicum coloratum*
	Digitaria milanjiana	*P.* sp. (KLT 1873)
	D. swazilandensis	*Urochloa mosambicensis*
	Echinochloa stagnina	*U. pullulans*
	Eriochloa stapfiana	*Vossia cuspidata*
Sedges	*Mariscus hemisphaericus*	
Forbs and Suffrutices	*Aeschynomene indica*	*Sesbania sesban* fr
	Heliotropium ovalifolium	*Sida alba*
	Melochia corchorifolia	*Tephrosia pumila*
	Neptunia oleracea	
Woody Plants	*Acacia xanthophloea*	*Mimosa pigra*
	A. robusta	*Ziziphus mucronata*
PLANTS	DRY SEASON (May–Oct.)	
Grasses	*Brachiaria deflexa*	*Heteropogon contortus*
	Cynodon dactylon	*Panicum coloratum*
	Digitaria swazilandensis	*P. infestum*
	Echinochloa stagnina	*Setaria eylesii*
	Eragrostis lappula	*Vetiveria nigritana* (post-fire flush)
	Eriochloa fatmensis	*Vossia cuspidata*
	E. stapfiana	
Sedges	*Mariscus hemisphaericus*	
Forbes	*Abutilon spp.*	*H. ovalifolium*
	Achyranthes aspera	*Indigofera microcarpa*
	Amaranthus graecizans	*I. tinctoria*
	Duosperma quadrangulare	*Sida alba*
	Gomphrena celosioides	*Solanum panduriforme*
	Heliotropium indica	*Tephrosia pumila*
Woody Plants	*Acacia albida* + fr	*Mimosa pigra* + fr
	A. robusta	*Ziziphus mucronata*
	Capparis erythrocarpos	

RED DUIKER

PLANTS	WET SEASON (Nov – Apr)	
Forbs	*Dicliptera mossambicensis*	*Psilotrichum scleranthum*
	Justicia flava	
Woody Plants	*Acacia kraussiana*	*Phyllanthus kirkianus*
	A. welwitschii	*Sloetiopsis usambarensis*
	Berchemia discolor fr	*Strychnos mitis*
	Landolphia kirkii	
PLANTS	DRY SEASON (May – Oct)	
Woody Plants	*Acacia nigrescens* fl, fr	*Coffea racemosa*
	Alchornea laxiflora	*Hippocratea* spp.
	Boscia salicifolia fr	*Xanthocercis zambesiaca* fr
	Cassine schlechterana fr	*Xylotheca tettensis*

REEDBUCK

PLANTS	WET SEASON (Nov – Apr)	
Grasses	*Cynodon dactylon*	*Eriochloa stapfiana*
	Digitaria swazilandensis	
Forbs	*Sesbania sesban*	
PLANTS	DRY SEASON (May – Oct)	
Grasses	*Panicum coloratum*	*Urochloa mosambicensis*
	Paspalum scrobiculatum	*Vossia cuspidata*
	Setaria eylesii	

SABLE

PLANTS	WET SEASON (Nov – Apr)	
Grasses	*Chloris gayana*	*Panicum maximum*
	Hyparrhenia dichroa	*Sporobolus pyramidalis*
	Hyparrenia filipendula	
PLANTS	DRY SEASON (May – Oct)	
Grasses	*Bothriochloa glabra*	*Panicum coloratum*
	Chloris gayana	*P. maximum*
	Digitaria milanjiana	*Paspalidium obtusifolium*
	Heteropogon contortus	*Phragmites mauritianus*
	Hyperthelia dissoluta	*Themeda triandra*
	Hyparrhenia rufa	*Urochloa mosambicensis*
	Ischaemum afrum	*Vetiveria nigritana* (post-fire flush)

WARTHOG

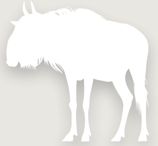
PLANTS	WET SEASON (Nov – Apr)	
Grasses	*Digitaria swazilandensis*	*Paspalidium obtusifolium*
	Echinochloa stagnina + ro, fr	*Sporobolus pyramidalis*
	Panicum maximum + ro, fr	*Urochloa mosambicensis + ro, fr*
Woody Plants	*Diospyros mespiliformis* fr	*Kigelia africana* fl
PLANTS	DRY SEASON (May – Oct)	
Grasses	*Cynodon dactylon* + ro	*Panicum coloratum*
	Digitaria milanjiana	*Urochloa mosambicensis*
	Echinochloa stagnina	*Vossia cuspidata*
Sedges	*Mariscus hemisphaericus* ro	
Woody Plants	*Acacia albida* fr	*Hyphaene benguellensis* fr
	Borassus aethiopum fr	*Tamarindus indica* fr

