THE ECOLOGY OF LARGE HERBIVORES IN THE MIOMBO WOODLANDS OF SOUTH EAST TANZANIA

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'A thesis submitted in fulfilment for the Degree
of Doctor of Philosophy in the University of
of Nairobi

1972

"This thesis is my original work and has not been presented for a degree in any other University".

Signed: W.A. RODGERS 1979

"This thesis has been submitted for examination with my approval as University supervisor".

Signed: J.B. SALE 1979.

This thesis is dedicated to the memory of the late

Constantine John Phillip Ionides

and to

Brian Dearnley Nicholson,

who, as Game Rangers in South East Tanzania from 1937 to 1973, created and developed the Selous Game Reserve, Africa's largest wildlife sanctuary.

and to

Bobbi, who shared the fun of the field work and the horrors of the writing.

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SUMMARY

The studies described in this thesis arose from an ecological survey of part of the eastern side of the Selous Game Reserve in south east Tanzania from 1967 to 1975. The intensive study area contained two major, ecologically distinct habitats, an area of tall grass miombo woodland and a smaller area of short grass scattered tree grassland. Several species of large grazing ungulate utilised these habitats, namely: buffalo, hartebeest, impala, sable, warthog, wildebeest and zebra. Seasonal changes in the environment such as the six month drought and widespread annual fires affect the pattern of habitat utilisation exhibited by each species. This thesis examines such utilisation and shows that each species has developed its own ecological and feeding strategies in order to maximise nutrient inputs and reproductive success in what is seasonally a harsh environment.

In many ways the miombo (Brachystegia) woodlands remain the least studied of the East African habitats. This lack of data on the miombo in general and the Selous Game Reserve in particular means much of the thesis is taken up by descriptions of the physical and biotic environment of the study area. Following an introductory chapter the thesis is divided into three parts. Part one, with three chapters, describes the physical environment: geology, soil, climate, water and prehistory; the vegetation: community description, distribution and species composition, floristics and vegetation dynamics; and range factors of productivity and forage nutrient content. Part two contains chapters on animal numbers, distribution patterns, feeding and nutrition and a chapter examining growth and reproduction as indices of population performance. Part three concludes the thesis with a chapter reviewing the miombo woodlands and the Selous as a wildlife habitat and a final chapter discussing management policy for the Selous Game Reserve.

The study area is low lying (100 - 700m asl) with a single rainy season from late November to early May (average 760mm p.a.). Despite a long hot dry season, surface water is relatively plentiful. Habitat distribution is primarily controlled by geology and soil type with major modifications by fires and past human activity. The upland Karoo and post karoo sandstones give rise to infertile acidic red sandy soils which carry a climax-thicket formation. These have been degraded into woodland by fire and settlement activity. Lower down the drainage slope the flat Pleistocene river terrace of grits and sands has produced a hard alkaline sodic soil carrying short grass scattered tree grassland. The drainage sump of recent alluvial clay carries tall floodplain grasses.

The vegetation is diverse, collections to date totalling over 1200 vascular plants including 150 grass species. The woodland vegetation shows strong affinities to the Zambezian flora, and the thicket, riverine and alkaline communities show affinities to the East African coastal flora. The thesis contains species lists and a vegetation community map. Fire has opened up the thickets producing

tall grass woodlands of various types. Grasses, mainly Andropogonae, are coarse tussock perennials with very low nutritive values when dry. No burning allows the spread of woody and climbing species which engulf the grass layer and rapidly reduce grazing values. Late dry season fires reduce woody elements and plant diversities and leave coarse grass growth throughout the dry season. Cooler early dry season fires maintain mixed woodland communities and a mixture of grass species and, where water tables allow, rapidly produce a flush of nutritious regenerating grass growth. Crude protein content of such growth can reach 20% although standing crop is low.

The alkaline soils carry a short grass sward of mixed annual perennial species of high nutritive values in the rains. There is no flush after burning and dry season grazing values are low.

Chapter 5 discusses techniques of animal census in detail. A vehicular ground sample census using fixed systematically placed transects was used for common ungulates. Rainy season densities on the short grass habitats are as follows: Impala 28.7/km^2, wildebeest 27.2/km^2, zebra 16.2/km^2 and warthog 9.4/km^2. Wildebeest and impala densities have remained unchanged for six years, zebra and warthog densities have increased significantly. Less detailed data are given for other species. Distribution data have been collected at several different scales from Tanzania wide, to the Selous, to the study area, to the different facets of a miombo valley-ridge catenary system.

It is shown that sable and Lichtensteins [illegible] hartebeest are restricted to tall grass woodland habitats, wildebeest and impala must have access to short grass areas in the rains and that buffalo, zebra and warthog, are more habitat tolerant but achieve higher densities on short grass habitats.

Within the study area virtually all impala, warthog, wildebeest and zebra concentrate on the short grass areas in the rains, moving into the woodlands following the onset of burning. Within the woodland habitat wildebeest and impala concentrate on the green flush of the valleys and avoid the unburnt areas and ridge tops. Sable and hartebeest are distributed throughout all categories and warthog and zebra are intermediate showing some selection of valley and green areas. The onset of the November rains signals a return to the short grasslands.

Studies of feeding behaviour showed buffalo, hartebeest and wildebeest to be total grazers whilst sable and impala took significant proportions of browse in the dry season and warthog diet changed to perennial monocot roots and rhizomes. Feeding studies concentrated on wildebeest and impala and much data was obtained from post morterm analysis. By assuming that extrapolation of data from other large ungulate studies was unlikely to cause large relative errors it was possible to make estimates of protein and energy intakes and of theoretical nutrient needs for these two species. During the rainy season both species had inputs greater than theoretical requirements for maintenance, i.e. they were in positive nutritional balance. As the dry season progressed both male and female wildebeest which remained on the dry short grass habit entered a period of negative nutritional balance. However wildebeest moving to fresh flush in the woodlands were shown (albeit on less evidence) to maintain a positive balance. Impala at the onset of the dry season changed their diet to nutrient rich browse components and so maintained a positive nutritional balance. These two strategies of habitat change and dietary change have resulted in peak nutritional inputs at different times of year. Impala have peak inputs in September and wildebeest in December. Onset of parturition coincides with these peak periods. The nutritional load of gestation is minimal compared to that of lactation. Calving season therefore allows lactation and wearing of calves at the nutritional optimum time of year. Other species show different strategies, which allow a separation of niche space reducing competition for food resources. Chapter eight shows that individual growth rate, body condition and fecundity rates are as high or higher than other populations in Africa, and that populations here are well adapted to the ecological conditions of this part of the Selous Game Reserve. This chapter discusses why the wildebeest population is stationary when nutrition is adequate, condition is good and fecundity is high. Predation by lion is put forward as a major limiting factor. The concluding chapters look at the miombo woodlands throughout Africa as wildlife reserves and suggest that only when tall grass woodlands are adjacent to other habitats

such as short grassland or floodplains do animal densities reach levels high enough to warrant major conservation inputs. The importance of fire in providing dry season graze is stressed and fire management polices for the Selous are discussed. Past, present and future human impacts on the wilderness values of the Selous are examined and a plea is made for definite land use policy statements for south east Tanzania and the reserve.

ACKNOWLEDGEMENTS

The studies contained within this thesis have been undertaken over a ten year period and in a very remote area of East Africa. I have been fortunate in that many people and institutions have given advice and assistance at all stages of my work. I trust I can remember them all!

The first six years were basically field work and I owe a great deal to my assistants and guides - the staff of the Selous Game Reserve and the Miombo Research Centre. both for making sure I am alive today and for teaching me much about the ecology of the miombo woodlands. Game Assistants Mohammed Athumani and Saidia Mwambezi took me on my first foot safaris. Field Assistants Marombe, Goryama, Daudi and Makonila were the mainstay before the Research Centre became a reality. Ali Makonila then became my driver until I left the Division. Hemedi Menge, Saidi Mpapa, Mshamu Mkopoka and Hemedi Matali helped in the field and with post mortem studies. Alfred Mponda helped me wrestle with maps and air photographs. Wazee Mohammed Ligogi and Nchigagi Mfaume lived and hunted in what became the study area well before I was born. They still know more about this area of wilderness than I will ever learn. My two Senior Research Assistants helped in many ways, Rashidi Ludanga with botanical aspects and Henry Desuzo with post mertems, census work and data analysis. I will miss their companionship.

Gordon Matzke, Patrick Stobart, Franc Mes, Bob Gainer and Kaj Vollesen, biologists at the Centre all contributed to my studies, Kaj still does - thank you!

Wardens, Engineers and Administrators of the Game Division have helped me with my work, kept vehicles going, built roads and lightened my load of non research tasks. I too acted as warden, engineer and administrator during my service. Hemedi Mahinda OBE, John Capon and Raphael Jingu

Directors and Acting Directord of Game approved my activities and gave considerable support in terms of finance, staff and equipment. Bakari Mbano who has replaced me as officer in charge of the M.R.C. (and as pilot!) was a welcome companion in the field office and the air.

C.J.P. (Iodine) Ionides, whom I had the privelege of knowing, provided inspiration; if he could live there for thirty years I could manage ten! Piet and Minnie Wessels taught me how to live in and enjoy the bush in my early years. Allen & Margaret Rees (Principal Game Warden & Ecologist in the Selous) themselves knowlegeable naturalists, gave much welcome assistance, advice and hospitality.

Brian Nicholson, my "boss" was heard to say that "he didn't want any schoolboy interfering in his reserve" when I was first posted to his range. I did interfere and we became friends. I trust this thesis justifies his support and enthusiasm. Brian has done more than any other person to protect the superb natural wilderness that is the Selous.

Then there were the students, nameless now, who helped during field courses, and their intructors from C.A.W.M. Mweka; Tony Mence, Les Robinette, John Kundaeli, Clive Spinage and especially Pat Hemingway. Pat and I have argued for years over census methodology, he in calculus and myself in rude English. I think he has the answer, but I cannot understand it.

Some biologists braved the wilds of the Selous, visited the M.R.C. and gave me much advice - some of which I took. To Anton de Vos, Ken Ashby, George Petrides, Hugh Lamprey, Ray Lawton, Colin Pernycuick, Bob Wingfield, Peter Jarman, Ron Skoog, Dennis Herlocker, Rudi Sachs, Hans Jacob and Pat Duncan, my thanks!

The Central Veterinary Laboratories undertook Chemical analysis and veterinary investigations. Laboratories in Tanga, Dar es Salaam, Ifakara and Kilosa analysed soils. Williamsons Diamonds supplied old aerial photographs and maps. The East African Herbarium and the Botany Department of the University of Dar es Salaam identified plants. Old men of Ngarambe village told me of the Selous in the good old days, when they lived there.

The East African Wildlife Society gave a generous grant in the early days of 1968, which provided the first of the permanent buildings at the M.R.C. The Government of Denmark gave a very large grant in 1969, this grant supported the study for the next five years and gave a lasting research base to the Tanzania Government.

Professor Prasad, Professor Jolly, Dr. Ian White and Dr. David Griffiths gave statistical advice. Staff of the Department of Botany at the University of Aberystwyth held my hand through the intricacies of computing and taught me much plant ecology. Drs David Griffiths, Kim Howell and Katherine Bulstrode read draft chapters and Professor Msangi encouraged the completion of thesis. Mrs Lena Guy and Miss Jennie Morris helped with drawings, Miss Erica Khuri with reproduction.

My supervisors, Dr. Brian Harris and Dr. Andrew Agnew gave assistance during the early stages of the study. Andrew Agnew gave me hospitality and organised my stay in Wales. Dr. John Sale remained patient and understanding for ten long years a supervisor. I owe him much, I don't think he expected me to complete the study.

My parents and my wife nagged for six years for me to finish the thesis. They were successful - it is done. Bobbi typed innumerable drafts for five years, I'm glad it is over for her sake.

CHAPTER ONE

INTRODUCTION

1.1 Aims of this study and Structure of the Thesis

Miombo (Brachystegia - Julbernardia)species woodland is estimated to cover half of Tanzania's land surface but until the last decade has been little studied from an ecological or agricultural view point. Despite the scale of wildlife resources within this ecological zone (which includes the 50,000 km^2 Selous Game Reserve and 25,000 km^2 Ruaha - Rungwa complex) there had been no intensive wildlife research input until this study commenced in 1967. This thesis has been compiled from data collected during my ten year ecological study of the eastern Selous, as Game Research Officer with the Tanzania Game Division.

The thesis examines the utilisation of the miombo woodland and associated grassland and floodplain communities by a spectrum of seven species of large grazing herbivore. The extremes of six month wet and dry seasons and the prevalence of dry season fires are responsible for great seasonal variation in the levels of forage production and nutrient content in the different habitats. In response to this variation the animal populations modify their utilisation patterns resulting in changed habitat occupance and feeding behaviour. Each species appears to have developed distinct strategies to obtain adequate nutritional inputs to allow for bodily maintenance and population growth. The evolution of these different strategies has resulted in a greater separation of niche space between sympatric herbivores at a time of scarce resources (Westoby 1974).

The objectives of this thesis are to demonstrate that such different strategies exist, to elucidate the reasons for the change in strategy and to measure the ecological benefits from such strategies. Such a task required the integration of several different lines of study, including:

(a) The detailed description of the environment and the different vegetation communities, and the seasonal change in the quantity and quality of their forage resources.

(b) The development of methods of animal census in woodland environments and the assessment of population density in each habitat in each season from year to year,

(c) The determination of animal population movements and habitat utilisation patterns, and the analysis of feeding activity and nutrient input in these habitats,

(d) The assessment of species performance in terms of population growth, body condition and reproductive activity,

(e) An attempt to relate the factors necessary for population success to the environment of the Selous Game Reserve and the miombo woodlands in general and to identify management inputs necessary to promote such success.

Thesis structure is detailed in the table of contents. The thesis contains nine chapters apart from this introduction and they are divided into a section describing the physical vegatation environments, a section describing the animal population and their use of the environments and a section reviewing the ecology and the management wildlife resources of the miombo woodlands and the Selous Game Reserve. There are ten appendices which either describe studies peripheral to the central theme of the thesis or contain extra details of methodolgoy or discussion to that of the main text.

Part One.

The physical environment is described in chapter two with sections on geology and geomorphology, soils, climate, water resources and past history. These topics have not been examined in depth but they do serve as relevant background information to the main study.

The vegetation is examined in much greater detail. Chapter three has sections on floristic affinities, vegeatation communities and distribution patterns, vegetation succession and dynamics, and vegetation diversity. The parameters of forage production and nutrient (mainly crude protein) content in relation to grazing pressure and annual fires are described in chapter four. The lack of previous descriptions of the vegetation of south east Tanzania and the complex role of fire in controlling woodland dynamics and forage parameters have meant this section is extremely lengthy.

Part Two.

This part commences with details of the animal census studies and shows change in numbers for four species (Wildebeest, zebra, impala and warthog) from 1968 to 1977, A discussion of the merits of the census technique is included in appendix 9. Chapter six discusses distribution patterns of the animal species on several different scales ranging from the whole of Tanzania, to the Selous Reserve, to the study area and to a small ridge slope valley catenary system in the miombo woodlands. The chapter concludes with a description of each species in terms of habitat occupance and compares this with other areas in Africa.

Details of feeding and nutritional studies are contained in chapter seven. Animal species are classified as to feeding type on the basis of their distribution, morphology and behaviour. The concept of selection in diet is discussed in some detail. Estimates of nutrient input are made for wildebeest and impala and these compared with theoretical requirements. Nutritional parameters are frequently taken from published studies on domestic stock. The use of such parameters is discussed in appendix 10. The chapter concludes with a discussion of the feeding strategies of the different herbivores.

Details of animal species population growth rates, reproductive parameters and condition levels are described in chapter eight. These values together with data on individual growth rates and disease-parasite levels are used to quantify "how well the populations are performing" in their habitats.

Part Three.

Part three brings together the conclusions of earlier chapters into a discussion of wildlife ecology in the miombo woodlands and the Selous Game Reserve, and the thesis finishes with a review of conservation, management and development options for the wildlife resources of the Selous Game Reserve.

1.2 THE SELOUS GAME RESERVE

The Selous is not only the largest but also one of the oldest wildife reserves in Africa, part being gagetted by the German Colonial Administration in 1905. Reserve boundaries are not static however, the latest additions b being gazetted in 1976. Matzke (1975, 1977) describes the history of the reserve and Nicholson (1969) documents the development and utilisation of the resources of the Selous. Rodgers (1976 and appendix 2) describes past human occupance of the eastern part of the reserve and Rodgers (1977b) discusses the ecological values of the Selous in the light of plans for large scale hydro-electric dam development.

The reserve is situated on the coastal plains in South East Tanzania, ranging in altitude from 80 to 1300m (300 to 4,200 ft) and is included in four administrative regions and ten districts (Fig. 1.1). To coordinate development, the reserve is controlled directly from Division Headquarters in Dar es Salaam and not from each region.

The Selous is dissected by the large Rufiji River System, whose major tributaries, Great Ruaha, Kilombero, Luwegu and Mbarangandu flow across the reserve. The difficulties of access and communications caused by these rivers have been important in allowing such a large area (6% of Tanzania's land surface) to be retained as a wildlife sanctuary. Being a reserve the area has no human habitation or human rights of access. Before their evacuation in 1945-1947 (due to trypanosomiasis) Selous area inhabitants were shifting cultivators, hunters and fishermen, predominantly of the Wangindo, Wapogoro and Warufiji tribes. The area has no history of domestic livestock. The prolonged dry season, poor infertile soils and the ubiquitous tsetse fly (Glossina morsitans) have meant the area is little suited for agriculture, cattle or forestry.

In 1964, the Tanzania Government implemented a policy of long term development for the Selous Game Reserve involving revenue from tourist trophy hunting and game viewing. This development necessitated the creation of 7000 km of roads and tracks, plus airstrips, ferries and bridges. Such a policy of resource utilisation required information on the ecology of the Selous, and in particular, knowledge of the abundance and distribution of the large mammals. This was the reason for my posting to the Selous in September, 1976.

The reserve is largely covered with miombo woodland although as is to be expected in an area of this size there is considerable variation in climate, soils and topography which give rise to several different vegetation types. These types with an estimate of their relative cover are as follows:

Thicket-forest	5%
Woodland	85%
Miombo communities	50%
Combretum communities	35%
Wooded grassland	8%
Swamp-floodplain	2%

A description of the miombo woodlands of East Africa can be found in Burtt (1942), Gillman (1949), Russell (1962) Lind & Morrison (1974) and in chapter three of this thesis. Broad detail of vegetation cover of the Selous are shown in Fig. 6.2b. General features of the Selous Game Reserve are shown in plates 1 and2.

Table 1.1 lists large mammals found in the Selous Game Reserve and in the study area (see below). This table gives the scientific names for all mammal species mentioned in the text of the thesis. Preliminary estimates of large mammal population size for the Selous and immediate environs are given in table 1.2. These figures were obtained from a 3% aerial census of the Selous undertaken in 1976 by Douglas-Hamilton, Rodgers & Mbano (unpublished data).

1.3 THE STUDY AREA AND MIOMBO RESEARCH CENTRE

As it was clearly impossible to study the whole reserve in detail, especially before the impact of light aircraft on wildlife research in East Africa, a smaller study area was needed. A large area in the eastern Selous was found to be adequate (blocks LL1 & LL2, named after the Lukiliro River) in that it had relatively easy access, large wildlife populations and it contained examples of all major vegetation types. The fact that the vegatation types were arranged in a distinct sequential fashion across an east-west drainage basin made study very much easier. Animal population move across the vegetation zonation and, with the exception of elephant, do not leave the study area in significant numbers. The study area therefore, can be thought to contain populations of finite size for the purposes of analysis and discussion. This block of some 1900 km^2, became the site for intensive ecological studies; less intensive surveys were made of other areas in the Selous The study area is shown in Fig. 1.2, the pattern of animal movement in fig. 1.3 and general features in plates 3-10.

In 1969, the Game Division benefited from a very generous grant from the Government of Denmark for the construction, equipping and running a wildlife research centre to investigate the miombo habitat and its fauna. This centre was built at Kingupira in the study area (38°30'E, 8°30'S). I administered the centre from its inception until 1975.

1.4 CONVENTIONS IN DATA PRESENTATION

(a) Within each chapter I have attempted to keep to a logical introduction - mehtods - results - discussion format. However, within very large chapters such as chapter three, or very diverse chapters such as chapter two I have resorted to the

(b) Numerical data are given in metric units, imperial equivalents are given in the case of altitude and hydrological data.

(c) The numberring of diagrams and tables follows that of of the chapter they refer to; thus table 4.2 is the second table in chapter four. Pages are numbered within chapters and appendices, e.g. page 7.28 is page 28 in chapter seven, page A3.4 is page four in appendix 3.