WATERBUCK

PLANTS	WET SEASON (Nov.–Apr.)	
Grasses	*Brachiaria* sp.	*Panicum coloratum*
	Cynodon dactylon	*P. maximum*
	Digitaria milanjiana	*Paspalidium obtusifolium*
	D. swazilandensis	*Setaria eylesii*
	Echinochloa sp.	*Urochloa mosambicensis*
	Eriochloa fatmensis	*Vossia cuspidata*
	E. stapfiana	
Sedges	*Cyperus esculentus*	
Forbs	*Cissempelos mucronata*	*Ludwigia stolonifera*
	Eichornia crassipes	*Sesbania mossambicensis*
	Hibiscus cannabinus	*Tephrosia pumila*
PLANTS	DRY SEASON (May–Oct.)	
Grasses	*Chloris gayana*	*Panicum coloratum*
	Cynodon dactylon	*Paspalidium obtusifolium*
	Digitaria swazilandensis	*Paspalum scrobiculatum*
	Eragrostic atrovirens	*Setaria eylesii*
	Echinochloa stagnina	*Sporobolus pyramidalis*
	Eriochloa fatmensis	*Urochloa mosambicensis*
	E. stapfiana	*Vetiveria nigritana* (post-fire flush)
	Heteropogon contortus	*Vossia cuspidata*
Sedges	*Cyperus esculentus*	*Mariscus hemisphaericus*
	Cyperus michelianus	
Forbs and Suffrutices	*Aeschynomene indica*	*Gomphrena celosioides*
	Amaranthus graecizans	*Heliotropium indicum*
	Basilicum polystachyon	*Sida acuta*
Woody Plants	*Mimosa pigra*	

WHITE RHINO

PLANTS	WET SEASON (Nov.–Apr.)	
Grasses	*Cynodon dactylon*	*Echinochloa stagnina*
	Digitaria swazilandensis	*Eriochloa fatmensis*
	Echinochloa sp. nr. *haploclada*	*Vossia cuspidata*
Forbes	*Sida alba*	*Tephrosia pumila*



WILDEBEEST

PLANTS	WET SEASON (Nov.–Apr.)	
Grasses	*Bothriochloa glabra*	*Eriochloa stapfiana*
	Brachiaria deflexa	*E. fatmensis*
	Chloris gayana	*Panicum infestum*
	Cynodon dactylon	*P.* sp. (KLT 1873)
	Digitaria milanjiana	*Paspalidium obtusifolium*
	D. swazilandensis	*Sporobous pyramidalis*
	Echinochloa sp. nr. *haploclada*	*Urochloa mosambicensis*
	E. stagnina	*Vossia cuspidata*
	Eragrostis atrovirens	
Sedges	*Cyperus esculentus*	*Mariscus hemisphaericus*
	C. digitatus	
Forbs	*Aeschynomene indica*	*Tephrosia pumila*
	Heliotropium ovalifolium	
PLANTS	DRY SEASON (May–Oct.)	
Grasses	*Chloris gayana*	*Panicum coloratum*
	Cynodon dactylon	*P. maximum*
	Digitaria aethiopica	*P.* sp. (KLT 2016)
	D. milanjiana	*Setaria eylesii*
	D. swazilandensis	*Sporobolus iocladus*
	Echinochloa stagnina	*S. pyramidalis*
	Eragrostis atrovirens	*Urochloa mosambicensis*
	Eriochloa fatmensis	*Vetiveria nigritana*
	E. stapfiana	*Vossia cuspidata*
	Heteropogon contortus	
Sedges	*Cyperus esculentus*	*Mariscus hemisphaericus*
Forbs	*Alternanthera sessilis*	*Heliotropium ovalifolium*
	Heliotropium indicum	
Woody Plants	*Hyphaene benguellensis*	*Lonchocarpus capassa*