(d) Most statistical analyses used standard techniques and, as such, few detail are given in the text. Unusual analyses are explained more fully and source references given. The significance value of the results of statistical tests are starred in tables and in the text, according to the scale:

* = probability less then 0.05
** = probability less than 0.01
*** = probability less than 0.001

PART I

THE ENVIRONMENT

Chapter 2: The physical environment
Chapter 3: The vegetation
Chapter 4: Forage production and nutrient content.

CHAPTER TWO: THE PHYSICAL ENVIRONMENT

2.0 INTRODUCTION

This chapter gives a brief description of the physical features of the study area; covering the geology, geomorphology, soil types, climate and water distribution. The chapter finishes with an outline of the prehistory of the Miombo woodland formation in terms of past climates and human history. Appendices on the dynamics of water hole formation and a recent history of Wangindo settlement in the study area, (Rodgers 1976) add to the chapter content.

Descriptions are based on published material, field observations and measurements, and analyses undertaken by specialist institutes in Tanzania. This chapter does not go into detail on any of the topics, but as the environment of South East Tanzania is poorly known and documented, I do draw extensively on published material from elsewhere in Africa. This is considered essential for an understanding of the ecology of the study area. Plates 1-10 show general features of the Selous and the study area.

2.1 GEOLOGY AND GEOMORPHOLOGY

The geology of South East Tanzania and the area of the Selous Game Reserve in particular has been poorly documented.

Williamson's Diamond Mines, Mwadui, produced a small scale geological types map in 1975. Published descriptions are based on early exploratory traverses and a detailed survey of the Rufiji River basin in connection with proposed irrigation and hydro-electric schemes, (Haldemann 1968, and F.A.O. 1961). Rodgers (1969) gives a summary of the available geological information.

The oldest geological formation within the Selous is the Usagarian system of basement rocks, composed of quartzites, limestones, schists and gneisses. The most widespread formation is the Karoo sandstone system (Jurassic/Cretaceous) of which one bed, the Rufiji bed, is found in the study area. Surface rocks vary from coarse and fine sandstones to lime nodules, mud pellets, shales and mudstones. A fossil gymnosperm (probably *Dadoxylon dantzii* Potonii) is characteristic and widespread.

During the early Cainozoic era, degradation or base levelling reduced the Karoo formation to a smooth land surface with few pre-Karoo or Gondwanaland relict surfaces, Nandanga mountain (37°45'E, 8°25'S) in the central Selous is an example of such a relict surface. Later degradation further reduced the early Cainozoic surfaces, of which one example, the Libungani hills (800m) is found in the west of this study block. These surfaces are referred to as the Neogene or African surfaces, (King, 1967), and have led to "the very distinctive topographic features, flat topped mesas bounded by cliffs of friable cream coloured gravels", (Spence, 1957). Further degradational cycles are distinguished as Late Cainozoic 1 and 2 and a Recent cycle.

The first of these later cycles ended in the Miocene leaving an undulating landscape characteristic of much of southern and western Tanzanian miombo. This second cycle, which ended in the Pleistocene, is characterised by the deposition of alluvial grits and sands, found in many African river terraces eg. the Kafue and Luangwa valley systems in Zambia and the Ruvuma valley and this study area in Tanzania. The recent cycle has caused further deposits of alluvial clays in many river valleys. A scaled profile diagram of the study area is shown in figure 2.1 indicating land surfaces and basic geology.

Present erosion is accentuated by annual fires enabling severe surface run off to occur early in the rainy season. As a result sand rivers are widening, and horse-shoe shaped erosion basins are cutting into the African land surface. The fact that the Rufiji river carries 13.5 million metric tons of sediment per year from a 155,000 km^2 basin is an indication of the extent of erosion, (F.A.O., 1961). The geological boundary of the Karoo sandstones and Pleistocene alluvial deposits is of importance in that it produces a line of permanent springs and seepages. This is discussed in appendix one.

Secondary to the major topography described above are a series of minor ridges and valleys, many of which are catenary. These catenary systems are discussed in chapter 2.2 and 3 as geomorphology through its role in determining soil type and drainage patterns, plays a major part in the causation of vegetation distribution (Cole 1963).

This general correlation between geomorphology, soil and vegetation allows the delimitation of easily recognized landscape units suitable for land use planning and land scape mapping. This has been attempted in the Luangwa valley system in Zambia by Astle et al, (1969), and many of their landscape units are easily recognizable here. The similarity between the Luangwa system and this study area will be further demonstrated in this thesis (Chapters 3 and 9).

2.2. SOILS.

2.20 Introduction.

This section describes the soils of the study area in terms of their distribution, physical characteristics and chemical constituents. As the taxonomy of tropical soils is complex and controversial no attempt is made at classification. Soils are named by reference to their physical characters, following the system of Anderson, (1952, 1963). The section finishes with a discussion of some soil features of importance to vegetation growth and distribution: the soil nutrient content, the properties of alkaline-sodic soils and the soil catena within the Karoo system.

2.21 Methods.

Major soil types were immediately recognizable in the field by their colour, physical composition (sand, silt, clay) and from their drainage and site situation. Such soil types were tabulated for all vegetation communities, (see chapter 3. Soil pits were examined in each soil type, at first in collaboration with the Ministry of Agriculture/U.S. Peace Corps "land use and soil survey team" in 1968. Later soil samples from known depths were collected from other sites, e.g. smaller communities, topographic profiles, burning plots etc.

Soil samples were air dried and sent for analysis either to the Agricultural Research Centre at Ilonga, Kilosa; or to the Water Department's Soil Laboratories in Dar es Salaam. In 1971 soil samples from 10cm depth were collected from vegetation sample sites (chapter 3) and analysed for pH and clay content at the Department of Botany at the University of Dar es Salaam.

2.22. Results.

2.221. Soil types and distribution.

The following soils dominate the study area:

a) Non laterised red and yellow soils on sandstones.

b) Leached ferruginous soils in valley bottoms,

c) Alkaline-sodic soils (solonetz) with hard pan characteristics,

d) Alluvial clays on flood plains.

These may be described as follows:

a) Non laterised soils: these are zonal for much of the Karoo/Cretaceous systems of southern Tanzania. They are equivalent to the red latosals, tropical red earths or ferralitic soils of other classificatory systems. Sub surface soil colour varies from bright red through yellow browns to grey, depending on iron oxide content. Red soils dominate on drier sites on upper slopes and ridge tops. These soils are old, inherently infertile, well drained, acidic and very low in major nutrients; Nitrogen (N), Phosphorous (P), and Potassium (K), (tables 2.1 & 2.2). Organic matter content is low especially where sheet erosion and surface run off occur. Clay content, principally kaolinite, increases downslope.

These soils dominate the African land surface and the upper levels of the late Cainozoic surfaces in the study area. They are catenary with the ferruginous soils described below.

The soils have a poorly differentiated profile and no real structure or form. A stone line may occur at depth, and in areas of cliff erosion a thin iron concretionary layer may be seen.

b) Leached ferruginous soils: these soils do not reach their full development in this area and are similar to a) in many ways. They are distinguished by their situation in valley bottoms with poor or sluggish drainage, by iron staining of roots and surface puddles and by an increase in clay content. Colours range from red to chocolate brown. Clay content (kaolinite with some montmorillonite and illite) is variable. Structure and horizons are poorly differentiated.

c) Alkaline-sodic soils: these soils are typical of the Pleistocene alluvial/colluvial deposits of the river terrace. Calcium in the profile is replaced by sodium entering through ground water, sodium levels are high and soils are strongly alkaline. Calcium is lost by leaching and some is deposited lower down the profile as calcium carbonate concretions. The soils are predominantly sandy especially on the surface as the sodium causes clay dispersion through the profile giving the soil its black colour and hardness. This hardness makes the soil impervious to water and so the soil is poorly drained with considerable surface wash. In some areas the loose sandy top soil may be removed leaving a very hard cement like surface. This is characteristic of the southern part of the study area.

Crossing these deposits are low east to west ridges of more acidic sandy soils which are similar to the soils of 'a' above.

d) Alluvial clays: these are restricted to recently deposited flood plains (Lungonyo valley and Nangue). They resemble the tropical black earths of Anderson (1963) but here calcium is replaced by magnesium. Characteristically they are heavy black clays, exhibiting dry season cracking (to 3cm wide) and rainy season flooding. Clays are predominantly montmorillionite and illite and the profile exhibits a massive columnar structure. This soil type carries an edaphic perennial grassland. From the air a ridge furrow appearance is seen and its is thought this may be an ordered form of gilgai relief with annual flooding and water flow causing the symmetry. Ridges are about 3m apart and up to 10cm high.

2.222 Physical and chemical composition.

Physical and chemical analyses for three major soil types are shown in table 2.1. Horizons are not labelled but shown by depth. It must be stressed that horizon delimitation is not at all clear and the dimensions shown are very subjective.

Analyses for the major vegetation associations are shown in table 2.2. Here, data is averaged for all sites and horizons pertaining to each association and figures are to show differences between vegetation types. It is clear that the soils of the thicket and woodland associations are very similar. These similarities are discussed further in chapter 3.

Figure 2.2 illustrates some of the characteristics of the alkaline-sodic soils, and figure 2.3 is a traditional soil physical composition diagram used in naming soils into clay, loam and sand classes.

2.23. Discussion.

2.231. Nutrient status and fertility.

Major nutrient levels are low in all soil types and the area is classed as one of low fertility on the Tanzania Land Potential Map (Tanzania Survey Division, 1969).

The non lateritic red soils are old and highly weathered, their permeability and topography favours the leaching of soluble salts down profile and down slope, causing a deficit on high ground and an accumulation in the lower alluvial deposits (eg. sodium on the Pleistocene terrace). The high proportion of magnesium in the upland soils, table 2.2, is an indication of long term weathering and leaching (Black, 1968).

Nitrogen levels are low, in part a function of high temperatures (Black, 1957), and in part due to annual burning of the vegetation cover in which N is lost to the atmosphere. A dry season grass cover of 300gm/m^2 (dry matter) with a 4% protein content will release some 15-20 Kg per hectare of N to the atmosphere. Woody material will release another 5-10 Kg. To balance this is a possible input of up to 20Kg per hectar of N from rainfall (Eriksson, 1952), and further nitrogen may come from the nitrogen fixing bacteria of legume root nodules. Miombo woodland soils respond well to N fertilisation (Allen, 1965). Organic carbon is also lost through burning and the thicket soils (where fire is excluded) show a C content some 40% higher than adjacent woodland soils.

Potassium levels are low and continuous agricultural production requires fertilisation of most miombo soils. Phosphorus levels are low enough to cause P deficient forage in terms of animal husbandry. (Rodgers 1976 & appendix 5).

Subsistence agriculture in the miombo of East and Central Africa requires a system of shifting cultivation. A large part of the available nutrients are tied up in the vegetation layers (Nye and Greenland 1960 and Rodin and Bazilevitch, 1968), and their release through slashing and burning allows good crops for 3 to 5 years. On poor miombo soils a 30-50 year replenishment cycle is necessary before further agriculture (Allen 1965).

2.232. The alkaline-sodic soils.

Soils with an exchangeable sodium content of over 15% of all exchangeable bases are classified as sodic. (Black, 1968; Russel, 1961). Figure 2.2 shows soils in this area to have sodium levels of up to 25%. These soils are found along the whole eastern boundary of the Selous from north of the Rufiji River southwards to the Matandu River. Hot springs, soda lakes, salt deposits and alkaline seepages are a feature of these areas. This soil type has a characteristic vegetation cover of a scattered tree grassland with short annual and perennial grasses. This association forms an important wet season animal concentration area with large mammal densities of up to 80 per km^2 (see chapter 5).

The combination of excess sodium and high alkalinity in the soil tends to inhibit phosphorus uptake in the plant and to a lesser degree calcium and magnesium. Vegetation on such soils appears as a more arid type than is normally associated with the rainfall. This may be due to two factors: firstly, the hard impervious nature of the soil causing excessive surface run off and, secondly, a decrease in water absorption by the plant due to changes in soil hydraulic conductivity and osmotic potentials.

Black (1968) and Russell (1961) discuss the chemical and physical properties of these soils in detail.

2.233. The soil catena of the Karoo system.

The concept of the catena or soil topo-sequence was first used by Milne (1947), who later used it as a term of mapping convenience for Tanzanian soils. Burtt (1942) described the importance of the catenary concept to miombo vegetation distribution in Tanzania. Stanley-Price (1974) gives a brief review of the water and particle movement characteristics of an East African catena.

Within the Karoo system of the Eastern Selous a soil catena with correlated vegetation changes is clearly seen. The vegetation aspects are discussed in chapter 3. Many of the soil characteristics can be briefly described as follows:

Soil	Catenary Position		
Character	Upper Slope	Lower Slope	Sump.
Soil colour	Red	Orange, Yellow, Grey	Black, Grey, Brown
Physical Composition	Sand	Loamy sand	Sandy clay loam
Clay type	Kaolinite (very little)	Kaolinite	Montmorilllionite & Illite
Drainage	Free	Free	Impeded
Water table	Very Deep	Shallow	Shallow.
Leaching	Severe	Little	Very little
Base status	Very Low	Low	Higher

Chapter six examines animal distribution with respect to slope position (water and grass availability) across a catenary sequence in the Nakilala valleys of the Karoo system.

2.3. CLIMATE.

2.31. Introduction.

The Selous Game Reserve and immediate surrounds has the lowest density of rainfall recording stations of any area in East Africa. Data for 23 years are available from the Steiglers Gorge water gauging station on the Rufiji River, for 8 years from the Miombo Research Centre and sporadic data from two other stations in the reserve and eight stations within 25 Km of the reserve boundary. Clearly quantitative climatic analysis of the complete reserve is not possible and this section merely examines data from the Miombo Research Centre in detail and from south east Tanzania (5°30'c to 12°S and 35° 30'E to 39° 30'E) in general terms. In broad climatic terms the area is classified on Thornthwaites scale as "Dry Subhumid," (Sansom, 1954).

2.32. Rainfall.

The whole of the Selous falls within the unimodal rainfall belt of south Tanzania and central Africa, rainfall concentrating from late November to early May . with a partial drying up period in January or February.

Trend surface analysis (computerised production of isohyets) was attempted for 160 rainfall stations with data sets of 3 years or longer within the whole of south east Tanzania. This did not produce meaningful results due to the clumped distribution of recording stations and the great variation in mean annual rainfall, which varies from 500 mm in Mikumi National Park to 2400 mm in the Mahenge mountains to the west of the reserve. Visual examination of the data shows a trend of increasing rainfall from a low of some 700 mm p.a. on the eastern boundaries to a high of up to 1200 mm p.a. along the western boundary. This trend is supported by the preliminary isohyet maps for the Rufiji River Basin (F.A.O. 1961). It is possible that mountainous areas in the North West and South West may have rainfalls of up to 1600 mm p.a. Within the study area there is probably a slight increase in rainfall from the flat eastern area to the hills of the west.

Annual rainfall for the period 1924 to 1964 for Liwale (37° 5'E 9°50'S) is shown in figure 2.4. Data is shown in its raw form and after smoothing with a 4 by 4 smoothing function, (Lamb et al, 1966), where rainfall for year "x"

$$= \frac{1}{16} x \left(1(x-3)+2(x-2)+3(x-1)+4x+3(x+1)+2(x+2)+1(x+3) \right)$$

The raw data suggest a 5-6 year cycle of successive peaks and troughs in annual rainfall but this trend disappears after smoothing. The smoothed data show some indication of a 10 year cycle in successive troughs.

I was fortunate in that I was able to subject long term rainfall data for eight stations in South East Tanzania to Fourier Analysis. This analysis (a form of harmonic or spectral analysis) is a rigorous statistical technique which evaluates cyclical phenomena on the basis of a series of sine wave harmonics. The analysis was undertaken at the University of Oxford computing centre by Dr. S. Cobb & Dr. L. Pennycuick. Data sets for the eight stations varied from 48 to 54 years, which is minimal for satisfactory analysis of long term cyclical phenomena (Cobb, pers. comm.). As the stations were scattered within a 100,000 km^2 area, data for individual stations were not amalgamated.

Fourier analysis results for these stations are shown in Figure 2.8 and whilst there are indications of cycles close to the 2.5, 5.5, 17 and 25-year wavelengths, these cycles differ from station to station and the variance content for each wavelength also differs from station to station. Detailed investigation of rainfall cycles must await longer term data. At present one can only conclude that a 5-6 year cycle appears prominent in the data sets.

Table 2.3 shows the detailed monthly rainfall data for the Miombo Research Centre from 1968 to 1976, and mean monthly rainfall together with temperature is shown in a climatic diagram (Walter, 1973) in figure 2.5. The intensity of rainfall can be high, some 40 mm falling in 20 minutes in January 1969, a total rainfall of 136 mm on January 28, 1969; and a total of 295 mm (some 40% of the annual mean) falling in 3 day consecutive days in February 1970.

2.33. Temperature and Humidity.

Temperatures in the eastern Selous are high, a maximum of 40.1°C being recorded in November 1970. Temperatures reach their highest in the early rains and are lowest at the beginning of the dry season in May and June.

Mean monthly temperature data are shown in Table 2.4 and graphically in the climatic diagram of figure 2.5.

Figure 2.9 shows typical thermohygrograph tracings for both the rains and the dry season. Readings were made in shade at the Miombo Research Centre.

Table 2.5 gives further climatic data for two long term agro-mete orological recording stations in south east

Tanzania. Whilst some distances from the study area these data serve to show the prevailing climatic pattern of the Selous Game Reserve.

2.4 WATER AVAILABILITY

2.40 Introduction

The Selous Game Reserve is extremely well-watered in comparison with other large game areas, despite a six-month annual dry season. Water is available in the form of major rivers, streams, water holes, seepages and from sub-surface flow in sand rivers. The study area, situated in the driest part of the game reserve has a water scarcity only at the end of an exceptionally dry season. Normally no area is more than eight km from available water. Typical mid-dry season water availability is shown in Figure 2.6.

2.41 Rivers

No permanent rivers flow in the study area. The Lungonyo shows a small flow for two km at the northern end of the flood plain (now dammed by the Research Centre) otherwise there are permanent pools only at Kingupira, Matawatawa and Nambule. The other major rivers: Lukiliro, Lihangwa, Namamba and Mwende, have sub-surface water available to elephant digging and occasional

2.44. Run Off and Watershed Management.

Run off maps for the eastern Selous, (FAO, 1961) show mean annual run off to be of the order of 200 acre feet per year ($98,500m^3/km^2/p.a.$) or some 15% of the total annual precipitation. Whilst this is low compared with the mountains to the west of the Selous ($995,000m^3/km^2/p.a.$ or approximately 50% annual precipitation) the loss is more serious as the water deficit in the eastern Selous is much greater due to a 6 month drought, high temperatures and a consequent high potential evaporation.

Within the study area, the main water sheds are still forested and it is from these forested areas that flowing streams and seepages originate. It is probable that if forest cover decreases, run off will increase and permanent seepages disappear, (Colman 1968). The need for water shed conservation is discussed further in chapter 9.

2.5. PREHISTORY.

2.50. Introduction.

The prehistory of Africa with respect to past climate and palaeoecology is still poorly understood and a subject for controversy (Moreau, 1966; van Zinderen Bakker, 1966). However, the past historical record of climatic regimes, fire and human settlement is of considerable importance in understanding present vegetation and animal distribution in eastern and central Africa. This section outlines the major climatic influences of the past and discusses these influences and the history of man as they relate to the ecology of the Tanzanian miombo. A more recent historical study of human settlement in the eastern Selous Game Reserve is given in Appendix 2, (Rodgers, 1976b).

2.51. Past climates.

The concept of a series of pluvial and drier interpluvial periods in the Pleistocene period has dominated African prehistory for the past fifty years (Cole, 1954; Moreau, 1966). Four major pluvials have been postulated, although it has not been possible to correlate these periods with the temperate ice ages. As Sonia Cole (1954) said, "That there were times when the climate was definitely wetter than today, and other times when it was drier, is not disputed; it is the intensity and timing of these changes that is questionable." Evidence from geology, archaeology, palynology and botany point to a major pluvial period, peaking some 21,000 years before the present (B.P.). This is the Gamblian or last pluvial period to be recognized.

Moreau (1966) gives evidence that there was a 5-8°C temperature drop during the Gamblian and he suggests this could have resulted in a rainfall regime some 50% higher than at present. Moreau argues that under these climatic conditions montane and upland forests would have moved downwards to some 400m above present sea level. This would have meant an almost continuous forest cover from Ethiopia to Cape Province of South Africa. Wetter areas would bear montane or rain forest and drier areas would have deciduous forest or thickets.

At this time, two centres of arid conditions still existed: the horn of Africa around Somalia and the Kalahari Desert in Namibia. That these two centres have been in past contact during dry interpluvials is shown by strong botanical affinities (Wild, 1964; Moreau, 1962). Since the Gamblian period the climate has steadily ameliorated. Moreau (1966) discusses two further minor wet periods and one dry period, 12,000 BP, since the Gamblian. Most authorities view the Pleistocene as a dry period with occasional wetter periods, the pluvials, rather than vice versa.