ZEBRA		
PLANTS	WET SEASON (Nov – Apr)	
Grasses	*Brachiaria* sp. nr. *glauca*	*Panicum* sp. (KLT 1734)
	Chloris gayana	*P. coloratum*
	Cynodon dactylon	*P. maximum*
	Dactyloctenium aegyptium	*Sporobolus ioclados*
	Digitaria swazilandensis	*S. kentrophyllus*
	Echinochloa sp. nr. *haploclada*	*Urochloa mosambicensis*
	Eriochloa fatmensis	*Vossia cuspidata*
	Panicum sp. (KLT 1738)	
Sedges	*Cyperus esculentus*	*Cyperus tenuispica*
Forbs	*Alternanthera sessilis*	*Eichhornia crassipes*
	Caperonia serrata	*Sphenoclea zeylanica*
PLANTS	DRY SEASON (May – Oct)	
Grasses	*Bothriochloa glabra*	*Panicum maximum*
	Chloris gayana	*Paspalum scrobiculatum*
	C. pycnothrix	*Setaria eylesii*
	Cynodon dactylon	*Sporobolus ioclados*
	Digitaria milanjiana	*S. kentrophyllus*
	D. swazilandensis	*S. pyramidalis*
	Eriochloa fatmensis	*Urochloa mosambicensis*
	Hyparrhenia dichroa	*Vetiveria nigritana*
	Panicum coloratum	

APPENDIX 3

UPDATED BIRD NAMES SINCE ORIGINAL THESIS

COMMON NAMES IN TEXT	COMMON NAMES ROBERTS VII 2005	SCIENTIFIC NAMES ROBERTS VII 2005
Black-bellied Glossy Starling	Black-bellied Starling	*Lamprotornis corruscus*
Black-eyed Bulbul	Dark-capped Bulbul	*Pycnonotus tricolor*
Black-necked Heron	Black-headed Heron	*Ardea melanocephala*
Blue-eared Glossy Starling	Greater Blue-eared Starling	*Lamprotornis chalybaeus*
Cape Robin	Cape Robin-chat	*Cossypha caffra*
Cinnamon Dove	Lemon Dove	*Aplopelia larvata*
Delagorgue's Pigeon	Eastern Bronze-naped Pigeon	*Columba delegorguei*
European Golden Oriole	Eurasian Golden Oriole	*Oriolus oriolus*
Golden-rumped Tinker Barbet	Yellow-rumped Tinkerbird	*Pogoniulus bilineatus*
Green Tinker Barbet	Green Tinkerbird	*Pogoniulus simplex*
Green-crested Turaco	Livingstone's Turaco	*Tauraco livingstonii*
Green Pigeon	African Green-pigeon	*Treron calvus*
Grey Hornbill	African Grey Hornbill	*Tockus nasutus*
Grey Lourie	Grey Go-away-bird	*Corythaixoides concolor*
Gurney’s Thrush	Orange ground-thrush	*Geokichla gurneyi*
Heuglin's Robin	White-browed Robin-chat	*Cossypha heuglini*
Lesser Blue-eared Starling	Miombo Blue-eared Starling	*Lamprotornis elisabeth*
Mocking Chat	Mocking Cliff-chat	*Thamnolaea cinnamomeiventris*
Natal Robin	Red-capped Robin-chat	*Cossypha natalensis*
Palm-Thrush	Collared Palm-thrush	*Cichladusa arquata*
Plum-coloured Starling	Violet-backed Starling	*Cinnyricinclus leucogaster*
Rameron Pigeon	African Olive Pigeon	*Columba arquatrix*
Red-eyed Turtle Dove	Red-eyed Dove	*Streptopelia semitorquata*
Sombre Bulbul	Sombre Greenbul	*Andropadus importunus*
Starred Robin	White-starred Robin	*Pogonocichla stellata*
Stripe-cheeked Bulbul	Stripe-cheeked Greenbul	*Andropadus milanjensis*
Terrestrial Bulbul	Terrestrial Brownbul	*Phyllastrephus terrestris*
White Breasted Alethe	White-chested Alethe	*Pseudalethe fuelleborni*
Yellow-billed Hornbill	Southern Yellow-billed Hornbill	*Tockus leucomelas*
Yellow-fronted Tinker Barbet	Yellow-fronted Tinkerbird	*Pogoniulus chrysoconus*
Yellow-streaked Bulbul	Yellow-streaked Greenbul	*Phyllastrephus flavostriatus*
Yellow-breasted Bulbul	Yellow-bellied Greenbul	*Chlorocichla flaviventris*
Yellow White-eye	African Yellow White-eye	*Zosterops senegalensis*