More recent work in Uganda has cast doubt on the occurrence and the timing of the Pleistocene dry and wet phases. The work of Livingstone (1967), Kendall (1969) and Hamilton (in Lind and Morrison 1974, and pers. comm.) suggests that at the time of the Gamblian the climate was colder (by 6°C) but drier than at present. At sometime after 12,000 BP the climate became warmer and wetter culminating in a period of forest maxima at some 6,000 to 4,000 BP. Studies of fossil lake levels in Kenya (Richardson, 1966) give evidence of high lake levels at 8,000 and not 20,000 BP. Martin (1966) argues on faunal evidence for drought conditions around 12,000 BP.

Extensive deposits of Kalahari sands in the soil profile of southern Zaire tropical forests aged at some 12,000 BP is the only definite evidence of the events postulated for Uganda taking place further south as well. There is a dearth of detailed palynological or fossil climate studies from the woodland areas of East and Central Africa. Lawton's (1963) data appears to fit the Gamblian pluvial theory but could be reanalysed to agree with Hamilton. For the purposes of this thesis, the concept of a forest maximum around 6,000 BP is accepted. It is suggested that as a result of fire and vegetation clearing, especially in the last 2,000 years, the miombo woodlands have developed as a fire held disclimax from the preceding forest or thicket vegetation types. This premise is developed more fully in Chapter Three.

2.52 The history of man and fire

West (1965) and Phillips (1965) show that natural fires must have been a major ecological factor throughout the tertiary period. Hoffman (1974) mentions the early tertiary as the age of dominance of grasses and the rise of the ruminant artiodactyls at the expense of the non-ruminant perissodactyls. Such radiation of the grasslands must have occurred with the presence of fire.

Man in Africa has had the use of fire for at least 53,000 years (Phillips, 1965, quoting Clarke). Van Zinderen Bakker (1966) gives Carbon 14 dates of over 40,000 years for charcoal deposits associated with stone age cultures. Man the cultivator has developed since the Gamblian ice age in the last 10 - 20,000 years (Allen, 1965; Clarke, 1969; Martin, 1970). The practise of shifting cultivation would have necessitated the clearing and burning of large areas of climax forest. Hamilton (pers. comm.) considers that the major impact of man on vegetation has occurred in the last 2,000 years and Martin (1966 & 1970) states evidence on the basis of faunal extinctions that man in Africa has only recently had major effects on the ecology.

2.53 The effects on vegetation and animal distribution.

Since the forest maximum large areas of climax forest and thicket have been destroyed and fragmented by man's clearing and burning, coupled with a gradual change to a slightly drier climate. The continuous belt of forest is shown today by relict vegetation types in East and Central Africa, and pollen spore analysis from swamp sediments shows the botanical nature of previous forests. That these relict forests have been joined and fragmented several times in the past is shown by close botanical similarities and by the degree of endemism in both plants and animal species (Lawton 1963). Woodland formations (the miombo) adapted to frequent fires have replaced the climax forests. This is discussed in detail in chapter 3.

The arid areas of Somalia and Kalahari show considerable faunal similarities (Careasson (1962, Wild 1964). These refuge areas provided centres of radiation for grassland animals, shown today by the great array of grazing mammals on the East African and South African plains. The presence of many allopatric species and subspecies pairs such as white rhino, oryx and spring hare show previous faunal connections. These grassland areas are separated by the miombo woodland formation of Central Africa, a zone with few large mammal endemics, notably sable and Lichtenstein's hartebeest.

Wildebeest, an animal of short grasslands, is an example of subspeciation in isolated grassland habitats. Their distribution can be shown as follows (after Sidney, 1965).

Species or Subspecies	Area	Notes
Black wildebeest	South African plains	Almost extinct
Blue wildebeest	Zambezi valley	Isolated valley grassland systems in Miombo woodland
Cooksons wildebeest	Luangwa valley	
Nyassa wildebeest	Rufiji & Ruvuma valleys	
White bearded wildebeest	East African plains	Races either side of the rift valley.
Eastern Wildebeest		

Figure 2.7 shows the extent of forest and thicket in Africa during the Gamblian, the present distribution of the miombo woodland formation separating the East and South African plains and the present distribution of wildebeest subspecies in their isolated grassland habitats.

2.54. Conclusions.

It is now accepted, if not proven, that the vast expanse of woodlands in Central Africa has developed from the forest and thicket formations by human agencies of fire and clearing, aided by a shift towards a more arid climate. This woodland formation separates the present day centres of grazing ungulate radiation, the East and South African plains. Within the woodlands can be found forest relics whose botanical composition in terms of floral similarities and degree of endemism indicate past cycles of fusion and isolation. Localised edaphic conditions have formed grassland islands in the woodlands which created areas of subspeciation for wildebeest along its range from East to South Africa.

CHAPTER THREE: THE VEGETATION

3.0. INTRODUCTION.

3.01. The Miombo woodlands of South East Tanzania.

This study area, and virtually the whole of the Selous Game Reserve, fall into the south-east Tanzania block of deciduous woodland or "miombo" (Gillman 1949, Russell 1961). This vegetation type covers large areas of East and Central Africa, from Rhodesia in the south through parts of Mozambique, Angola, Zaire and Zambia into south-western and eastern Tanzania. A physiognomically similar woodland exists in West Africa, the "Guinea savanna" (White 1965, Ramsay & Rose-Innes 1963). The distribution of the "miombo woodland" in Africa is shown in figure 2.6.

Within Tanzania this formation is estimated to cover almost 450,000 km^2 or just under half the total land surface. The south-eastern block is separated from the western areas by a drier zone running from the Rukwa valley to Dodoma. This dry belt had possible importance as part of a past link between the arid communities of Somalia and South West Africa, (Carcasson 1964, van Zinderen Bakker 1967). The south-eastern block differs from the more typical western Tanzania and Zambezian miombo floras by having fewer endemic miombo elements and by the inclusion of coastal elements, especially in the riverine and thicket communities. (Rodgers 1969, Hedberg 1966).

The miombo formation can be defined as follows: "A deciduous unarmed woodland occurring in the unimodal rainfall areas of East and Central Africa on old, acid, sandy soils. It is characterised by Caesalpinaceous trees, especially species of Brachystegia and Julbernardia. The ground cover varies from a dense coarse grass growth to a sparse cover of herbs and small grasses. The shrub layer is variable in density and species composition, often dominated by Diplorhyncus condylocarpon and species of Combretum. The whole is maintained by periodic dry season fires."

As the vegetation of south east Tanzania has been poorly collected and described, this chapter is necessarily large. An understanding of the seasonal movement of grazing ungulates and the management of the study area depends on a knowledge of the plant cover, its dynamics and seasonal change. Consequently the vegetation is discussed at some length, and for ease of presentation, this chapter is split into six sections, viz:-

1) The vegetation communities and vegetation map
2) A computerised analysis of the ground layer communities.
3) Floristic composition and affinities
4) Vegetation and the environment
5) Succession and community dynamics and
6) The concepts of diversity, equitability and maturity.

Where possible each section is split into introduction, methods, results and discussion. In addition, three appendices dealing with vegetation are enclosed with this thesis. One contains the detailed annotated species list, the second contains a description of the computer analysis techniques and the third, already referred to in chapter two, discusses the effect of past settlement on the vegetation of the study area.

3.02. General Methods:

In order to be able to identify and name plants in the field a self-contained reference herbarium was initiated in 1967. The collection is maintained as a fully mounted and annotated herbarium and duplicate specimens kept at the East African Herbarium in Nairobi and the herbarium of the Department of Botany at the University of Dar es Salaam.

To date the collection contains over 4,000 specimens covering almost 1,100 species from this study area, in addition to collections from other parts of Tanzania. In 1975 a plant taxonomist was appointed to the Miombo Research Centre and he has maintained and revised the plant collections and species check list since then.

Using local assistants a Latin-vernacular dictionary for over 400 woody species has been prepared and checked in order to facilitate discussions on plant ecology and distribution with field staff.

Full aerial black and white photographic cover of the study area was available as follows:

1947 to 52	Occasional flight lines: R.A.F.	1:32,000
1965	Complete stereo cover: Tanzania Survey.	1:48,000
1970	Stereo cover of selected flight lines within the study area	1:10,000

Vegetation communities were recognized qualitatively over 4 years of field studies (1968 - 1972) and located and marked on aerial photographs. Such communities are shown in Plate 9 for a typical air photograph of the woodland karoo system.

Species lists and determinations of dominants were made for several sites within the different communities. This information and data from collected herbarium material were mounted on punch cards, cross referenced for habit, dominance, distribution, community and regional affinities. An example of such a card is shown in figure 3.1.

Fire plots and grazing exclosures were set up early in the study to monitor vegetation changes due to fire and grazing. This is discussed in detail in Chapter 4.

3.1. VEGETATION COMMUNITIES AND THE VEGETATION MAP.

3.11 Introduction.

No standardised procedure of hierarchical classification exists for African vegetation. The following procedure is adopted for this thesis. The miombo woodlands of Africa as a whole are referred to as a "formation type". The word formation is used to denote separate physiognomic vegetation categories, e.g. forest or grassland. These formations are divided into associations, which are frequently occurring vegetation groupings characterised by similar species dominance, physiognomy and ecology. Their terminology follows that described by Pratt, Greenway and Gwynne (1966), in their paper on the classification of East African rangeland. In this method, association names are compounded of dominant genera and physiognomic characteristics. In some cases, as in thickets, the choice of dominants is difficult, and I have resorted to geographical and ecological criteria. Two vernacular terms are partly retained in the terminology and text, both of which have extensive usage in East and Central Africa. These are "miombo", which now specifically refers to the Brachystegia/Julbernardia communities, and "chipya", a Zambian term used to describe the fierce fire woodland communities with dense grass cover. The terms "upper valley" and "lower valley" as defined by Trapnell (1953), are useful categories, and they are partly retained in association names. Their relevance is discussed in the text.

Five physiognomic formations are recognized. These are:

A) Forest - here defined as a closed stand of trees over 8 metres in height whose canopies interlock. There may or may not be an understory of shrubs or small trees. The ground layer, if present, is sparse.

B) Thicket - here defined as a closed vegetation type dominated by shrubs and trees of less than 8 metres. A sparse ground cover may be present.

C) Woodland - here defined as a vegetation type dominated by trees, but whose crowns are not touching and the ground layer is predominantly grass. An understory of trees or shrubs may or may not occur. Canopy cover is from 20 to 80%.

D) Scattered-Tree Grassland - defined as an open vegetation type, dominated by grassland, with occasional trees or groups of trees. Canopy cover is cover is less than 20%.

E) Grassland - a completely open type with no, or very few, woody elements.

3.12. Methods:

Using field notes and marked aerial photographs 19 constant and discrete vegetation associations were recognized qualitatively. These were recognizable on the ground, on photographs (see Plate 9) and by listing dominant species.

By examining herbarium records and species data cards, the species dominating, frequently occurring in, or constant to, each association for each of the tree, shrub and grass layers were identified and used to form a brief description for each association.

Where an association showed several sub-types based on minor but real changes in species composition, these sub-types were also described as communities within the association.

A vegetation map at a scale of 1:125,000 was drawn onto a base map from the marked aerial photographs using a Zeiss Sketchmaster to reduce the photo scale of 1:48,000. A base map showing rivers was prepared by photographically reducing and tracing the published 1:50,000 survey maps for the study area.

This base map was overdrawn with the photo flight lines and photo centres. A geometric diagram of a scaled down photograph showing photo centre, photo limits, stereo overlap and diagonals was used to minimise edge distortion. A Casella mirror stereoscope was used to clarify vegetation boundaries (Howard 1970).

Vegetation mapping at this scale necessitated some sacrifice of detail for final visual clarity. In practice any vegetation unit of less than 2mm on the final map was not shown. This has meant some riverine communities could not be portrayed and the map shows only 16 of the 19 associations. Several vegetation boundaries were not discrete, and communities tended to merge rather than end abruptly; in such cases boundary lines were subjectively positioned after checking in the field. Final colouration of the map was chosen (within the limits of the printers) to show major physiognomic formations as well as individual associations (Kuchler 1967).

3.13. Results.

Nineteen associations were recognized. These are:

A) Forest Formation:

1. Ground Water Forest
2. Riverine Forest
3. Coastal Dry Evergreen Forest

B) Thicket Formation:

1. Riverine Thicket
2. *Brachystegia microphylla* Thicket
3. Coastal Dry Thicket on Alkaline Soils.
4. Coastal Dry Thicket on Sands

C) Woodland Formation:

1. *Brachystegia* Woodland (Miombo)
2. *Pterocarpus-Pseudolachnostylis* Woodland (Chipya)
3. *Pteleopsis-Millettia* Woodland (Chipya)
4. *Combretum-Terminalia sericea* Woodland
5. Upper Valley Mixed Woodland
6. Lower Valley *Combretum-Sclerocarya* Woodland

7. Shallow Soil Stunted Woodland

D) Scattered Tree Grassland Formation:

1. *Terminalia spinosa-Spirostachys* Wooded Grassland
2. *Acacia-Combretum* Shrub Short Grassland
3. *Cassia-Combretum* Shrub Medium Grassland

E) Grassland Formation:

1. Seasonally Flooded Tall Grass Swamp

F) Oddments:

1. Anthill Communities

Association descriptions, revised slightly from Rodgers and Ludanga (1973) follow. Many of the associations are shown in Plates 1 - 6.

A.1 Ground Water Forest:

This association occurs as a discrete 10 km^2 area at the northern end of the large Lungonyo flood plain, where there is permanent water seepage. The southern half of the forest consits largely of mature wild date palms, *Phoenix reclinata*, overlooking muddy swamp pools. The northern half, away from the water seepage, becomes more similar to riverine forest. The canopy cover is dense, but no well-defined layering exists. Forest trees have buttressed boles and lianes are common, but not epiphytes. A ground cover exists only where the canopy is broken. The whole area is criss-crossed by the trails of hippopotamus, for which the forest offers a dry season refuge. The edge is sharply defined by the action of fire. Several small alkaline streams enter from the east, and saline plant species occur - e.g. *Haplocoelum mombasense*, *Salvadora persica* and *Sporobolus virginicus*.

Common trees are *Phoenix reclinata*, *Hyphaene spp*, *Lepisanthes senegalensis*, *Alangium salviifolium*, *Balanites wilsoniana*, *Celtis wightii*, *Azanza garkeana*, *Sorendeia madagascariensis*, *Mimusops kummel* and *M. fruticosa*, *Calancoba* and *Memcylon spp*, which present a continual evergreen aspect.

The understory contains many *Rubiaceae* and *Celastraceae* eg. *Tarenna*, *Canthium*, *Coffea*, *Psychotria* and *Tricalysia*, and *Elaedendron*, *Salacia* and *Mystroxylon*. *Commiphoria* species are common.

Several small isolated forest clumps are scattered around the main forest edge. *Tamarindus indica*, *Afzelia quanzensis*, *Hyphaene* and *Euphorbia* species are common elements.

Grasses are mainly forest species - e.g. *Leptochloa* and *Eleusine*. *Cynodon dactylon* and *Chloris Gayana* are common in the clearings. These species indicate the alkaline nature of the forest.

A small area of ground water forest occurs to the north of the study area, at Maua ($38^{0}10$'E, $8^{0}20$'S), around a fresh water spring. Dominant species are *Khaya nyassica*, *Ficus* spp. and *Sterculia appendiculata*. *Syzygium guineense* and *Majidea zanguebarica* are common in the understory. This is more similar to the ground water forests of Zambia (Lawton, 1963; Wild, 1964).

A.2 Riverine Forest:

This is a varied association, occurring as true gallery forest along only two rivers - the Lungonyo and lower Lihangwa, and isolated patches occur on the Mwende river. In all these cases the forest is rapidly decreasing due to both fire and river bank encroachment.

The gallery forest varies from a few metres to over 100 metres in width, with discrete fire maintained edges and several game trails. Where the forest has been cleared, many such trails lead to severe erosion gulleys. Dominant trees are *Pterocarpus holtzii*, *Diospyros kirkii* and *D. mespiliformis*, *Sterculia appendiculata* and *Terminalia sambesiaca*. *Albizia amara* and *A. zimmermanii* are occasional elements. Common understory trees are *Garcinia livingstonei*, *Dalbergia arbutifolia*, *Erythroxylum emarginatum*, *Haplocoelum mombasense*, *Commiphora zanzibarica*, *Cleistochlamys kirkii*, and *Cola* species.

The shrub layer contains many species, especially *Rubiaceous* elements - e.g. *Lamprothamnus*, *Pavetta*, *Polysphaeria*, *Tricalysia* etc. Grasses such as *Leptochloa*, *Rottboelia*, *Heteropogon melanocarpus*, and *Oryza* are common in open glades.

Climbers such as *Artabotrys*, *Abrus*, *Monodora* and *Entada* are frequent. A fringe zone of shrubs such as the *Malvaceae* - *Thespesia*, *Urena* and *Hibiscus* species with *Deinbollia borbonica* and *Combretum goetzei* is a characteristic feature.

One small relict forest of primarily riverine species occurs on clay soils away from major rivers. Examination of air photographs from 1949 shows these patches were more frequent even twenty years ago. Dominant trees are *Diospyros*, *Mimusops*, *Sterculia* and *Afzelia*.

There are a very few forest patches in the upland areas on more sandy acid soils. Where they occur *Pterocarpus* holtzii is common as a riverine tree. Mention must be made of a small (one hectare) forest at Mpapule on alluvium by permanent water. This forest patch is dominated by tall Trichilia emetica trees, with Ficus spp. The understory is largely composed of Markhamia acuminata, Vangueria acutiloba and Cleistochlamys.

A.3 Costal Dry Evergreen Forest:

This association is restricted to the higher areas (above 700 metres) of the western watershed, with an estimated rainfall of 1000 to 1200 mm per annum. The forest shows a dense stunted aspect on steep slopes with a closed shrub layer. Taller stands with a bare ground layer occur on deep soil ridge tops. Usnea is common, but other epiphytes are rarely seen. The soil shows a permanent litter/humus layer of up to 5 cm and the top soil is a rich sandy loam.

Common canopy trees are Mimusops busseana, Albizia adianthifolia, Trachylobium, Brachylaena, Dracaena, Ricinodendron tomentellum, Ficus zanzibaricus, Manilkara discolor and M. sulcata, Pteleopsis, Strychnos sp. and Lannea sp.

Sapium, *Drypetes*, *Fagara chalybea*, *Byrsocarpus bovinianus*, *Calancoba gigantocarpa* and *Hymenocardia* are common in the understory.

Typical thicket species occur on the slopes as a shrub layer - e.g. *Croton pseudopulchellus*, *Grewia conocarpa* *Salacia senegalensis*, *Lingelsheimia*, *Memecylon*, *Maerua* and *Uvaria* species.

Climbers such as *Combretum trothae* and *C. padoides*, *Acacia brevispica* and *Schlecterina mitostemmatoides* are frequent.

Polyneura squarrosa, a sparse creeping grass on the open floor is endemic to the sandy soil forests of south east Tanzania.

B.1 Riverine Thicket:

As with the gallery forest, analysis of photographs reveals a general decrease in extent since 1949. This formation occurs in several forms:

1. Degraded riverine forest, still with occasional emergents such as *Pterocarpus holtzii*. Dense groves of *Lamprothamnus*, *Polysphaeria*, *Haplocoelum* etc.

2. Flood plain, fringing the major channels - *Combretum constrictum* with small composite shrubs - e.g. *Pluchea dioscoridis*, *Vernonia exsertifolia*.
3. Drier areas on clay - *Maytenus putterlickiodes*, *Albizia anthelmintica*, *Capparis tomentosa*, *Harrisonia abyssinica*, *Dalbergia melanoxylon* and the occasional baobab - *Adansonia digitata*.
4. Wetter areas on clay - *Markhania acuminata*, *Heinsia crinita*.
5. On deep alluvial sands, often in association with trees such as *Stereospermum*, *Trichilia*, *Kigelia* and *Dalbergia boehmii*. Typical shrub species are *Xylotheca glutinosa*, *Antidesma venosum*, *Psorospermum febrifugum*, *Canthium zanzibaricum*, *Dichrostachys cinerea* etc.
6. In miombo valleys where fire protected - *Ziziphus abyssinica*, *Dichrostachys*, *Harrisonia*, *Maytenus senegalensis* etc.

B.2 *Brachystegia microphylla* Thicket:

This is restricted to the steep upper slopes of major hill systems, on poor shallow soils. The canopy, which is light and feathery, is almost entirely composed of

B. microphylla and the occasional *Rhodognaphalon schumannianum*. On better sites such trees as *Cleistanthus*, *Afzelia*, *Cussonia zimmermanii*, *Albizia petersiana* and even *Tamarindus indica* have been seen as occasional emergents.

Common shrubs and small trees are *Gardenia resiniflua* and *Gardenia sp.* = *Mgaza 272* (both restricted to this association), *Hymenocardia ulmoides*, *Strychnos henningsii* and *S. panganensis*, *Maerua kirkii*, *Lingelsheimia*, *Croton*, *Paropsia braunii*, *Rothmannia englerana*, *Vernonia zanzibarica*, *Acokanthera schimperi* and *Alchornea laxiflora*. *Usnea* is common, grasses are rare, the ground usually being covered by *B. microphylla* seedlings.

B.3 Coastal Thicket on Alkaline Soils:

This association occurs in small patches in this study area, but occupies a high proportion of the alkaline soil to the north. The soil is highly sodic (pH 9.0 with a high sodium content) and sets very hard in the dry season. The association is semi-deciduous and xeric in character.

Common emergents are *Spirostachys africana*, *Afzelia*, *Manilkara mochisia* and *M. sp.* (Muhike), *Tamarindus* and

and Millettia stuhlmannii. Diospyros cornii and D. bussei are common, as is Euphorbia candelabrum. Several shrub species occur, chiefly Cola species, Cleistochlamys, Commiphora, Suregada zanzibarensis, Erythroxylum emarginatum, Euphorbia grandicornis, Sansevieria species, Lamprothamnus, Teclea simplicifolia, Securinega virosa, Indigofera schimperi, Toddaliopsis, Dichapetalum, Croton and Harrisonia.

Several large seasonal water pans occur, often with hippopotamus, especially when fire produced open woodland areas are close.

B.4 Coastal Thicket on Sands:

This association occupies several large areas in the study area (totalling almost 150 km^2). It is nearly always restricted to ridge tops or the upper slopes on deep sandy soils. It is semi-deciduous, with a virtually bare ground layer and a sharp fire controlled edge.

Dominant emergents are Pteleopsis myrtifolia and Millettia stuhlmannii with occasional to common Commiphora serrata, Lannea sp. (Mumbo), Vitex species, Manilkara discolor and Oldfieldia somalensis.
Understory trees are: Calancoba, Markhamia obtusifolia

Drypetes gerrardii, *Ochna holstii*, *Citropsis daweana*, *Cola microcarpa*, *Hymenocardia ulmoides*, *Memecylon* sp, *Fagara chalybea*, *Haplocoelum inopleum*, *Wrightia* sp, *Erythroxylum emarginatum* and *Strychnos henningsii*. Common shrubs are *Polyalthia* sp., *Uvaria acuminata*, *Salacia senegalensis*, *Dichapetalum* spp., *Croton pseudopulchellus*, *Grewia conocarpa*, *Lingelsheimia* sp., *Leptactina bussei*, *Strophanthus hispidus*, *Lindackeria* sp., *Alchornea laxiflora*, *Chassalia umbraticola*, *Clerodendrum* spp., *Pentas parvifolia* and *Mildbraedia carpinifolia*.

Climbers are common, viz: *Hugonia castaneifolia*, *Combretum trothae* and *C. padoides*, *Acacia brevispica* (sp. aff), *Schlecterina*, *Monodora junodii*, *Ancyclobothrys petersiana* and *Landolphia* sp.

Small ephemeral herbs appear in the ground layer - e.g. *Triumfetta kirkii*. Thicket grasses such as *Megastachya mucronata* and *Panicum heterostachyon* occur.

An occasional variant of this type is a thicket dominated by *Manilkara discolor* and *M. sulcata* often found just above the *Brachystegia microphylla* zone.

The thicket to the west of Balani is unusual in that it is completely deciduous and poor in species composition.

Pteleopsis and Millettia are complete dominants, and Leptactina bussei the commonest shrub. This community gives rise to the adjacent Pteleopsis, Millettia woodlands when opened up by fire.

Isolated thicket and pioneer thicket clumps are occasionally found. Landolphia spp., Markhamia obtusifolia, Grewia conocarpa, Monodora junodii, Hymenodictyon floribundum and Vernonia zanzibarica are amongst the earliest pioneer species.

On isolated steep scarps a drier variant occurs, composed almost entirely of Diospyros bussei, Croton pseudopulchellus and Strychnos henningsii.

C.1 Brachystegia Woodland (Miombo):

This association is the true "miombo" of Central Africa. It rarely reaches the height, density or species richness of the Zambian form, and often contains coastal elements. Here it is dominated by Brachystegia spiciformis and Julbernardia globifera, either together or separately. Julbernardia appears to dominate on poorer soils. The shrub layer is dominated by Diplorhynchus condylocarpon and Byrsocarpus orientalis;

occasional *Xeromphis obovata*, *Tetracera masuiana*, *Ximenia caffra* and *Flacourtia indica* occur. *Hugonia busseana* and *Lonchocarpus eriocalyx* are common understory trees. The ground layer is more open than the fierce fire woodland; rarely are dense, coarse stands of grass present. Herbs, sedges and suffrutices are common. Grasses are sweet, chiefly *Panicum infestum*, with several small species such as *Sporobolus ioclados* and *Sporobolus subglobosus*.

Other *Brachystegia* species are more restricted in their distribution. Mention has been made of *B. microphylla*, which can occur as a woodland dominant on steep, rocky soils, without a thicket understorey.

B. utilis is rare in this area, but can be found on steep slopes below the *B. microphylla* zone.

B. bussei is usually restricted to poor, steep slopes, but is occasionally found in dense groves in valley bottoms.

B. boehmii is common on lower slopes of higher clay content, often in poorly drained areas.

In deep shade, and usually fire protected, thicket pioneer clumps occur: *Landolphia* and *Leptactina bussei* are common.

Throughout this association, occasional trees of *Afzelia*, *Ficus* sp., *Pterocarpus angolensis*, *Pteleopsis*, *Millettia stuhlmannii*, *Pseudolachnostylis* and *Strychnos innocua* occur.

C.2 Pterocarpus-Pseudolachnostylis Woodland (Chipya):

Referred to as "chao" in this area, this is the basic fierce fire woodland, with a dense coarse grass cover. Dominant and common trees are *Pseudolachnostylis*, *Pterocarpus angolensis*, *Pteleopsis myrtifolia*, *Millettia stuhlmannii*, *Combretum zeyheri* and *C. collinum*, *Strychnos innocua*, *Boscia salicifolia* and *Xeroderris stuhlmannii*.

Shrubs are rare and subject to severe die back due to fierce annual fires. *Terminalia sericea* seedlings may be common. Grasses are sour and coarse, and dominated by *Andropogon schirensis* and *Hyparrhenia* spp. Sedges, small grasses and herbs are not common. Herbs, where they do occur, are semi-suffruticose, such as *Crotalaria* and *Phyllanthus*.

A richer form occurs, dominated by Burkea, Amblygonocarpus and Erythrophleum africanum. It is not known whether this is a successional series or edaphically controlled.

A related form occurs on the slopes of the Tundu Hills, which is dominated by Boscia salicifolia, Pseudolachnostylis and some Pterocarpus and Millettia. Grewia monticola is a common constituent of the shrub layer.

On the lower slopes of upland valleys, a woodland dominated by Pseudolachnostylis is common. The grass layer is dominated by Loudetia arundinacea and Tristachya bequartii. The lack of fire sensitive elements, and a dense grass layer, warrants its inclusion in this association.

C.3 Pteleopsis-Millettia Woodland (Chipya):

Possibly a variant of C.2 (above), but is discrete and readily identifiable. Trees are almost exclusively Millettia stuhlmannii and Pteleopsis, with a few Schrebera trichoclada. One occurrence of this community is adjacent to the deciduous thicket variant discussed under B.4. Markhania obtusifolia and Millettia micans are dominant shrubs. Pseudolachnostylis has only been seen as a rare seedling and sapling.

C.4. Combretum-Terminalia Tall Grass Woodland:

As will be shown later, this is a successional stage following cultivation, and will proceed to a miombo or chipya form in time.

The woodland is dominated by trees of *Terminalia sericea*,, *Combretum zeyheri*, *Pseudolachnostylis* and *Xeroderris*. Suffrutices of *T. sericea* are very conspicuous in the ground layer. Grasses are predominantly tall and coarse, *Andropogon schirensis*, *Loudetia simplex*, *Tristachya* and *Themeda* are common.

Other trees found are *Combretum collinum* and *C. molle*, *Lannea stuhlmannii*, *Lonchocarpus eriocalyx* and *Pterocarpus angolensis*. Mature woodland contains more *Pterocarpus*, *Burkea*, *Erythrophloeum*, *Millettia* and *Afzelia*. Shrubs are more common, especially *Diplorhynchus*, *Byrsocarpus orientalis* and *Xeromphis*. Saplings of *B. spiciformis* occur. The grass cover becomes more open and sweet, with *Panicum infestum* and several herbs.

Occasional copses of mature *B. spiciformis* occur.

C.5 Upper Valley Mixed Woodland:

A complex and heterogenous zone with many variants. They occur in the valley bottoms of all upland sandy alluvial valleys or "dambos". As such they are aptly described by the blanket association term "upper valley mixed woodland."

Type 1: Dominated by *Pericopsis angolensis*, *Vitex doniana* and *Hyphaene* species. *Albizia versicolor*, *A. harveyi* and *Acacia nigrescens* are common, with the occasional *Tamarindus*, *Dalbergia boehmii*, *Kigelia aethiopum* and *Cleistanthus*. *Tamarindus*, *Ziziphus* sp. and *Boscia angustifolia* are common on anthills. Grasses are tall and dense, and include *Panicum maximum*, *P. aphanoneurum*, *Cymbopogon giganteum* and the occasional *Setaria*.

Type 2: One more sandy soils. *Acacia sieberiana*, *Piliostigma thonningii*, *Lonchocarpus capassa* and several *Combretum* species - e.g. *C. collinum*, *C. psidiodes*, *C. fragrans* and *C. molle*. *Annona senegalensis* is common. *Ricinodendron rautanenii* sometimes occurs.

Shrubs of *Xeromphis*, *Maytenus senegalensis*, *Mimosa pigra*, *Securinega*, *Dichrostachys* and *Ziziphus* are common to both forms.

C.6 Lower Valley, *Combretum*-*Sclerocarya* Woodland:

An equally heterogenous association found on the more extensive and gentle slopes of the lower valleys. It also shows sandy and clay communities. Soils are usually pale, and the community is an inter-zone between the woodland and scattered trees grassland.

Type 1: On more sandy soils of drainage lines such as Chimbiriri and Balenje, *Sclerocarya caffra*, *Crossopteryx febrifuga*, *Combretum* species, *Manilkara mochisia* and the occasional *Brachystegia boehmi*; *Pseudolachnostylis* and *Xeroderris* are common.

Type 2: On clay soils, drying hard and slightly alkaline, the following are common: *Dalbergia melanoxylon*, *Acacia nigrescens*, *Albizia harveyi*, *Dobera glabra*, *Berchemia discolor*, *Sclerocarya caffra*, *Combretum* species, *Lonchocarpus capassa* and *L. eriocalyx*; *Combretum imberbe* and *Balanites aegyptiaca* in some lower areas. *Mimusops schliebenii*, *Manilkara mochisia* and *Tamarindus* are common on anthills. The occasional water pan occurs with fringing thicket. The baobab and *Sterculia africana* are characteristic elements.

In both types the shrub layer is poorly developed. *Diospyros usumbarensis*, *Ziziphus* spp., *Turraea nilotica* and *Cassia auriculata* are common. *Acacia nilctica* and *A. robusta* occur.

Grasses vary from tall *Themeda*, *Hyparrhenia*, *Loudetia* communities to medium height *Hereropogon contortus* and *Digitaria milanjiana* on heavier soils. *Panicum infestum* is common in shade.

C.7 Stunted Woodland on Stony Slopes:

Common in other parts of the Selous, here restricted to small areas near Balenje and from Nunga to Mpapule. Stunted *Julbernardia* and *Brachystegia boehmi* occur. *Uapaca nitida* is restricted to this community in this area. *Diospyros bussei* and *Dalbergia melanoxylon* are common, as is *Acacia robusta*. *Alloteropsis semialata* is a characteristic grass species.

D.1 Terminalia spinosa-Spirostachys Wooded Short Grassland:

The dominant vegetation type on alkaline, poorly-drained, sandy clay soils in the absence of thicket.

Terminalia spinosa is the characteristic dominant, although in some areas it gives way to pure *Spirostachys africara*.

Other common trees are *Acacia nigrescens*, *Afzelia*, *Sterculia africana*, *Cassia abbreviata*, *Albizia harveyi*, *Sclerocarya caffra*, *Dobera glabra* and, on anthills, *Tamarindus*, *Euphorbia candelabrum*, *Mimusops schliebenii*, *Manilkara mochisia* and *Berchemia discolor*.

Common small trees and shrubs are *Diospyros usambarensis*, *Cassia auriculata*, *Acacia senegal*, *A. zanzibarica*, *A. robusta* and *A. gerrardii*; *Dalbergia melanoxylon*, *Turraea nilotica*, *Markhamia acuminata* and *Combretum hereroense*.

The grass cover is short, usually less than 60 cms., and sweet. Common species are *Sporobolus ioclados*, *Digitaria milanjiana*, *Panicum infestum* and many annual species of *Eragrostis*, *Brachiaria*, *Dactyloctenium*, *Urochloa*, *Aristida* and *Chloris*. Sedges, especially *Mariscus mollipes*, are common. The herb layer is dominated by *Cyathula lanceolata*, *Heliotropium strigosum*, *Cassia mimosoides*, and *Tephrosia pumila*. Patches of ungrazed fire-resistant *Bothriochloa pertusa* are a characteristic feature of some areas.

To the south on harder soils, trees, especially *Terminalia spinosa*, become less conspicuous, although several dead stumps indicate greater densities in the past. The grass cover becomes more dense and dominated by *Heteropogon contortus* and *Digitaria milanjiana*.

Several permanent and semi-permanent water pans occur with a fringing thicket of *Markhamia acuminata*, *Lamprothamnus* and *Polysphaeria*, and trees of *Mimusops* and *Tamarindus* and the occasional baobab.

D.2 Acacia-Combretum Shrub Short Grassland:

Small areas in the vicinity of the Miombo Research Centre headquarters show a community dominated by *Acacia robusta*, *A. senegal*, and *A. gerrardii*. *Combretum hereroense* and some *C. zeyheri* are present. Both *Terminala spinosa* and *Spirostachys africana* are absent.

D.3 Cassia-Combretum Shrub Medium Grassland:

Running across types D.1 and D.2 are low sandy ridges which bear a characteristic vegetation type. Both *Terminala spinosa* and *Spirostachys* are absent, and common trees are *Xeroderris*, *Sclerocarya* and the occasional *Pseudolachnostylis*, *Burkea*, *Lonchocarpus eriocalyx* and *Lannea stuhlmannii*. *Combretum zeyheri*, *C. molle* and *Cassia auriculata* dominate the shrub layer, with some *Diospyros usumbarensis*, *Turraea nilotica* and both *Markhamia acuminata* and *M. obtusifolia*.

Grasses are dense, and chiefly *Themeda*, *Heteropogon* and *Hyparrhenia* spp., with some *Panicum infestum* in shade. *Astripomoea malvacea* is dominant in the herb layer.

E.1 Seasonally Flooded Tall Grass Swamp:

Occurs in two major localities, the main flood plain of the upper Lungonyo River (c.125 km^2) and a smaller plain at Nangue (c. 25 km^2).

Nangue is dominated by *Setaria sphacelata*, *Echinochloa haploclada* and *Andropogon gayanus*. Several dead trees stumps (mainly *Dalbergia melanoxylon*) indicate a possible recent increase in area.

The Lungonyo flood plain is bordered by trees of *Combretum imberbe* and *Balanites aegyptiaca*. The larger channels are bordered by *Combretum constrictum*.

Grass dominants are *Echinochloa haploclada*, *Ischaemum afrum*, *Setaria sphacelata*, *Andropogon gayanus*, *Bothriochloa glabra* and *Vetiveria nigritana* and *V. zizaniodes*. The edges are characteristically *Echinochloa*, *Themeda* and *Digitaria milanjiana*, and tussock *Sporobolus* such as *S. pyramidalis*; *Imperata cylindrica* occurs in small areas.

There is a rich herb flora and occasional outcrops of *Sesbania hirtistyla* and *Aeschynomene* spp.

F.1 Ant Hill Communities:

These present a very diverse flora, only partially related to the surrounding community. In general, anthills provide a more alkaline, base rich habitat and this is reflected by the vegetation cover.

Tamarindus, *Mimusops schliebenii* and *Manilkara mochisia* have already been mentioned as common anthill trees. Smaller trees are *Commiphora* spp., *Salvadora*, *Cleistochlamys*, *Ziziphus* spp., including *Z. pubescens*, and *Ehretia amoena* and *Cordia* spp. *Euphorbia candelabrum* and several fleshy climbers are common, as are species of *Pavetta* and other *Rubiceae*. Grasses are often sweet, and include *Leptochloa*, *Cynodon*, *Sporobolous* and *Chloris virgata*.

3.2. COMPUTER ANALYSIS OF THE GROUND LAYER VEGETATION

3.20. Introduction.

During the course of the study the ground layer vegetation was analysed quantitatively in order to stimulate plant collecting, gather base line data for species composition change and to be able to describe and compare different plant communities and associations. Analysis was undertaken by random quadrats and assessing plant presence or absence and percentage frequency for each site. In 1970 I decided to extend these assessments into a grid coverage of the entire study area and to analyse such data by standard computer techniques (Kershaw 1973; Greig-Smith 1964). The analysis was intended to show ecological relationships between different species and different sites of the study area,,and to compare the computer generated association map with the more subjective vegetation map on figure 3.2.

This section describes the field data collection, presents the computer analysis results and discusses the biological value of these results. Details of computer techniques, programmes, choice of methods and parameters etc are given in appendix 4.

3.21. Field Methods.

Data were collected at each mile post along the road transect system of the study area. This system was designed for animal census and is described in chapter 5. Five transects were used: Lihangwa, Kilunda, Chimbiriri, Malemba and Mwende with 30, 25, 18, 11 and 25 sites respectively, (total 109 sites). In addition 68 sites along a transect network in a miombo catenary system were analysed. Four transects of 20, 18, 18 and 12 sites, each 300m apart on transects 1000m apart were used. This transect system is described in chapter 6. Later in the study a transect of 33 sites across the Lungonyo floodplain and 6 additional sites in minor associations were analysed. This gave a total of 216 sites examined between 1970 and 1973 in the months of March and April when most grasses and herbs were flowering.

At each site 100 quadrats (25cm square) were thrown in a pattern of 25 quadrats per compass quadrant within 100m of the site central mile post or marker. Quadrats landing on bare soil, litter, trails, wallows etc were discarded. Each quadrat was examined for herbaceous species rooting within the square and each species was identified and tabulated. Data could be expressed as presence/absence for each site and as species percentage frequency for each site. In 1973 only 33 quadrats were thrown per site in the relatively homogenous vegetation along the woodland parts of Lihangwa transect and the floodplain transect.

Within the miombo catena system woody vegetation was analysed by tabulating all tree and shrub species over 25cm high within a 15m radius circle around the marker for each site. These plots were used only for presence/absence data a total of 108 species (ignoring those occurring in less than 3 of the sites) were used for the ground layer analysis, and 42 woody species were used for the miombo catenary system.

3.22. Computer Analysis.

Data were analysed in late 1974 at the Botany Department of the University College of Wales, Aberystwyth, using prepared programme modules. Programmes were available for classification analysis (using only presence/absence data) and ordination analysis (using both presence/absence data and the quantitative data of percentage frequency). Details of these techniques and their application are described in appendix 4.

Classification programmes involved the use of association analysis in both the normal and inverse modes and also cluster or constellation analysis. Association analysis examines the levels of chi-square correlations between pairs of species or sites and in the normal mode produces groupings of sites with similar floral characteristics and in the inverse mode produces groupings of species with similar site characteristics. Cluster analysis involves the plotting of species chi-square correlations into a web of constellation of species linkages, a technique used by Welch (1960) in his study on the woodland vegetation of Morogoro, East Tanzania.

The complete data set was analysed first and this, as expected, split the data into separate formations; the floodplain, the wooded grassland and the woodland system. Following this the data for each formation, as determined by the computer, plus adjacent sites as "edge areas" were analysed separately. This technique was followed for normal and inverse analysis and cluster analysis. The miombo catena data were run separately and together with the woodland data from the grid transects.

The ordination technique chosen was principal component analysis, but due to data size limitations this was run for the woodland set, the miombo catena set and the flood plain set using percentage frequency data. The flood plain data was also analysed using presence/absence criteria. Principal component analysis examines the variance-covariance matrix of species or sites pairs and generates gradients of variation which can be portrayed linearly with the variables ranked along the gradient. Output is in the form of two dimensional (two gradients of variation) graph plots of either sites in normal analysis, or species in inverse analysis. The proximity of such species or sites on the plot is taken as an indication of their ecological similarity.