UPDATED BOTANICAL NAMES SINCE ORIGINAL THESIS

NAME IN TEXT	UPDATED NAME
Abutilon guinense	*Abutilon indicum subsp. guinense*
Acacia albida	*Faidherbia albida*
Acacia borleae	*Vachellia borleae*
Acacia karroo	*Vachellia karroo*
Acacia kraussiana	*Senegalia kraussiana*
Acacia nigrescens	*Senegalia nigrescens*
Acacia nilotica	*Vachellia nilotica*
Acacia polyacantha	*Senegalia polyacantha*
Acacia robusta	*Vachellia robusta*
Acacia schweinfurtii	*Senegalia schweinfurtii*
Acacia seyal	*Vachellia seyal*
Acacia sieberiana	*Vachellia sieberiana*
Acacia welwitschii	*Senegalia welwitschii subsp. delagoensis*
Acacia xanthophloea	*Vachellia xanthophloea*
Acalypha senensis	*Acalypha villicaulis*
Acrocephalus chirindensis	*Haumaniastrum dissitifolium*
Adhatoda bagshawei	*Justicia francoiseana*
Adina microcephala	*Breonadia salicina*
Allophylus alnifolia	*Allophylus rubifolius*
Aloe bainesii	*Aloidendron barberae*
Ambrosia maritima	*Ambrosia artemisiifolia*
Andropogon flabellifer	*Andropogon mannii*
Anthospermum ammanioides	*Anthospermum welwitschii*
Aulacalyx diervilleoides	*Heinsenia diervilleoides*
Beckeropsis uniseta	*Pennisetum unisetum*
Bergia mossambicensis	*Bergia salaria*
Botriochloa glabra	*Botriochloa bladhii*
Brachystegia glaucescens	*Brachystegia microphylla*
Byrsocarpus orientalis	*Rourea orientalis*

NAME IN TEXT	UPDATED NAME
Canthium crassum	*Multidentia crassa var. crassa*
Canthium huillense	*Psydrax livida*
Canthium setiflorum	*Bullockia setiflora*
Cassia mimosoides	*Chamaecrista mimosoides*
Cassia petersiana	*Senna petersiana*
Cassine papillosa	*Elaeodendron croceum*
Cassine schlechterana	*Mystroxylon aethiopicum*
Cassipourea congoensis	*Cassipourea malosana*
Chlorophora excelsa	*Milicia excelsa*
Combretum fragrans	*Combretum adenogonium*
Crassula argyrophylla	*Crassula swaziensis*
Cymbopogon validus	*Cymbopogon nardus*
Cyperus holostigma	*Cyperus schinzii*
Dicliptera mossambicensis	*Dicliptera heterostegia*
Digitaria apiculata	*Digitaria maitlandii*
Digitaria swazilandensis	*Digitaria didactyla*
Diospyros usambarensis	*Diospyros loureiriana*
Dracaena reflexa	*Dracaena mannii*
Elionurus argenteus	*Elionurus muticus*
Enicostema hyssopifolium	*Enicostema axillare subsp. axillare*
Entada pursaetha	*Entada rheedii*
Enterospermum littorale	*Coptosperma littorale*
Eragrostis atrovirens	*Eragrostis inamoena*
Eriocaulon subulatum	*Eriocaulon abyssinicum*
Erythrophleum suaveolens	*Erythrophleum lasianthum*
Euphorbia minutiflora	*Euphorbia serpens*
Ficus capensis	*Ficus sur*
Ficus kirkii	*Ficus scassellatii*
Ficus soldanella	*Ficus abutilifolia*