3.231. Results.

3.231 Classification Techniques.

3.2311 The total data set.

The complete data matrix of 109 species and 216 sites was analysed. Normal analysis resulted in 12 associations or groups of sites of similar floristic composition. The first division was on Brachiaria leucranthra at a high level of total chi square and this split off 68 sites of the wooded grassland formation. The second division on Ischaemum afrum removed 12 flood plain sites and a later major division on Hyparrhenia divided the woodland formation into 49 valley sites and 71 upland sites. A dendrogram of the hierarchy of divisions is shown in figure 3.3A. The chi-square levels are scaled which tends to mask the high level of the primary division into alkaline soil sites and others. As there are no further divisions until a much lower level of chi-square, this grouping is relatively homogenous.

The spatial distribution of sites into the 12 associations is shown in figure 3.3B, and the associations can be classified as shown in table 3.1.

The inverse analysis produced 12 associations or groups of similar species. The first split at a very high level of chi square out off a group of 8 woodland perennial grasses with no further division, indicating a high degree of similarity. The second split, also at high chi square level, out off 16 alkaline terrace species but subdivided them at a low chi square level into 3 subgroups of little apparent ecological meaning. Further divisions at lower significance levels split off 2 floodplain groups, one from the centre and one from the edge, 2 Combretum ridge groups, 3 woodland forbs and short grasses groups and a large "noise" group of species of little information content.

The dendrogram of divisions is shown in figure 3.4 and group species composition in table 3.2.

The constellation diagram of species affinities as determined by cluster analysis is shown in figure 3.5.

Five major clusters of species are shown, one for the flood plain, three for the wooded grassland and one for the woodland habitat. These clusters are shown as circles in figure 3.5 and the letters in the circles refer to association groups as determined by inverse association analysis. A few major species are shown to characterise each grouping. The notation 'n' and 'd' under each circle indicates the number of species making up the cluster and the density of species linkages within the cluster. For example, if every single species of the cluster was significantly associated (a positive chi square level) with every other species then 'd' would equal 1.0; a 'd' of 0.8 indicates 80% of the possible linkages do occur. It is evident that the 3 grassland clusters have more species associations than the 2 woodland clusters.

Each cluster is related to other clusters by intermediate species which are shown in figure 3.5. The intermediate species have positive associations with species in both the adjoining clusters; for example *Echinochloa haploclada* is a constituent of both the flood plain and the wooded grasslands.

3.2312. The flood plain data set.

This data set contained 18 sites and 42 species. The sites were 12 designated as the floodplain unit under the total data set and 6 edge sites of the wooded grassland.

Normal association analysis produced 3 associations; a central floodplain community of 8 sites characterised by *Andropogon gayanus*, C; an edge community of 5 sites characterised by *Mariscus mollipes*, A; and an intermediate community of 5 sites, B.

Inverse analysis produced 7 groups of species, but ignoring divisions at low chi square levels 4 ecological groups of species can be picked out. These groupings are shown in table 3.3.

Cluster analysis (fig. 3.5) shows 3 groupings: a discrete edge community of wooded grassland species labelled D in the figure and in table 3.3, a group of herbs from the periphery of the flood plain, labelled C, and a central swamp group of grasses and herbs only roughly divisible into the A and B communities of inverse association analysis.

3.2313. The scattered tree grassland data set.

This data set consisted of 81 sites and 78 species. Normal analysis showed 9 groups of sites. The dendrogram of divisions is shown in figure 3.6 and a table of group characteristics in table 3.4. The first division splits off 18 sites which are ectonal with the woodland formation. *Borreria subvulgata*, a herb of *Combretum* ridges, is the divisive species. The second split removes 14 species without *Brachiaria leucrantlra* as a "noise" grouping. These sites border the flood plain and include the Hyparrhenia communities to the south of the wooded grassland area. The third division seperates 12 sites with *Indigofera* which resemble the *Borreria* sites and include the *Combretum* - *Cassia* ridge communities. The remaining 35 sites, equivalent to the D, E&F groups of the total data set are relatively homogenous and are split at lower chi square levels into 6 small communities.

Inverse analysis produced 13 groups of species classifiable as 4 ecological groups and one large noise group. The dendrogram is shown in figure 3.7 and the species groupings in table 3.5.

Cluster analysis, as shown in figure 3.5, produced 2 discrete constellations, relating to groups A-F and H-I of the association analysis and two lesser groups with affinities to the flood plain and woodland habitats.

3.2314. The woodland data set (including the miombo catena data).

The data set consisted of 132 quadrats and 78 species. Normal association analysis produced 6 groups of sites, with all divisions well above the minimum level of chi square. The first division, on Heliotropium strigosum split off 5 sites which are ecotonal to the wooded grasslands and the second division on Hyparrhenia virtually separated the miombo catena sites from the rest. Further subdivisions removed small groups of sites on rather uncommon species. The dendrogram is shown in figure 3.8 and the site groups tabulated in table 3.6.

Inverse association analysis was rather unsatisfactory due to the "chaining effect" in the divisions (see appendix 4). Ten groups of species were produced. The first group comprising ~~the~~ woodland tall grasses and sedges, split off at a chi square level nearly 4 times as high as the next split. It is of interest in that the woodland tall grasses are separated from the forbs and shorter grasses as was done in the total data set. The dendrogram is shown in figure 3.9 and species groups listed in table 3.7.

Cluster analysis produced a complex array of linkages with many negative and few very high positive associations. One tight cluster of 16 species is associated with the ridge communities of the wooded grassland and also with the 'valley' communities (Hyparrhenia, Heteropogon) of the woodlands. There is a diffuse grouping of tall grasses associated with two different groups of forbs, but linkage chi-square values are not high.

3.2315. The miombo catena: ground layer and woody species data sets.

This combined data set was composed of 68 sites and 90 species (42 woody species and 48 herbs). As woody and herbaceous data were collected by different methods and at different times inverse analysis was not attempted. Normal analysis produced 13 groups of sites, 7 groups (38 sites) with Brachystegia spiciformis, the first division species, and 6 groups (30 sites) without. Of the 12 division species only 3 were herbs. It was felt that the small quadrat size (710m^2), tended to exclude tree species and as such site classification on the basis of species presence or absence was not feasible. Many groups produced by association analysis were heterogenous.

Cluster analysis of the combined data set did produce data of value, although 35% of all associations were negative.

The constellation diagram is shown in figure 3.10; two seperate groups are formed, a small' 'valley' group and a much larger woodland group. The woodland group is dominated by a 'ring' of miombo species ($n=11, d=0.51$) with a thicket grouping to the right, *Euclea* and *Markhamia* and a chipya group to the top with *Andropogon*, *Tristachya* etc.

Association analysis of the ground layer data set gave 10 site groups in the normal mode; the first split on *Panicum infestum* giving 12 valley sites and 56 upland sites. The dendrogram of divisions is shown in figure 3.11 and the site groups are classified in table 3.8. Inverse analysis was not run for this data set.

3.232. Principal Components Analysis (P.C.A)

Details of terminology and the basis of the PCA technique are given in appendix 4. Table 3.9 gives analytical data for all the PCA analyses described below.

3.2321. The floodplain data set.

This analysis utilised the same 18 sites and 42 species as the association analysis.

Normal P.C.A. clearly showed a separation of sites which gave general agreement with the sites separated by association analysis. The first axis contained over 35% of the data variance and for both the frequency and presence/absence analyses, the loading species for the first axis were a wooded grassland and a major floodplain grass species. Both analyses emphasised the difference of sites 1 and 2 which was not brought out in association analysis. The two analyses are shown in figure 3.12. The 3 groupings of the association analysis A, B and C are shown in the diagram.

Inverse P.C.A. using the presence/absence criteria worked well, separating species into groups readily identifiable with the groupings of inverse association analysis.

P.C.A. using % frequency data presented a problem, in that dominant grass species which have a high % frequency suppress the information of the rarer smaller grasses and herbs, which tend to cluster at the negative side of the graph plot axis origin. This tendency is repeated for the woodland and for the miombo catena data sets for inverse P.C.A. All graph plots raveal a characteristic pattern similar to a "proportional sign", with the arms including dominant grasses and the fulcrum all the small plants of low cover and low % frequency values.

Enlargement of the graph plot scale around the origin does show that species are grouped into ecological entities, but these are completely masked by the dominant grasses. Graph plots for both criteria are shown in figure 3.13.

For both normal mode P.C.A.s it is fairly obvious that the first components reflects the major ecological changes from the wooded grassland (sites 1 and 2) to the central floodplain, these changes being an increase in moisture and an increase in clay content. The second component is more difficult to assess and appears to differ between the P/A and the % frequency plots. Note from table 3.9 that the proportions of the variance explained by the first components are similar but differ for the second components for the P/A plot and the % frequency plot. Loading species for the second component are in both cases species from the central flood plain against species from the flood plain margin, so this component is not to do with the great disparity between flood plain and grassland communities.

For the inverse presence/absence plot the components are not readily identifiable in environmental terms, despite the first component accounting for 45% of the variance. Site loadings are positive on grassland sites and negative on the edge/central sites, but the species associated with the central sites are placed in an intermediate position.

The inverse % frequency plot appears to be dominated by species of high frequency of occurrence, and whilst species are ordered in groups identifiable with association analysis groups, it is not possible to pick out ecological criteria for the components.

3.2322. The woodland data set.

The restriction of data matrix size for P.C.A. resulted in the exclusion of all but 65 woodland sites, made up from Kilunda, Lihangwa, Chimbiri, Malemba and the first (out of four) of the miombo catena transects. 62 species were used.

Normal PCA resulted in a satisfactory spread of sites but beyond a separation of the miombo catena sites and a partial separation of valley sites, the sites are not sharply divided. The variance content of the first two axes is only 35% of the total and loading species are *Andropogon* and *Hyparrhenia* on the first axis and *Panicum* and *Andropogon* on the second, possibly showing an ordering into "dryness/wetness" and "miombo/chipya" respectively. The graph plot is shown in figure 3.14.

Inverse PCA showed the same trend as the floodplain plot in that 8 grasses and sedges dominate, leaving an extremely tight cluster of smaller plants at the negative side of the origin. The major grass species do show a dry trend and a wet trend with *Panicum maximum* in an intermediate position. It is of interest to note that the grasses with the highest value on the first axis, *Andropogon*, *Digitaria* and *Panicum* are not restricted to the woodland community but are commonly found in the alkaline wooded grassland as well. The graph plot is shown in figure 3.15.

3.2323. The miombo catena data set.

All 68 sites and 44 ground layer species were included for analysis (woody species had no % frequency data).

Normal PCA gave a good spread of sites but with little ecological meaning except a separation of valley sites. Variance content of the first two axes totalled 39% and species loadings were <u>Andropogon/Panicum</u> and <u>Panicum/Loudetia arundinacea</u> respectively showing a possible ordering into miombo/chipya and upland/valley sites.

Inverse PCA showed a domination by tall grasses and a near origin cluster of smaller grasses and forbs. The spread of grasses shows a separation of upland and valley species. Normal and inverse plots are shown in figures 3.16 and 3.17.

3.24. Discussion and Conclusions.

A discussion of the computer programmes and analytical techiques is contained in appendix 4. This section deals only with the results. Methods of classification and ordination undertake the "mathematical sorting" of biological data; as such the interpretation of results needs considerable care. Changes in the preset termination levels for analysis (number of species occurrences, chi square levels etc) can lead to considerable differences in the computer output of results.

As was expected the analysis of the total data set showed the study area vegetation to be highly stratified and classification produced little more than the major formations with their linkage or transitional species. This sharp stratification is shown clearly in the cluster analysis diagram of figure 3.5. The gross homogeneity of these formation clusters masked internal relationships at the total data set level.

Comparing the associations of sites produced by N.A.A. (fig 3.3B) with the subjective vegetation categories of the map in figure 3.2 shows a high similarity. Use of a simple matching coefficient, (Sokal and Sneath, 1963).

$$\text{where} \quad S = \frac{\text{No. of agreements (+ve or -ve)}}{\text{No. of characters (sites)}} \times 100$$

gave a similarity of 72.4%. The similarity can only be partial as the vegetation was mapped mainly by reference to the woody vegetation and the computer analysis was confined to ground layer data.

Within the confines of the technique the wooded grassland formation proved the most complex system, showing a tenuous link with the floodplain communities through such species as <u>Echinochloa</u> and <u>Eriochloa</u> and a much stronger link to the woodland system through the *Combretum* ridge communities which are clearly ecotonal or transitional.,The placing of *Themeda* and *Heteropogon* is of interest as these two species occur in two distinct habitats, the *Combretum* ridges (giving way to *Andropogon* closer to the woodlands) and the flat, hard, clay sands to the south of the study area.

The profusion of small associations from both NAA and IAA for the wooded grasslands is difficult to explain. One division appears to be the broad-leaved, more nutritious species of less disturbed (less grazing pressure?) or more fertile sites, eg. *Brachiaria*, *Sporobolus*, *Urochloa* (table 3.5), as opposed to the *Chloris*, *Cyathula*, *Euphorbia* group typical of highly grazed sites. The many groups typical of the *Combretum* ridges may represent a gradient or successiorary series to the woodland communities.

The floodplain community is relatively simple (possibly due to less "noise" from a single transect at right angles to the gradient). The edge sites of the wooded grasslands are separated immediately by all analyses and the community boundary is very sharp. PCA further divides these grassland sites into 2 groups, a group of sites 1 and 2 and a group of sites 3, 4, 5 and 6.

The woodlands as analysed here have few internal groupings or relatively few positive associations in the cluster analysis. This may be attributable to:-

1) The dominance in real terms and by number of occurrences of five grass species: Andropogon, Tristachya, Schizachyrium, Panicium and Digitaria, these species tend to show only negative associations.
2) The low occurrence and seemingly random distribution of forbs and smaller grasses.
3) The low mean number of species per site (11.8 compared with 21.4 for the wooded grassland).
4) The relative homogeneity of the formation.

It is of interest that the inverse PCA produced axes of greater variance content than the normal PCA. Figures for each formation are shown in table 3.9. As the first axis is much greater than the second for inverse PCA, this seems to indicate that species may be responding heavily towards one environmental factor, whereas sites can only be characterised by several factors of less individual importance.

In conclusion it can be stated that the objective analysis of the herbaceous vegetation has revealed patterns that are understandable in ecological terms and are in agreement with the earlier more subjective survey and delimitation of vegetation associations. The apparent lack of internal communities within the large woodland formation and the close association of most species (figure 3.10) indicates the formation is a continuum of possibly several successional stages and not an assemblage of discrete communities separated by edaphic or topographic factors. This point is discussed in greater detail in later sections of this chapter.

SECTION 3.3. FLORISTIC COMPOSITION AND AFFINITIES

3.30. Introduction.

Plant collections in the Selous have shown the heterogeneity of the vegetation with elements of the Kenyan, Mozambican and Zambia floras common in certain habitats. It was considered of value to assess quantitatively the level of these inclusions and to show the degree of similarity and affinity with major floristic zones. As the Selous is close to the North eastern limit of miombo woodland such an analysis is necessary to describe the Selous flora in phyto-geographical terms.

This section also analyses the flora in terms of numbers and sizes of taxonomic units.

3.31. Methods.

The herbarium collection and plant species list was checked to provide data on botanical family and genus content and size. The checklist (appendix 3) and punch card sorting system (as illustrated in figure 3.1) was used to compare the woody element of this flora (as known in 1973, and including taxa identified to species level only) with the

Kenyan flora, Dale and Greenway (1961), and with the Zambian flora, White (1962), to show similarities or affinities in plant species composition. Similar comparisons were made with smaller area check lists from Zambia, Lawton (1963) and Fanshawe (1960-1969), and from Tanzania, Harris (1970).

It was not possible to carry out statistical analyses of affinity and similarity as described by Exell and Wild (1961) as no comparable species lists were available for areas of similar size to this study area. However, simple percentile similarity figures were obtained by using Sokal & Sneath's (1963) formula of:

$$S(\%) = \frac{N}{N + D} \times 100.$$

where S is coefficient of similarity, N is the number of shared species and D the number of different species.

White (1965) described phytogeographical regions for the African woodlands and showed quantitative similarities and dissimilarities between the West and Central African woodlands. His paper and accompanying species list of savanna and woodland trees served as a basis to compare the Selous flora with the Zambezian and Sudanian phytogeographical domains. Selous species were checked against the distributions in White's list and tables of similarity drawn up.

3.32. Results.

To date (1 January 1977) using Vollesen's additions to the checklist of Rodgers and Ludanga (1973) 1250 species of vascular plants have been collected from the immediate study area. This compares with a present collection of 1800 species from the whole of the Selous Game Reserve, Vollesen (pers. comm.); and an estimated 10,000 species for the flora of Tanzania, Wingfield (pers. comm.). The study area flora is contained in 118 families and 541 genera.

Of these families; 53 contain 1 genus, 41 contain 2 to 5 genera and 24 contain more than 5 genera. The largest families are: Gramineae (135 species), Rubiaceae (75), Cyperaceae (48), Euphorbiaceae (57), and Papillionaceae (101).

Of the genera, 326 contain 1 species, 175 contain 2-5 species and 40 contain more than 5 species. The largest genera are: Indigofera (19 species), Crotalaria (16), *Combretum* (   ), *Ipomoea* (18), *Vernonia* (13), *Acacia* (13) and *Cassia* (11). Note that *Indigofera* and *Crotalaria* are the two largest genera in East Africa.

A total of 135 grasses have been collected, including 42 annuals and 155 legumes. Note that herbs and sedges are under represented in this collection as compared with woody elements and grasses. It is probable that the riverine and thicket associations, with many species that flower irregularly, are under-collected as compared to the woodland and grassland associations.

The Eastern Selous flora as described in this thesis shows strong affinities to both the Kenyan (mainly coastal) flora and the Zambian flora. 323 woody species from this study area were used to assess the affinities quantitatively. Of the 323 species:

64 did not occur in Kenya or Zambia,
95 occurred in both Kenya and Zambia,
93 occurred in Kenya but not Zambia,
71 occurred in Zambia but not Kenya,
188 occurred in Kenya (total), and
166 occurred in Zambia (total).

Sneath's coefficient of similarity shows that this study area has comparable levels of similarity with both Kenya and Zambia, eg. E. Selous and Kenya: 58.2%

E. Selous and Zambia: 51.4%.

However, closer examination of separate vegetation types reveals a very different picture. The woodland elements of this area show a close affinity to Zambia (especially the legumes), and the thickets and riverine communities show a close affinity to Kenya.

eg. E. Selous woodland species (total 108);

E. Selous and Kenya 45%

E. Selous and Zambia 79%

E. Selous thicket, riverine and ground water forest species (total 251)

E. Selous and Kenya 63%

E. Selous and Zambia 37%

Note that some species in the eastern Selous are found in both vegetation types and so are included in both comparisons.

Comparison of the species restricted to Kenya or Zambia showed that:

Of the 93 species restricted to Kenya (50 to the Coast Province);

10% are miombo species

43% are riverine species
42% are thicket species
20% are ground water forest species
8% are legumes.

Of the 71 species restricted to Zambia;

64% are miombo species
18% are riverine species
20% are thicket species
1% is a ground water forest species
37% are legumes.

Analysis of vegetation checklists from smaller areas in Zambia reveals a close similarity with the woodland flora but little with the thicket or riverine floras. From the brief species lists of Lawton (1963), out of 47 species from Brachystegia woodland 62% occur here; out of 46 chipya species 67% occur here; whilst of 70 riverine and forest species only 13% occur here. Similar patterns emerge from the Zambian district species lists of Fanshawe (1960-69).

Comparison with a species list from the University campus of Dar es Salaam, Harris (1970), shows that out of

402 identified indigenous species, 48% also occur in this study area. A comparison of the Ruaha National Park's flora (Central Tanzania), with this study area's complete flora (as per 1973, 894 species) by Bjornstadt (1976), showed a 44% similarity.

White's (1965) list includes 132 tree species found within the Selous. Of these 2 were present in West Africa and not in Zambia, 86 were present in Zambia and not in West Africa and 48 were common to both. Of the 134 species common to Zambia, White notes that 38 are widespread, 35 are miombo species and 24 are _Acacia_ - _Combretum_ - _Terminalia_ woodland/wooded grassland species. No Selous species are recorded in the Katangan or Barotse centres of endemism but 29 are common to the Kariban centre of endemism (species confined to low lying hot valleys). Ten Selous species have small restricted distributions in Zambia. Only 7 species are constituents of thickets in Zambia.

3.33. Discussion.

The ecological system in this study area is closely duplicated through central and southern Africa. Upland ridges of miombo and chipya woodland interspersed with areas of thicket and forest, descending to an alkaline river terrace of more open scattered tree grassland and shrubland and eventually to a riverine system of channels or floodplains are a common pattern. The Ruvuma valley in southern Tanzania has many resemblances (Rodgers aerial survey). The Luangwa valley of Zambia (Astle et al 1970), the Zambezi valley, (Jarman pers. comm.); the Saabi-Lund valley of Rhodesia (Farrell 1968 and Rattray and Wild 1964), and the areas surrounding the Kruger National Park in South Africa, (Hirst 1975)· all duplicate many of the land systems, vegetation communities, genera and very often the species of this study area.

I was able to see these similarities on a visit to South Luangwa National Park in Zambia in March 1970. In Luangwa a plateau woodland of *Brachystegia* species descends over a steep escarpment with patches of scarp forest and thicket, through a transitional *Combretum* - *Terminalia* zone to a flat highly alkaline wooded grassland with a short mixed annual perennial grass cover. *Terminalia spinosa* is replaced in Zambia and Rhodesia by *Colophospermum mopane* (Kirk ex Benth) Kirk, a tree of very similar habit and ecology. This association merges into the Luangwa river communities of floodplains and lagoons.

Farrell (1968) describes several vegetation communities in the Saabi - Lund system which closely resemble this study area, in particular the *Pteleopsis* - *Millettia* - *Spirostachys* woodland and thicket systems. The *Brachystegia glaucescens* (a southern ecotype of *B. microphylla* (White 1962), thicket is similar in distribution, ecology and species composition to *B. microphylla* thickets here. The Saabi - Lund area contains several coastal elements of the Mozambique flora and the riverine and *Acacia* scrub associations show strong affinities to this area.

Plant collections from this study area, and even more from the south Selous (Rees specimens, lodged in the MRC herbarium) illustrate the strong link between the Selous and Mozambique floras, with the Selous collections turning up several new E. African species which are common in Mozambique. These species tend to be restricted to riverine or thicket habitats.

Similarly, the coastal forests of Kenya as described by Dale (1939) and Moomaw (1960), show strong affinities to the Selous forests. In particular the Boni forest of Kenya, Dale's Evergreen Dry Forest and Moomaw's *Manilkara* - *Diospyros* Lowland Dry Forest, resembles the coastal thickets on alkaline clay sands described here. Moomaw's *Manilkara* -

Cynometra Lowland Dry Forest resembles the coastal evergreen forests of this area. The woodland forest system of Kenya's Shimba Hills Game Reserve has strong similarities with this area and many of the woodland trees and grasses are the same.

To conclude it seems probable that in historic times the Selous was covered by forest and thicket communities which are now more restricted to the coastal areas of East and Central Africa. The postulated climax and past forest cover for Central Africa of Khaya - Trichilia - Diospyros (see section 5 of this chapter) possibly did not reach the drier areas of the coast, but are now more common in the West Selous and South and Western Tanzania in areas of higher rainfall.

With the decrease in forest cover as a result of climate amelioration and human activities, the predominantly coastal forests have given way to woodland systems with origins in the Zambian flora. Thus the Selous has a bivalent flora with past links to Kenya and the coast in its thicket and riverine communities and more recent affinities to Zambia in the woodland communities.

In phytogeographical terms the Selous is an integral part of the Zambezian Domain with a low index of similarity with the Soudanian Domain. The affinities with the Zambezian flora are through the miombo and wooded grassland floras, not through the riverine or thicket floras. There is no contact with the western (Katanga and Barotse) centres of endemism. Superimposed on the dominance of the Zambezian Domain is the strong influence of the coastal flora (especially in the thicket/forest formations) with elements of both the Kenya and Mozambique floras.

3.4. VEGETATION AND THE ENVIRONMENT.

3.40. Introduction.

This section describes the distribution of the vegetation formations and associations with regard to the environmental factors of soil and topography. Such factors affect vegetation not only at the association level but also at community and individual species levels. Soil and topographic factors have been described in chapter two and are not discussed in detail here.

The section concludes with a discussion of the topics of the vegetation catena, the distribution patterns of the miombo and chipya woodlands, an ecological classification of grasses, the phenonoma of spatial and temporal grassland mosaics and a brief analysis of factors affecting the annual or perennial nature of grassland composition.

3.41. Methods.

Formation and association distribution patterns were examined by drawing scaled profile diagrams across the whole or parts of the study area from published 1:50,000 contour maps. Vegetation boundaries were superimposed on these diagrams by reference to air photographs or composite air photograph mosaics.

The woodland thicket systems were further analysed for slope position by selecting random points on air photograph stereo pairs and allotting such points to three slope positions: upper, middle and valley; and three vegetation associations, thicket, miombo and chipya. Some 272 points were so chosen and data analysed by a 3 x 3 chi square contingency table. Points falling on other minor communities or community boundaries were ignored.

Finally, and as was mentioned in chapter 2, soil samples from 10cm depth from 56 woodland sites in the eastern Selous and from 110 transect mile posts in the study area were analysed for pH and clay content. Vegetation at these sites was assigned to the association types listed in chapter 3.1.

3.42. Results.

3.421. Profile Diagrams.

a) Distribution at the formation level.

Scaled East-West profile diagrams were drawn for every 15' of lattitude across the study area. One example, for 9^{o}S., is shown as figure 3.18. These diagrams showed that grasslands are confined to low lying flats or flood plains.

The wooded and shrubbed grasslands are confined to the alkaline river terrace and the woodlands are confined to the upland areas of Karoo sandstones. The thicket and forest patches (excluding riverine or groundwater communities) were restricted to the karoo sandstones and usually to the upper slopes or ridge tops. Formation distribution is thus topographically (and edaphically) controlled.

(b) Distribution at the community level.

Profile diagrams across a steep valley ridge system (A-B), across the miombo catena system (C-D), and across the alkaline river terrace (E-F) are shown in figures 3.19, 3.20 and 3.21 respectively. Letters in brackets identify these profiles on figure 1.3.

Examination of these (and other) profiles shows the following features:

1) Within the Forest/Thicket formation
   (a) Coastal dry forest is restricted to the western watershed on flat topped ridges.
   (b) <u>Brachystegia</u> <u>microphylla</u> thicket is confined to steep scarp slopes on shallow stony soils.
   (c) Costal dry thickets on sandy soils are absent from valley areas.

2) Within the Woodland formation.

There is virtually no difference between the various associations as to their topographic position. Valley communities are, of course restricted.

3) Within the Wooded Grassland formation.

(a) Cassia - Combretum communities are restricted to the low ridges of sandy loam traversing the river terrace.

(b) Terminalia - Spirostachys communities are restricted to the river terrace. These communities also contain small areas of wetter conditions with their characteristic species which are not mappable. The profile diagram of 3.21 illustrates these communities.

(c) Distribution at the species level.

All species can be defined in terms of their autecology and distribution, but only three grass species are given here as an example.

1) Sporobolus virginicus is confined to saline seepages
2) Oxytenanthera abyssinica (bamboo) is confined to steep rocky gorges.
3) Alloteropsis semialata is confined to rocky shallow soil hillocks.

(d) The effect of treeshade.

A transect of contiguous 25cm square quadrats across a patch of dense tree shade (Cassia abbreviata) from the wooded grassland is shown in figure 3.32. Broad-leaved grasses such as Panicum infestum and Urochloa trichopus tend to dominate in the moister area of tree shade.

3.422. Woodland associations and topography.

The 3x3 chi-square contingency table for 272 points analysed on stereo photo pairs is shown in table 3.10.

Comparing expected with observed values, the thickets show a significant association with the upper slopes, miombo woodland middle and lower slopes, and chipya occurs with equal frequency in all positions.

3.423. Vegetation association and soil types.

Results for all 166 sites are shown in table 3.11. There is no significant difference between miombo and chipya distribution in terms of soil acidity and clay content. Wooded grassland and shrubbed grassland associations are dominant on sites of higher alkalinity and clay with the Terminalia - Spirostachys community areas showing especially high alkalinities.

3.43. Discussion.

3.431. The vegetation catena.

The concept of a soil catena was discussed in chapter 2.2.

Vegetation communities are associated with such soil and topographic sequences, especially on the karoo sandstones where the relief is greater than on the flat river terrace and floodplain. Burtt (1942) showed the existence of vegetation catenas both on a small scale within a woodland association and on a larger scale from formation to formation. The distribution of associations as shown in figures 3.18 to 3.21 may be described as catenary.

Howard (1970) discusses the miombo woodland - *Combretum* woodland - clay soil grassy mbuga sequence so typical of the western Tanzania miombo formation type. In this case the *Combretum* woodlands are transitional on the lower slopes of the toposequence. *Combretum* woodlands on the large scale appear to be transitional between the miombo and *Acacia* - *Commiphora* formation types in Central and Western Tanzania.

In this study area the *Combretum* woodlands act as an ecotone between the miombo - chipya associations and the valley associations ; their position on better soils of a high water table makes them a favoured dry season habitat for several grazing mammals.

The genus *Combretum* with some 18 species in this study area does show a distinct zonation in species distribution which follows a catenary pattern viz:-

Thickets on upper slopes:-	*Combretum padoides.*
Woodlands on upper slopes:-	*C. zeyheri*, *C. collinum taborense*, *C. psidiodes*
Woodlands on lower slopes:-	*C. molle*, *C. collinum suluense*, *C. fragrans*.
River valleys:-	*C. goetzei*, *C. pentagonum*.
Alkaline river terrace:-	*C. hereoense*
Flood plain edges:-	*C. imberbe*
Flood plain channels:-	*C. constrictum* *C. mossambicensis*

Similar patterns could be described for species of *Brachystegia* (6), *Acacia* (7) and some grasses.

3.432. The Miombo-Chipya distribution pattern.

Cole (1963), working in Zambia, believed geomorphology (and hence soils) to be the major factor affecting woodland association distribution and stated that fire and human agencies of succession are secondary factors. Briefly, she states that:-

"miombo woodland is restricted to undissected plateaux on old infertile sandy soils; chipya woodland is restricted to dissected undulating country on well-drained, mature chocolate loams; open woodland forms (scattered tree grassland and the Zambian 'mopane' and 'munga' associations) on alkaline clays and valley slopes and that grassland is restricted to poorly drained pediplains and valley bottoms."

These conclusions agree with the data presented here, with the exception that in this area one cannot distinguish between the miombo and chipya communities using broad topographic or edaphic factors. Tables 3.10 and 3.11 show no real difference between slope or soil acidity and clay factors. However it must be stressed that in Zambia the term 'chipya' is used in a broader sense than in this study area and Cole's remarks could apply to several different communities.

Lawton (1964) working in Northern Zambia gives data (shown in table 3.12) to show a soil clay factor determining chipya and miombo distribution. He writes, "It is suggested that the edaphic factors determine distribution, miombo being confined to clay soils and chipyas to sandy soils." The very high clay values (falling into the heavy sandy clay class of the Zambian soil survey, Savory, 1963) given by Lawton are not found in the woodland soils of S.E. Tanzania where clay content of horizons down to 1m depth average much less than 10%. Lawton's data appear to contradict that of Cole given above.

Anderson (1952) working in the Nachingwea district of S.E. Tanzania (160km S.E. from the Miombo Research Centre), reaches the opposite conclusion. His data are shown in table 3.13 and he writes, "It is seen that miombo woodland is predominant on the sandy soils with clay content up to about 12% and chipya occupies the heavier soils with clay content over 12%." This he qualifies as follows: "More often texture differences are due to the development of a catenary sequence with the miombo predominant on the sands of the lower slopes with the chipya on the sandy loams of the ridge tops."

Again soil clay contents in this area do not reach 12% although there is a tendency for miombo types to associate with middle and lower slopes. However, as chipya and miombo occur with equal frequency on similar soil types it is concluded that edaphic factors are not important in this area. The next section introduces considerable evidence to show the two associations are seral stages in a pyrosere leading to or from a climax thicket.

3.433. Grass Species Distribution and Ecological Classification.

Mention has been made of the large numbers of grass species in this study area and how only a few species dominate in each association. This grass cover can be classified according to ecological characters, as well as on taxonomic features. An ecological classification has more relevance to a study of the array of grazing mammals. These ecological characters may be listed as follows:

1) Distribution patterns.

   (a) Species of restricted ecological tolerance. Mention has already been made of *Sporobolus virginicus*, *Alloteropsis semialata* etc.

   (b) Species of broad ecological tolerance but never dominant, eg. *Sporobolus ioclados*, *Digitaria milanjiana*. *Eragrostis superba*, *Panicum infestum*.

   (c) Dominant species but restricted to one habitat type, eg. *Andropogon schirensis* in chipyas, *Setaria sphacelata* in floodplain communities.

2) Growth type (excluding morphological habits of rhizomatous, stoloniferous or tussock growth).

(a) Short grasses, (less than 60cm) including most annuals and creeping grasses. These can be dominant as on the alkaline soils or inconspicuous as in the woodlands.

(b) Medium grasses, (from 60 to 10cm) including some annuals and many perennials. These are often edaphically caused stunted forms of taller grasses, eg. Heteropogon contortus and Themeda triandra on alkaline soils. They are also a common constituent of intermediate communities, eg. the Combretum - Terminalia woodlands and the Combretum - Cassia ridges.

(c) Tall grasses (100-300cm) which are nearly all perennials, but include some rare annuals, eg. Cleistachne sorghoides which grows to 250cm. These dominate the woodland and floodplain communities.

3) Nutritional and Grazing Values

(a) 'Sourveld', usually tall or medium grasses with a coarse tussock growth form, often perennial in habit with a high stem to leaf ratio. These are basically not palatable in the mature growth stages.

(b) 'Sweetveld', usually short or medium grasses, with soft stems and broad leaves, either annual or perennial in habit and have a low stem to leaf ratio. These are basically palatable in all growth stages, but tend to breakdown and fragment in the dry season.

4) Regenerative type:

(a) Annual species which regenerate from seed only, with a life span of one year or less.

(b) Perennial species which regenerate from seed and rootstocks and have a life span of several years.

(c) Occasionally species can exhibit either habit depending on habitat type eg. _Perotis_ and _Enteropogon_ spp.

Many of these characters are linked and characteristic of major habitat types, eg. tall sourveld perennials dominate the woodlands (some 42 common grass species including only 3 annuals). Short sweetveld annuals and perennials dominate the alkaline outwash plain, (42 species with 20 annuals). Tall coarse perennials dominate the flood plain with no annual species. These terms of short, tall, sweet and sourveld are of importance to grazing mammals and are used extensively in following chapters.

3.434. Spatial and Temporal Mosaics in Grass Distribution Patterns.

Superimposed on the broad edaphically controlled distribution pattern outlined above is a smaller pattern consisting of a mosaic of areas or synusia of single species or small group of species dominance. Such mosaics may vary from a pattern scale of 1 or 2m up to several hundred metres in size. Sometimes these may be immediately relatable to soil or micro relief patterns such as old termite mounds, animal wallows, depressions or deep shade, but often they are due to the species clumped growth and spread where a species competitive ability may be favoured by fire or grazing pressure.

Such single species mosaics are more typical of the non-wooded areas such as the scattered tree grasslands and the floodplains. A prominent example is _Bothriochloa pertusa_ in the more open areas of the scattered tree grassland, which exists as a pure monotype over areas of up to 100m^2. In this case _B. pertusa_ is non-palatable and fire resistant and spreads at the expense of more palatable heavily grazed grasses. This species growth and spread is further discussed in chapter 4. To the south of the alkaline terrace mosaics of _Themeda_ and _Heteropogon_ are common, forming pure species monotypes over large areas. Areas of the central floodplain are often monotypes, although in this case species diversity has decreased with an increase in clay percentage and duration of flooding.

Woodland grass layer mosaics are not so noticeable. Grass clumps are more discrete and further apart, allowing a second shorter grass and forb layer to exist under the tall perennials. The density of trees and shrubs with their attendant shade breaks up areas of species dominance.

Walker (1974) discusses the impact of canopy cover on grass species composition and describes a case similar to that of figure 3.22 where tree shade provides a habitat for broad leafed grasses, usually Panicum maximum, P. infestum and Urochloa species in Walker's Rhodesian lowveld study area. Walker ascribes this shade effect to lowered temperatures, increased nutrient status and better soil texture and moisture conditions under tree canopies.

In addition to such spatial mosaics, there exists a temporal or seasonal mosaic or pattern with different species germinating and flowering at different times. As the flowering grasses tend to dominate the sward, a gap of 2 months can give very different visual impressions of species composition and dominace

This effect is most pronounced in the scattered tree grasslands where at the onset of the November rains the sward is dominated by *Mariscus* species, a small sedge, and later *Dactyloctenium*. By mid rains in March the sward is covered by flowering *Digitaria* and *Sporobolus* and in April *Chloris virgata* starts flowering. Finally during the dry season, a short woody suffrutex, *Maerua edulis*, appears, flowers, fruits and dies back in less than 6 months. After an early fire this is virtually the only green plant in the entire ground layer.

, 3.435. Perennial or Annual Grasslands.

Several authors dealing with tropical grasslands state that misuse or overuse in terms of fire and grazing pressure causes a successional change from a perennial grass cover to a more annual grassland, eg. Humphrey (1962), Rattray (1960 a&b) Riney (1963), Savory (1966), Bayer (1955) and Walker (1974). There is however considerable evidence to show that for this area and other similar systems, the high annual grass content of the alkaline terrace is due to edaphic factors and only secondarily due to grazing pressure.

Studies in Central Africa indicate that heavy grazing pressure in the growing season (the rains) coupled with early dry season burning considerably reduces plant "vigour and competitive ability" (Bayer 1955). In this study area the scattered tree grasslands carry a very high rainy season density (of up to 100 animals per km^2, see chapter 5) of predominantly grazing mammals. Several areas do show signs of heavy utilisation, forage being removed almost to ground level and large bare areas, dominant unpalatable herbs and sheet erosion becoming common. This phenonomen can be accentuated by the brief drying up period in January or February when high radiant ground temperatures scorch and wilt young growing grasses. Areas relatively inaccessible to grazing animals such as around low thorn bushes and between branches of fallen trees show a medium height good grass cover including many perennial species.

Species such as *Mariscus mollipes*, a sedge, and annual grasses such as *Aristida barbicollis*, *Brachiaria deflexa* and *Eragrostis ciliaris* as well as unpalatable herbs such as *Cyathula lanceolata* dominate these heavily grazed areas. Better rangeland has a denser cover of *Digitaria milanjiana*, *Urochloa* spp, *Sporobolus ioclados* and *Panicum infestum*.

However, this does not necessarily mean that the high percentage of annual grasses in this zone is primarily due to overuse and a resulting succession from a perennial grass sward. There exists considerable evidence from Central and Southern Africa to show that edaphic conditions cause a high percentage of annuals. The Luangwa, Zambezi and Saabi-Lund **Valleys** and areas adjacent to the Kruger National Park, all have extensive areas of heavy alkaline sodic clay sands, with poor drainage. Plant species composition is very similar to that of this study area. Rattray (1966) for example, discussing the Saabi valley grass cover, states that *Urochloa*, *Chloris virgata*, *Dactyloclenium Brachiaria* spp, *Aristida* spp and *Eragrostis* spp are common, a list closely resembling this area. Anderson (1963) discusses Tanzanian saline, alkaline and hard pan soils at some length. Such soils characteristically bear a sparse ground cover including many ephemeral and annual grasses. The high sodium content restricts water uptake, and affects plant nutrient absorption, especially phosphorus. These soil properties cause the vegetation to exhibit a drier form than would be expected on the basis of the actual rainfall.

Bogdan (1958) discusses grass species distribution on halomorphic soils from the Kiboko area in Eastern Kenya. His suggested plant-soil relationships are shown in figure 3.23 which is modified and enlarged for this study area.

I conclude therefore that the grass cover of the alkaline terrace is edaphically controlled and the best quality forage contains a high percentage of short sweet perennial grasses such as *Panicum*, *Digitaria* and *Sporobolus*, with some annual species and herbs. The community is relatively delicate and susceptible to heavy grazing and trampling which will cause a rapid deterioration in range quality with perennials decreasiing and annuals, forbs, and bare ground increasing.

3.5. VEGETATION SUCCESSION AND DYNAMICS

3.51. Introduction:

Mention was made in Chapter 2 of the historical background to "miombo" and the effects of Pleistocene climatic change. Evidence was discussed showing that the open woodland forms have developed at the expense of mesic and xeric forest or thicket types by the effect of fire and human activities. Within the more rigid limitations of climate, geomorphology and soils, it is the effects of fire and cultivation that have the greatest effect on plant communities, both their physiognomy and species composition.

Unlike the physical limitations, fire and human factors are not permanent, and vegetation change may be modified or reversed by altering or removing the causative factor. Such factors change the seral stages in community succession. Without such factors succession would proceed to the climax type for the particular soil and climatic regime.

Boaler (1966b), in a monograph on the ecology of Pterocarpus angolensis, quotes evidence as to the age of the miombo formation type as being at least 38,000 years. He notes the miombo species as possessing certain non-forest characteristics such as fire resistance and annual seedling dieback. Boaler estimates that at any one stage, over 90% of the woody plants in a miombo community are growing as suffrutices. This is called a Cryptodrymion type by Glover (in Boaler, 1966).

Considerable evidence from tree growth plots and ring counts show the lifespan of many miombo dominants to be in the order of 100 to 150 years, and that woodland can reach maturity within 100 years of clear felling. (Glover 1946; Boaler and Sciwale 1966). This rapid turnover in a vegetation type marked by unequal fires and scattered settlement results in a mosaic of vegetation communities, in several different seral stages.