NAME IN TEXT	UPDATED NAME
Ficus vogellii	*Ficus lutea*
Fimbristylis hispidula	*Bulbostylis hispidula*
Fimbristylis hygrophyla	*Abildgaardia hygrophila*
Garcinia milanjiensis	*Garcinia kingaensis*
Glycine wightii	*Neonotonia wightii*
Gnaphalium hispidum	*Elytropappus hispidus*
Grewia transzambesiaca	*Grewia transzambesica*
Helichrysum gazense	*Helichrysum lepidissimum*
Helichrysum pilosellum	*Helichrysum nudifolium*
Heteromorpha trifoliata	*Heteromorpha arborescens* var. *abyssinica*
Heteropogon melanoleuca	*Heteropogon melanocarpus*
Hirtella zanguebarica	*Hirtella zanzibarica*
Hyphaene benguellensis	*Hyphaene petersiana*
Hypoxis dregei	*Hypoxis filiformis*
Ischaemum arctuatum	*Ischaemum fasciculatum*
Khaya nyassica	*Khaya anthotheca*
Knowltonia transvaalensis	*Anemone transvaalensis*
Lannea stuhlmannii	*Lannea schweinfurtii* var. *stuhlmannii*
Linociera battiscombei	*Chionanthus battiscombei*
Lobelia intertexta	*Lobelia trullifolia*
Lonchocarpus bussei	*Philinoptera bussei*
Lonchocarpus capassa	*Philinoptera violacea*
Loudetia superba	*Tristachya superba*
Ludwigia stolonifera	*Ludwigia adscendens*
Lycopodium carolinianum	*Lycopodiella caroliniana*
Markhamia acuminata	*Markhamia zanzibarica*
Maytenus senegalensis	*Gymnosporia senegalensis*
Melodorum gracile	*Sphaerocoryne gracilis*
Memycelon sansibaricum	*Warneckea sansibarica*
Mimusops fruticosa	*Mimusops obtusifolia*
Myrica pilulifera	*Morella pilulifera*
Najas interrupta	*Najas horrida*
Nemesia montana	*Nemesia zimbabwensis*
Nymphaea capensis	*Nymphaea nouchali* var. *caerulea*
Ochna oconnori	*Ochna arborea* var. *oconnorii*
Pachystela brevipes	*Synsepalum brevipes*
Paropsia schliebeniana	*Paropsia braunii*
Phillipia benguelensis	*Erica benguelensis*
Phillipia simii	*Erica simii*
Phillippia hexandra	*Erica hexandra*
Phyllanthus discoideus	*Margaritaria discoidea*
Phyllanthus kirkianus	*Phyllanthus pinnatus*
Phyllanthus niruri	*Phyllanthus fraternus*
Podocarpus milanjianus	*Podocarpus latifolius*
Protea gazensis	*Protea caffra* subsp.. *gazensis*
Pseudocassine transvaalensis	*Elaeodendron transvaalense*
Pterocarpus autunesii	*Pterocarpus lucens* subsp. *autunesii*
Rhus chirindensis	*Searsia chirindensis*
Rhus natalensis	*Searsia natalensis*
Rhyncheletrum rhodesianum	*Melinis nerviglumis*
Rhynchosia clivorum	*Rhynchosia clivorum* var. *clivorum*
Ricinodendron rautanenii	*Schinziophyton rautanenii*
Rottboellia exaltata	*Rottboellia cochinchinensis*
Saba floribunda	*Saba comorensis*
Sacciolepis luciae	*Sacciolepis spiciformis*
Sapium ellepticum	*Shirakiopsis elliptica*
Scabiosa austroafricana	*Scabiosa columbaria*
Scirpus fluitans	*Isolepis fluitans*

NAME IN TEXT	UPDATED NAME
Sclerocarya caffra	*Sclerocarya birrea*
Securinega virosa	*Flueggea virosa*
Sesbania mossambicensis	*Sesbania microphylla*
Setaria anceps	*Setaria sphacelata* var. *sericea*
Setaria chevalieri	*Setaria megaphylla*
Setaria eylesii	*Setaria incrassata*
Smilax kraussiana	*Smilax anceps*
Sopubia mannii	*Sopubia mannii* var. *tenuifolia*
Sphaeranthus gazaensis	*Sphaeranthus senegalensis*
Sporobolus kentrophyllus	*Sporobolus ioclados*
Sporobolus mauritianus	*Sporobolus subulatus*
Stoebe vulgaris	*Seriphium plumosum*
Strelitzia nicolai	*Strelitzia caudata*
Sutera carvalhoi	*Jamesbrittenia carvalhoi*
Swartzia madagascariensis	*Bobgunnia madagascariensis*
Syzygium masukuense	*Syzygium chimanimaniense*
Tabernaemontana angolensis	*Tabernaemontana pachysiphon*
Tarenna neurophylla	*Coptosperma neurophyllum*
Terminalia sansibarica	*Terminalia sambesiaca*
Thesium scabridulum	*Thesium nigricans*
Trachylobium verrucosum	*Hymenaea verrucosa*
Tricalysia nyassae	*Tricalysia coriacea*
Tristachya hispida	*Tristachya leucothrix*
Vincentella passargei	*Synsepalum passargei*
Xeromphis obovata	*Catanuregam obovata*
Xylotheca tettensis	*Oncoba tettensis*
Zygoon graveolens	*Coptosperma zygoon*

Index

Ken Tinley's D.Sc. thesis is a masterpiece. He's a tremendous intellect and a visionary, we really respect and appreciate what he did, and we are going to make sure that his pioneering work is clearly acknowledged in everything that we ever do that draws on his research, from now until I'm his age.

There's no way he could have been conscious at the time of how valuable his work was going to be — and in what ways.

Rob Pringle, Professor of Zoology, Princeton University.

www.gorongosa.org