Botanical evidence points to the centre of evolution of this leguminous woodland as Zambia and the Eastern Congo, which have 17 full species of *Brachystegia*, the dominant genus. The number of species decreases away from this centre, e.g. 11 in western and central Tanzania, 6 in eastern Tanzania, 1 in Kenya and none in Uganda (Wild 1964). The large number of hybrids between species in this genus would indicate considerable recent extension and or contraction of range. The Zambian flora also shows a high degree of endemism in other tropical genera, e.g. *Crotalaria* (another legume) with 70 endemic species (White, 196). Other taxonomic groups such as the Lepidoptera and birds show similar effects. (Carcasson 1962 and Moreau 1966). This evidence fits well with a history of recent climatic change.

3.52. Methods.

Detailed investigation of vegetation successionary trends requires the establishment and analysis of longterm experimental plots. Experimental fire plots were established in 1968 and have been used to investigate the effects of fire and grazing on the ground layer; these effects are discussed in chapter.4.

As a 7 year period is insufficient for obtaining data on woody species successionary trends, the bulk of the evidence presented in this chapter is taken from the literature and from a visit I paid to the Zambian Forest Research Division fire plots in 1970.

Within this study area the existence of documented settlement enabled me to investigate clearing and fire effects by the questioning of previous residents, by examining air photographs and by visiting sites of past settlement.

In 1971 an aerial survey of the eastern Selous was undertaken along 5 East-West flight lines some 30km apart. Flights were made twice, in the early dry season in late July and the late dry season in mid October. Data on the extent of burning was collected by using a stop watch to indicate the time of flight over burnt areas and expressing this as a percentage of the total flight time for each transect. Areas of thicket and forest were excluded.

Finally data from the woodland computer analysis records (as presented in chapter 3.2) were used to show community relationshipsin the woodland formation.

3.53. Results.

3.531. The Zambian Fire Plots.

The Forest Research Division of Zambia in 1933 set up 3 experimental fire exclusion plots of some 5 ha each at Ndola in homogenous Brachystegia woodland. The area recieves some 1100 mm rain per annum and soils are moderately high in nutrients. The woodland is taller and denser than that found in the Selous. Each plot is surrounded by a graded fire break, one plot is completely fire protected, one burnt early in the dry season and one burnt late in the dry season. I visited the plots at the end of the rains in May 1970 when the experiment was some 37 years old. The experiments are discussed by Trapnell (1957) and White (1966).

The early burn plot showed no structural change from the surrounding woodland (which is also burned early in the dry season). Species diversity was maintained, Brachystegia spp remained dominant with some 100 to 120 trees per ha. Annual and short perennial grasses and many herb species were encountered in the ground layer and small thicket patches occurred around termitaria and in deep shade.

The late burn plot showed a drastic change with virtually all trees except Pterocarpus angolensis having been killed. Tree stem density was 5-6 per ha. Grass growth was tall and tussocky and predominantly Hyparrhenia spp. Occasional patches of fire tolerant suffrutices remained. Herbs were scarce in the ground layer. Lack of vegetation cover at the start of the heavy rains had created a hydrophobic impermeable crust (pavement erosion) which severely decreases water infiltration. Soil height under grass tussocks was some 4-5 cm higher than the surrounding pavement.

Fire effects in the no burn plot were equally drastic.

All grass cover had disappeared, being replaced by evergreen shrubs, forbs and climbers amongst which Rubiaceae and Euphorbiaceae dominated. Miombo woodland elements remained dominant in the tree layer but were scarce or absent in the underwood, shrub and ground layers. Several forest species seedlings were encountered in the ground layer, notably Marquesia spp.

3.532. Extent of Burning in the Selous Woodlands.

The 1971 coverage of the Selous showed that in July 36% (± 19% as 95% confidence limits) had been burnt whilst in October 58% (± 27%) had been burnt (n was 10, each half transect counting as one sample). High confidence limits are partly due to the distribution of game scout patrols and legal trophy hunters who burn as a matter of policy. The September aerial survey gave further information on burning status for the east Selous, each 18 x 18 km sq. being assessed in five classes as: no burn, 1-25%, 26-50%, 51-75% and 76-100% burnt. Results were 12, 12, 18, 17 and 5% respectively. No hunters and reduced level of field patrols have caused the decrease in fire prevalence early in the season.

3.533. The effects of past human settlement.

Appendix 2 gives a detailed account of the history of human settlement in the eastern Selous Game Reserve and the effect of such settlement and its attendant agricultural clearing on the vegetation. A summary of these effects is given here.

Prior to 1920 much of the settlement was confined to the upland thicket areas as a means of defence against neighbouring tribes, slaving expeditions and German rule. Clearings lasted some 3-5 years and then were left to regenerate. Where clearings were enclosed by thicket communities, the clearings rapidly reverted to a thicket cover. Where clearings were open to woodland communities and fire a typical chipya woodland resulted.

Plate 7 is an air photograph of an area of past settlement known as 'Nunga' which is marked on figure 1.3. Within a few km^2 it is possible to find climax thicket, open chipya woodland and several intermediate stages of thicket reinvasion. One area shows an invasion of mature chipya woodland by thicket species. A tree canopy of chipya species covers a dense shrub canopy of Landolphia and Vernonia zanzibarica which has suppressed all grass growth. Within this shrub canopy can be found faithful thicket species such as Fagara, Gardenia, Grewia conocarpa, Suregada and Uvaria spp. Comparative species lists for adjacent plots of climax thicket, open chipya and chipya thicket are shown in table 3.14.

3.534. Air photograph analysis of thicket/woodland systems.

Plate 8.1 shows an air photograph of a thicket woodland system. The large dense blocks of thicket are edged with white, (a Markhamia obtusifolia - Millettia micans edge community) which merges into an evenly spaced chipya woodland turning more abruptly into denser Brachystegia woodland.

The successionary sequence from thicket could be observed around a large thicket to the north of the study area where one can see tree density increasing with distance away from a fire produced thicket edge. The vegetation passes through Markhamia to Combretum then chipya communities, culminating in a Brachystegia woodland.

Investigation of a xerophytic sandy soil thicket in Biharamulo Game Reserve, West Lake Region of Tanzania in October 1973, showed a steady increase in woodland tree height and girth away from a thicket edge. Trees were species of Combretum, Ozoroa and Pericopsis not found in the thicket. In this case a soil change had taken place, the woodland occurring on truncated shallow soils having lost up to 50cms soil depth since thicket clearing. Fire was the destructive factor (Rodgers, Ludanga & DeSuzo 1978).

3.535. The Woodland Formation Computer Analysis.

Chapter 3.2 detailed the results of a computerised association analysis of the tree and ground layer elements of a woodland complex. Results are displayed as a constellation diagram in figure 3.10. It is immediately obvious that all the woodland species are associated within one grouping whilst the valley community is separate. This can be used as further evidence for the fact that the woodland and valley associations are edaphically controlled distinct entities. In contrast within the woodlands the different communities are associated seral stages within one successionary series or a very close continuum of communities. Within the constellation diagram there are definite sub groups of stronger associations. These may be taken as the chipya community at the top of the diagram which includes the dominant chipya grasses, (_Tristachya_, _Andropogon_ and _Schizachyrium_)and a central grouping of _Brachystegia_ woodland species. This latter category gives rise to a thicket precursor group of species centred on _Landolphia kirkii_, and another smaller group centred on _Markhamia obtusifolia_.

3.54. Discussion.

3.541. Successional series and climax vegetation.

Three major successional series are put forward for this study area and the whole of the Selous Game Reserve. These series which may occur singly or together are as follows. Firstly a climatic succession which changed from mesic to more xeric conditions within the last millenium (Moreau 1966). This succession, which is very slow acting, could conceivably alter the species composition and structure of the climax communities. Secondly, and much more importantly, is a pyrosere or fire successionary series, and finally a succession following human cultivation and clearing.

Two major climax vegetation types are postulated for the woodlands of the study area, and the bulk of S.E. Tanzania. These are a xeroseric climax of dry thicket forest communities and a hydroseric climax of riverine thicket and forest communities.

All three successional factors, climate, fire and man, affect the development of both climax types. But the nature of their effects and the concept of a closed canopy climax in the miombo woodland formation type is a matter of much controversy in the literature. Most authors envisage the climax for the miombo woodlands as a forest or thicket type with variable degrees of evergreen or deciduous components depending on climate and soil conditions (Wild 1964; White 1965, Lawton 1963, Boughey 1959, Glover 1949, Anderson 1963; Fanshawe 1960; and Freson et al, 1974).

Ramsay and Rose-Innes (1963) in a detailed paper on fire effects in the Guinea savanna state that, "Complete fire protection ensures a rapid development towards a closed woodland or forest climax which would ultimately reduce or eliminate the present herbaceous cover. Protection encourages the spread and diversification of shrubs and trees whilst reducing the number of and percentage basal cover of grass species. Fire produces the opposite result. Given protection from all forms of disturbance over a long period it seems possible that this type of modified woodland subclimax would develop to a closed forest climax of deciduous trees with an evergreen shrubby ground cover. If such is the case, changes in composition would be extremely slow, owing to the lack of mobility and or scarcity of seed of suitable climax species in the surrounding country."

Keay (1959), working in West Africa suggests three distinct climaxes for the three major climatic/vegetation belts. Firstly, in the southernmost more mesic areas, the present derived savanna with large open woodland tracts with some forest remnants would, with complete fire protection, proceed to an evergreen forest. Secondly the submesic areas of the southern Guinea savanna which have a present open woodland of mixed composition, riverine forest and thicket remnants would move to a transitional climax with evergreen forest on the moister sites and a closed deciduous canopy of Afzelia, Vitex, Albizia and Khaya over an evergreen Guinea savanna (miombo) with an open deciduous canopy of Isoberlinia and Pterocarpus with no forest remnants. Fire protection would lead to a dense deciduous woodland of an open or closed canopy of present savanna elements over a partly herbaceous partly evergreen shrub ground layer.

Lawton (1963), Fanshawe (1960) and White (1965) working in Zambia describe several dry evergreen forest types which they believe to have covered much of the Zambian plateau during a wetter period of the Pleistocene, and are probably the present day climax vegetation types. Several components of these forests have montane or rainforest affinities, but the forests can maintain themselves under present day conditions in the absence of fire. Under fire conditions they are rapidly degraded to a chipya or Brachystegia woodland type.

Analysing the Ndola experimental fire plots, Trapnell (1957) hesitated to state fire protection would lead to a closed forest. This was following some 23 years of protection. The observations of White (1966) and my own in 1971 however, show that following some 37 years of protection, the protected plot is slowly turning into a forest community but the complete cycle may take over 100 years to complete.

Freson et al (1974) working in Katanga compared many parameters of a thicket, Brachystegia woodland and a fire degraded woody savanna (a poor chipya community) successionary series. They state that, "Late fires occur during the austral spring's vegetation flush and have a strong depressive effect. Early fires have a lesser impact as they take place at the end of the vegetative period. Spatial and temporal variability of fires induces a large heterogeneity of miombo communities which are in constant change. Their ecological measurements are summarised in table 3.15 which shows the intermediate position of the Brachystegia woodlands in most ecological parameters, leading to the greatest species diversity."

Glover (1949) suggested two climax communities for the Nachingwea area of S.E. Tanzania. These are a xerosere leading to a Brachystegia microphylla thicket and a hydrosere leading to a riverine forest community. This latter type (postulated for this study area as well) would equate to the Diospyros - Trichilia - Khaya lowland forests supposed to have covered much of Central and Eastern Africa during the Pleistocene pluvial periods (Wild 1964). Similar forest patches occur in this study area, (see association type A2 in chapter 3.1) but Khaya spp are more common to the west in wetter areas of the Selous reserve.

3.542. Fire and Thicket Destruction.

The thicket vegetation communities are extremely vulnerable to fire. Tree and shrub bark is thin and papery, and leaf loss to evergreen species can be fatal. The protective suffruticose habit is rare in forest or thicket communities. Fires attack thicket edges, and a fierce late season fire before the wind can cause considerable destruction. Human clearing, elephant paths and tree destruction can allow fire to enter. Grass species quickly invade and fires become annual events. Within this study area comparison of aerial photographs of thickets show their areas and shapes have remained relatively constant from 1949 to 1965. No significant decrease in size could be detected. Riverine forest has however been severely depleted and this is shown in plate 3.11.

In open areas adjacent to thickets, grass growth becomes vigorous and a dense sward of up to 1.5m height is normal. This sward can produce fires of 400°C and above (West, 1965). Such fires will prevent seedling germination of all but the most tolerant species. Two dominant thicket trees, <u>Pteleopsis myrtifolia</u> and <u>Millettia stuhlmannii</u> are also common in the chipya and miombo communities of coastal Tanzania. These species are often left unscattered after fire destroys the thicket and are frequently left standing by native cultivators. Such trees provide shade islands where grass growth is suppressed. Tangles of *Landolphia* spp are common and tree seedling growth often starts in these patches.

Mention has been made of a *Pteleopsis* woodland community (type C.3 in chapter 3.1) found in 3 areas adjacent to thickets in the study block. These communities reflect an early stage after thicket destruction and occur with shrubs of *Millettia micans* and *Markhamia obtusifolia*, two thicket edge species. Anderson (1963) quoting Glover's work in S.E. Tanzania, mentions a *Millettia* - *Markhamia* community which he ascribes to recent clearing and regeneration of upland thickets.

In the course of time the fired thicket will develop into a woodland community with fire tolerant species, i.e. a chipya community. Trees here are fire resistant with thick corky barks and have seedlings which can resist frequent burning. Fire destroys the above ground tissue but the woody root-stock continues growing. *Pterocarpus angolensis*, a common constituent of chipya, requires fire to crack the hard seed coat before germination can take place (Boaler (1966b). All thicket edges, except those on steep slopes, show an ecotone of some 20-40m width characterised by thicket relicts such as *Vitex sp c.f. altissima* (a tree resistant to fire when mature but with fire sensitive seedlings and saplings), *Pteleopsis*, *Millettia*, *Grewia conocarpa* and *Markhamia*. Outside this is a chipya woodland characterised by trees of *Pterocarpus*, *Pseudolachnostylis*, *Combretum zeyheri*, *Strychnos*, *Vitex mombassana* and *Millettia* and *Pteleopsis*.

The place of the *Brachystegia* woodlands in this scheme is not clear. Trapnell (1957), has pointed out that *Brachystegia* spp. are sensitive to fierce late season fires, and *Brachystegia* communities are never found adjacent to thickets. Previous sections of this chapter have shown no topographic or edaphic criteria separating the chipya cr *Brachystegia* woodlands. Where chipya wooodlands are burnt infrequently or early in the dry season, conditions may exist for *Brachystegia* components to develop. The shade islands under chipya trees would provide relatively fire-free starting points and developing *Brachystegia* saplings and seedlings have been seen in such situations. In support of this theory it is rare to find mature *Brachystegia* trees in a chipya community although many chipya species are frequent elements in *Brachystegia* woodland.

3.545. Succession Following Cultivation.

Boaler and Sciwale (1966) described the successional series following cultivation and clearing of Brachystegia woodland at Lupa in south west Tanzania. Mention has been made of the large number of suffriticose seedlings of miombo species, Boaler gives a figure of 10,000 per ha at Lupa which is similar to 7,200 per ha here (see chapter 4). Many suffrutices are left (up to 40%) following a 4-5 year cultivation period, and it is this seedling source which supplies the woody regeneration, much more so than seed. There is evidence to support a return to miombo conditions, within 100 years of cessation of cultivation (Boaler and Sciwale 1966).

Four periods of woodland growth are discussed by Boaler, these are as follows. Immediately after cultivation, a dense grass cover with suffrutices and fierce fires lasts some 4-7 years. This is followed by a period of sapling growth which may suppress much of the grass cover and hence fire effects. A part canopy may form at 20-25 years. In this case it is thought that where suffrutex densities are high enough they can eliminate grass and/or it is possible that a suffrutex with a big enough root stock may produce sufficient above ground growth for its apical meristems to escape a cool early season fire. Thirdly, a period of sapling competition opens out stands of woody plants, and grasses reinvade. Lastly a balance is achieved between woody and herbaceous growth and a mature woodland results.

At Lupa and this study area, there exist three stages of species composition. Following cultivation initial species such as *Terminalia sericea* and *Combretum zeyheri* dominate and then lose prominence. Secondly, the broad spectrum species which are relatively fire tolerant such as *Pterocarpus* and *Pseudolachnostylis* regenerate; and thirdly, the more fire sensitive species such as *Brachystegia* and *Julbernardia* regenerate under the initial canopy and then dominate the community. These growth stages are illustrated diagrammatically in figure 3.24.

Several of these stages may be seen in this study area. The *Combretum* - *Terminalia* woodlands south of the Lihangwa river illustrate stage 3 with many *Brachystegia* and *Julbernardia* saplings under a *Combretum* - *Terminalia* - *Pseudolachnostylis* canopy. Small patches of nature *Brachystegia* are found which may have regenerated in fire free areas or be relicts from cultivation in the 1930s. This area is shown in an aerial photograph as Plate 3.12.

3.544. A Successionary Model.

From the evidence discussed above a dynamic relationship between the thicket, chipya and *Brachystegia* communities can be suggested. The relationships as suggested by Anderson (1963) and Lawton (1972) are also shown in figure 3.25. Anderson's ideas presuppose an edaphic difference between chipya and miombo associations. This possibility was discussed earlier in this chapter and in my opinion the two woodlands are different stages of a successionary series and edaphic differences are negligible in this and similar areas.

3.545. Other Vegetation Formations.

Previous discussion has centred on the thicket and woodland formations. To conclude this section mention must be made of the grassland and scattered tree grasslands.

The grasslands of this study area are edaphically controlled and fire and cultivation will have no effect on their structure or physiognomy although they may very well affect species composition. All floodplains in the study area burn, at least in part,every year.

The scattered tree grasslands and shrubbed grasslands are affected by fire. Mention has been made of a shift to more annual grasses and forbs with an increase in fire and grazing pressure. Quantitative effects on grass structure are discussed in chapter 4.

Further, fire plays a role in preventing the wooded grasslands from reverting to its probable climax, the coastal thickets of clay sand alkaline soils. These thickets described as type B3 in chapter 3.1 are xeric in character and include many of the tree species common to the open scattered tree grasslands. Terminalia spinosa is affected by fire. With no burning its seedlings tend to form dense thickets and sapling clumps although these are frequently opened up by elephant. (Rodgers (unpublished data).

3.546 Comparison with Northern Zambia

In late 1976, the Land Resources Division of the British Ministry of Overseas Development published their assessment of the land resources of Northern Zambia. This resource assessment contains an analysis of the soils and vegetation of the region (M.O.D. 1976).

The very detailed soil survey has shown no significant difference between miombo and chipya soils, viz: "Chipya-carrying soils differ only marginally from miombo soils, contrary to frequently expressed opinion", (M.O.D. 1976; conclusion 67).

"Differences between soils under miombo and chipya vegetation types were generally insignificant and showèd no underlying trend" (M.O.D. 1976; page 93).

R.M. Lawton, who undertook the vegetation survey, used P.C.A. analysis to investigate site and species relationships within 206 sites using woody species only. He concluded: "The continuous spread of the samples on the graph indicates that the vegetation is a continuum. This is so, there is an overlap of species and groups of species, and the relationship between dry evergreen forest, chipya and miombo woodland is complex and dynamic." (M.O.D. 1976; page 119.)

These conclusions agree very closely with the ideas and conclusions presented in this thesis. Lawton's discussion of fire ecology and vegetation successionary trends under different fire treatments agrees well with observations I have reported here. With these new conclusions from Zambia the controversy reported for miombo-chipya soil types is now closed. Both vegetation types occur on a variety of soils within the acidic sandy loam series. Differences between them are successionary and fire induced and not edaphic.

3.6. THE CONCEPTS OF DIVERSITY, EQUITABILITY AND MATURITY IN THE VEGETATION COMMUNITIES.

3.61. Introduction.

The past decade has seen a growing interest by ecologists in the concepts of diversity, stability and maturity, eg. Krebs (1972), Margalef (1963) and a series of papers in the First Int. Congr. Ecol. (1974). These concepts aid the understanding of succession and have been used in studies on productivity, distribution and genecology. Given the variety of communities in many different stages of successional development and the frequent perturbations in terms of fire, it was thought to be of value and interest to determine values for these parameters for the ground layer communities of this study.area.

Diversity may be defined as a measure of species richness weighted by species abundance. Numerically the Shannon-Weiner function of information theory , 'H', is used.

Where $H = \sum_{i=1}^{s} - (Pi)(\log Pi)$ for all species

'Pi' is the proportion of the sample belonging to the 'ith' species, Krebs (1972).

Equitability is a measure of eveness of distribution patterns and numerically is the ratio of H : H (max) for each species in a community. In this case the Lloyd and Ghelardi function, 'E' is used where E is H/log S. Where H is the community diversity and S the number of species in the sample (Krebs 1972).

Stability and maturity are controversial terms and difficult to define and measure. Stability is the ability of a system or community to recover after disturbance or perturbation. Maturity is an attribute of climax vegetation and therefore should increase with time along a successional series.

Community Dominance Index (CDI) is the degree by which the community is controlled by the abundance of one or a few species and numerically is given as

$$CDI = \frac{y_1 + y_2}{\sum_{1-n} y} \times 100$$

where y_1 and y_2 are the abundances of the first and second most abundant species (Walker 1974).

3.62. Methods.

Data have been drawn from the computerised ground layer vegetation survey described in chapter 3.2. Calculations have been made as follows.

The index of diversity 'H' was determined from normal association analysis outputs which produces list of frequencies within associations. Data were used from the total data set for all positive associations as determined by the association dendrogram.

The index of equitability was also determined from these data. Values for the thicket community were estimated for woody species by a subjective evaluation of abundance on a 1-5 scale for all woody species recorded within the thicket on sand associations.

The CDI was calculated for each of 4 vegetation types by selecting 5 representative sites for each type from the survey data and using % frequency data as a measure of abundance. CDI and the number of species per community appear to be inversely proportional and a regression for these 2 parameters was calculated.

3.63. Results and Conclusion.

Values for diversity, equitability and CDI are shown in table 3.16 for up to 11 computer produced associations in 5 distinct vegetation types. The graph and regression line for CD1 and species number is shown in figure 3.26.

Four main conclusions may be drawn from table 3.16. Firstly the climax communities of swamp and thicket have the highest equitability (E 0.96) although all values are high (E 0.83). Secondly, the two climax communities have opposite diversities, very low for the swamp (H = 2.97) and high for the thicket(H = 4.62). Thirdly, the woodland associations generally have low diversity and equitability values. Lastly, the swamp and woodland associations with a low mean number of species per sample site have high dominance (CD I) values.

These results may be interpreted as follows. The floodplain and woodland associations are tall grass areas with little or no small scale spatial species mosaic in the major species. Within the floodplain formation <u>Ischaemum</u> and <u>Setaria</u> dominate over large areas and in the woodlands <u>Andropogon</u> is dominant. Smaller grasses and forbs appear to be at low levels of occurrence and hence the associations show high CD1 values.

Conversely the wooded grasslands with short grasses, many small scale mosaics and many forbs have low CDI values.

As equitability is an attribute of community maturity (Margalef, 1963), one would expect climax communities to have high equitability values. What is interesting is the disparity in H values. The swamp community is an edaphic climax with a demanding environment involving seasonal flooding and heavy clay soils. Maximum diversity and equitability involves the resource base being taken up by many genotypes as evenly as possible. For a harsh environment, fewer genotypes would be as adapted as for a more equable environment. This appears to be the case here, the swamp having few species (22) but with an even distribution pattern and the thicket with many species (118) with again a near equal resource sharing or distribution pattern. As a comparison values for diversity for a number of eastern USA deciduous forest communities vary from 1.69 to 3.09 (Krebs, 1972).

The woodland habitat has low E & H values. In the grass layer one species is dominating, leading to an uneven resource distribution and the species total is not high.

What do these values mean? The results agree with the previous choice of climax communities, in that climaxes have high equitability values. The two communities exhibit different levels of maturity as defined by Margalef (1963) in that maturity leads to an increase in biomass, diversity, stratification and individual life span, but a decrease in productivity per unit biomass. These would hold for the thicket but not the swamp, which as an edaphic climax is perhaps an anomaly.

3.64. The Effects of Fire and Grazing on Diversity Values.

Data from experimental fire and grazing plots as described in chapter 4 were used to show the effects of fire and grazing on diversity. Data are drawn from tables 4.1, 4.2 and 4.5 and 4.6. Results for 'H' are shown in table 3.17. Results are not conclusive because experiments lasted only a few years, but they do illustrate trends.

Late fires tend to reduce diversity both in the shrub and ground layers. No burning has increased diversity in the ground layer due to an influx of herbs and woody seedlings. The Woody layer shows a small but probably non significant decrease in diversity.

Diversity values from the grazing exclosures show no pattern of change. Grazing will tend to affect species composition balance in that perennials will replace annuals with a decrease in grazing pressure, but numbers of species may not be affected. The sharp rise in diversity in the Terminalia plot for 1975 is conspicuous and caused by an influx of herbs.

Kelly in Rhodesia (quoted in Walker 1974) has shown a decrease in productivity with an increase in community dominance index. Data from this study (table 4.6 and 4.7) agree with this finding.

CHAPTER FOUR: FORAGE PRODUCTION AND NUTRIENT CONTENT

4.1. Introduction

The rangeland parameters of forage production and nutrient content are important in determining animal distribution and densities within the more rigid strictures of vegetation type and water availability. Production and nutrient content are correlated and both seasonally and annually variable, they are therefore to some extent predictable. Through the use of fire levels of both production and nutrient content are controllable. Published information on these parameters for the woodland areas of Africa is scarce and often controversial. Soils, gross and microclimates; incidence, frequency and timing of fires; and different plant species will all affect production and nutrient content.

The woodland grasses are typically Andropogonae, tall, sour and generally considered as of low palatibility. Lind and Morrison (1974) quote evidence showing the Andropogonae as being inferior to other grass tribes, eg. Paniceae, in nutrient turn over. But judicious fire management of this coarse grass cover can provide good quality forage for a large part of the year.

West (1965) and Daubenmire (1968) provide a detailed review of fire effects on tropical grasslands. Bourliere and Hadley (1970) review the factors affecting savanna production.

The investigations detailed in this chapter were designed with the following objectives:

(a) to determine the effect of annual fires on the structure and floristic composition of the grass layer,

(b) to determine gross production and seasonal rates of production of forage grasses,

(c) to describe the nutrient content of such forage and its seasonal changes,

(d) to examine the role of grazing in range floristic composition and production,

(e) to examine the role of fire in controlling production and nutrient content.

As in previous chapters the overall aim was to describe these parameters and effects to allow an understanding of animal distribution and habitat utilisation and to allow the implementation of a fire management policy for the immediate study area and the Selous Game Reserve.

Investigations detailed in this chapter are presented in two sections: the field studies and analyses separated into the woodland formation and scattered tree grassland formation, and the laboratory analyses.

4.2. Limitations

Six years (1970-1975) are not sufficient to investigate floristic successional changes due to fire and grazing effects on complex communities. At best, trends in succession may only be suggested.

Difficulty was experienced in burning the short grass habitats due to the lack of fuel resulting from heavy grazing pressure and fragmentation of the annual grasses. Conversely, grazing was only detectable in the tall grass habitats, the woodlands, following burning. For this reason the effects of fire and grazing were not seperated for this zone.

Production and nutrient content sampling was restricted to forage grasses and did not include browse herbs or shrubs. Above ground tissues only were sampled, no estimate was made of root production. Sampling intensity for production studies was low as grazing exclosures were required for investigation of floristic change. No attempt was made at determining optimum quadrat size or shape, a standard square 25x25cm quadrat was used throughout for floristic sampling. Two 1m square quadrats were used per area and time period for production sampling. This small sample size precluded estimating variances for production data.

4.3. Field Investigations.

These included the setting up of fire experimental plots and grazing exclosures. These are located in figure 1.2.

4.31. Experimental Fire Plots.

Two sets of plots were set up in late 1968, one set in the *Combretum* - *Terminalia* tall grass woodland (chipya), and one set in the *Terminalia* scattered tree grasslands. Studies in the latter set were abandoned due to the impossibility of setting fires.

Plots consisted of early season fire, late season fire and unburnt areas, early fires being set in July and late fires in October. Each treatment area was 100m square and all 3 treatment areas were adjacent. Plot sites were chosen subjectively close to permanent tracks and in homogenous areas representative of the vegetation type. It was apparent that the unburnt plot had not burnt in the 1968 dry season, the other two plots had burnt. The unburnt area in the woodland plot was partially burnt by accident in 1970 (about 40%), this burnt portion was not sampled in later analyses. All plots were burnt in late 1974 during my absence from the study area. No further analyses were undertaken.

4.32. Grazing Exclosures.

Three exclosures were built, one adjacent to each fire plot and one in a heavily grazed area of short grassland to the north of the study area. Exclosures were built for the dual purpose of measuring above ground biomass in year one (1969) and studying vegetation floristic change in subsequent years.

The exclosures are 15m square and constructed with heavy gauge angle iron embedded in concrete and 2 inch heavy duty weld mesh. Exclosures were surrounded by an "anti-elephant ditch", one metre from the exclosure, one metre wide and one metre deep with the soil piled outside. Ditch efficiency can be judged by the fact that these have lasted seven years while two earlier less robust exclosures were destroyed by elephant within one month of errection. In some situations ditching can lead to an alteration of soil drainage and consequent changing moisture availability for the plants under study. In this case the very hard poorly drained soils of the area would minimize such changes, but no clippings or measurements were made within one metre of the exclosure fence to reduce possible drainage effect.

4.33. Clipping and Measurement Techniques.

All plant material clippings were taken from a 1m^2 quadrat, plant material being clipped to 1cm above ground by hand held scissors. Obvious ground litter was discarded, dead material being acceptable if joined to the plant base or root system. All clippings were packed in polythene bags and transported to the laboratory within an hour of clipping. Material was weighed, separated into grass green leaf, dry leaf, stem, sedge and forb components, reweighed, oven or sun dried to constant weight and then repacked for later analysis.

Quadrat positions within plots were chosen by random numbers from a numbered grid of squares of 1.25m square. Quadrats were placed centrally in the selected square. Quadrats outside exclosures were placed at random within subjectively chosen localities. Such quadrat sites were marked to prevent reuse.

Techniques of plant measurement, such as % frequency, density and cover were standardised and followed those described by Brown (1954) and Milner and Hughes (1968).

4.34. Investigation of Fire Effects.

4.341. Tall grass woodlands.

Ground layer species frequency values were determined by the use of randomly placed 25cm square quadrats. Species presence was noted for each of 100 quadrats within each of the treatment fire plots. Note that the early burning plot acts as a control in that the surrounding area is early burnt as a matter of management policy. Field data was entered in tables and % frequency of occurrence totalled for each species. The first analysis was carried out in April 1969 (peak flowering period) and the plots were reanalysed in April 1973. Results for each plot and each period are shown in table 4.1.

Woody seedling, suffrutex and shrub species frequency and density were determined by the total counting of individuals within ten 10m square plots per fire treatment plot. Small plots were located randomly on each sampling occasion. Results are shown in table 4.2 for the first analysis in late December 1969 and the second analysis in late December 1973. December was chosen as small woody plants were easily seen amongst the short green grass. Note that the unburnt plot had not been burnt for 2 seasons at the time of first analysis and so initial densities are considerably higher than those of the burnt plots.

Seedlings, suffrutices and shrubs above 25cm in height were measured as to height class in 25cm classes up to 2m. Results are shown in table 4.3.

Ground cover values were determined by an aerial pin projection technique as described by Brown (1954). 10 frames of 20 points were used per analysis time and site. Results are shown in table 4.4.

4.35. Investigation of Grazing Effects.

4.3511. Scattered tree short grasslands.

Both short grass habitat exclosures were used and as their initial and final species composition differs, results are shown separately. Plant species composition as indicated by % frequency was determined by recording species presence in each of 100 $25cm^2$ quadrats inside and outside the exclosure in April 1970, 1971, 1973 and 1975. Results for both exclosures are shown in table 4.5.

4.36. Investigation of Plant Production.

Clipping of different quadrats took place at monthly intervals in the grazing exclosure in the *Terminalia* scattered tree grassland habitat from November 1969 to October 1970, and at less frequent intervals in other grazing exclosures, fire plots, and other grassland habitats throughout the study area. Only one year's intensive measurements were taken as the exclosure plots were required to be free from both human and animal grazing to show species composition change. All woody growth was removed from the grazing exclosures before clipping commenced. Two quadrats per month were clipped in the main exclosure and two or more for other sample areas. Results for each quadrat were combined after drying and separation and weighing. Mean values only are given in the results in this thesis. Monthly growth increment quadrats were also used in the Terminalia exclosure. The same two quadrats were clipped to a uniform height of 5cm above ground every month from November 1969 to October 1970 to show the monthly growth increment or yield under an intensive clipping (simulated grazing) regime.

Data for the Terminalia grazing exclosure are given in table 4.6. Biomass or standing crop production is expressed as grammes dry matter per metre square (gm dm/m^2). Rainfall as measured at the research centre, a distance of 3km, is given in mm for the 30 day period prior to clipping. The linear relationship between plant growth and rainfall is shown in figure 4.1. Production and monthly increment results for each component of the grass layer is shown graphically in figure 4.2.

Data for the long grass woodlands exclosure are given in table 4.7 and figure 4.2. These results cover a 12 month period following burning in August 1970. Data for other sites in the study area are shown in table 4.8 where single values only are given, this is at the time of estimated peak production.

4.4 Laboratory Analyses

[illegible]

4.41. Investigation of Plant Nutrient Content.

Grass samples from many different growth stages, species and habitats have been analysed for nutrient content. All samples have been analysed by the Chemistry Section of the Central Veterinary Laboratories, Dar es Salaam, using standard analytical techniques. Samples for analysis were taken from the productivity clippings or collected especially in the field. All samples were sun or oven dried before despatch for analysis.

All samples were analysed for crude protein and crude fibre content. Many of these were further analysed for mineral (calcium, phosphorus, magnesium and copper) content. A few samples received full proximate analysis for crude protein, crude fibre, minerals, ash, fat and nitrogen free extract. Emphasis was placed on crude protein and crude fibre analyses as these are the two most seasonally variable nutrients in total content. Protein content alone is a commonly used indicator of nutritive value, (French, 1959, Long, Thornton and Marshall, 1969).

Table 4.9 gives data showing the seasonal variation in protein content for the monthly clippings from the *Terminalia* grazing exclosure. Total available protein as gms/m^2 is also shown for each month. These data are shown diagrammatically in figure 4.3. Similar results are shown in table 4.10 and figure 4.4 for the tall grass exclosure.

Table 4.11 shows full proximate chemical analysis for different grass species at different growth stages. Table 4.12 shows details of mineral analysis. Appendix 5 to this thesis

discusses the relationship between soil, forage and animal tissue mineral content for this study area.

4.42. Investigation of fire effects on plant nutrient content.

Forage samples have been collected from the fire treatment plots in the tall grass woodlands. Samples were separated into grass leaf and stem and analysed for crude protein. Figure 4.5 shows the change in protein content of grass leaf following burning over 120 day period.Calendar dates of burning are not considered but they vary from late July to early December from 1969 to 1971 and include several different grass species.

As there is virtually no regeneration following burning in the short grass areas until after the first rains, the question of fire effects on nutrient content has not been considered.

4.5. Discussion

4.51. Effects of fire on plant species composition, structure and ground cover, in the tall grass woodlands.

The time period since establishment of the fire treatment plots was not sufficient to show major changes in grass species composition, table 4.1. The late burning plot could be considered as tending towards species reduction, a trend also described from Zambia, in the Ndola fire plot (Trapnell, 1957). Chapter 3.6 showed a small decrease in plant species diversity in the late burning plot.

The unburnt plot has shown no real change in grass species composition, but an apparent increase in herbaceous and seedling material. Macrotyloma maranguense, a spreading herb which scrambles over the grass layer, accounts for much of the increase in forb content.

Shrub and seedling composition and density show marked changes between the three treatments, table 4.2. The early burn plot maintained the statusquo with the shrub layer being partially dominated by *Combretum*, *Terminalia* and *Lonchocarpus* species, but a wide range of species is present in the plot. Shrub density remained the same. The late burn plot shows a marked decrease in shrub and seedling density and a decrease in species diversity. *Terminalia sericea* increased in dominance. *Terminalia* here grows in clumps averaging some 80cm in height, which regenerate after burning each year. The 80cm height is reached some 2 months after burning and there is little vertical growth for the rest of the year. Difficulty was found in determining which were seperate plants and which were multiple shoots of one plant. The unburnt plot showed an increase in shrub density especially of *Combretum zeyheri* but also an influx of thicket pioneer species, eg. *Dichrostachys*, *Markhamia* and *Commiphora*.

Table 4.13 shows density data for similar fire treatment plots from other published studies on the African woodlands.

Height distribution classes of seedlings and shrubs, table 4.3, illustrate the development and growth of woody material in the unburnt plot. The dominance of the 50-100cm class in the late burn class in due to the uniform growth of regenerating

Terminalia seedlings described above. The decrease in bare ground due to leaf litter and falling grass stems in the unburnt plot is clearly shown in the ground cover data, table 4.4.

As was discussed in chapter 3, it is clear that in the absence of fire, miombo type vegetation becomes more and more dominated by woody growth until eventually the grass layer is excluded and a thicket type is formed. The results given here, albeit over a short period of time, support this conclusion.

Several grass species show different degrees of tolerance to fires. There is evidence that *Themeda* and *Hyparrhenia* spp. pastures are maintained by frequent burning, (Brockington, 1961). *Bothriochloa* sp. are aromatic and rarely utilised by wildlife in any but the youngest growth stage. Where grazing pressure on other species is high and fires are common, *Bothriochloa* spreads rapidly. In the Kruger National Park,a fire prevention policy has been introduced in selected areas to eradicate this unpalatable species, (Brynard, 1965).

Chapter 3.4 made mention of the loss of valuable grazing species such as *Panicum infestum* and *Urochloa* by the removal of shade trees by late season fires, This removal can be accelerated by elephant activity, (Rodgers, unpublished data).

4.52. Effects of grazing on plant species composition.

Table 4.5 gives data from two seperate sties of different initial species composition. The two sites show similarities in their response to grazing exclusion but also some apparent contradictions. Basically there is a decrease in grass species variety (especially annuals) and a tendency to domination by one or two perennial species, Digitaria milanjiana and Panicum infestum on one site and Eriochloa and P. massaiense on the other. The apparent reduction of Dactyloctenium and tremendous increase of Sporobolus outside the second exclosure is difficult to explain. Also difficult to explain is the increase in herb and sedge frequencies from one site or enclosure and not the other. Part of this due to an influx of Commelina species in one plot. Blepharis, a tough spiny herb not selected by grazing animals, seems to disappear with exclusion from grazing.

Although not directly measured, grass cover value appears to increase with exclusion from grazing.

The results give the impression of great variability and apparent trends of species, diversity value and annual grass content are certainly not significant. It would appear that a longer time period than 5 years is necessary to show real changes in species composition.

4.53. Plant production and biomass.

Data on primary production for the woodlands of Central Africa is extremely limited. There is some data from West African woodlands and Malaisse and co-workers at Lubumbashi, (Zaire) have accumulated much data on tree/shrub production but little on the grass layer (Malaisse, 1975; Freson, 1973). Table 4.14 lists comparable data from other published studies. Values of 360gms/m^2 for the tall grass sward of this study, table 4.7, are low for tropical grasslands but compare well with similar woodland areas of similar rainfall patterns.

The linear relationship between plant production and accumulative rainfall has been described by Khan (1970), Walker (1974) and is discussed briefly by Phillipson (1975) and Bourliere and Hadley (1970). Such linear correlations allow the prediction of primary production when rainfall is known.

The yield pattern of the short grass exclosures is as expected for a mixed annual/perennial sward. There is no growth until the first rain which stimulates a burst of leaf production followed later by stem and inflorescence production. Leaf production decreases as stem growth increases. Immediately after the rains there is a decrease in standing crop due to nutrient translocation of nutrients in perennials and the breakdown and withering of annual grasses. No new growth is recorded until the following rainy season.

Data for the tall perennial grass plot reveal the influence of fire. Following a clean burn, there is a rapid burst or flush of fresh leaf production up to some 10-15cms height or $20gm/m^2$ dry matter. This growth occurs on slopes with some soil moisture in the complete absence of rain. Deep excessively sandy ridge top soils and hard clay soils of valley bottoms do not exhibit the flush. Following there is a period of wilting and no production until the next rains when normal growth occurs. Leaf production decreases with the onset of flowering, and there is a decrease in standing crop after the rains due to nutrient translocation and some leaf fall.

The role of grazing in increasing yield has not been closely investigated in this study, although the experimental clipping of miombo grasses at different intensities and frequencies can significantly increase annual production (e.g. Van Voorthuizen 1972). In this study the monthly clipping of the short grass sward resulted in a total yield almost equal to the unclipped plots maximum standing crop. However yield of green leaf (the portion of greatest value to grazing mammals) is considerably in excess of the maximum green and dry leaf standing crop of the unclipped plot, 173gms compared to $122gms/m^2$ dry matter, table 4.6. In terms of protein yield the green grass leaf of the clipped plots average 9.1% crude protein giving an annual total of 25gms crude protein per m^2, compared with an annual average of 8.1% and a peak of 13.0 gms/m^2 for all growth in the unclipped plots, table 4.9. It is probable that a less vigorous clipping regime would have resulted in even greater yield.

Some investigators have shown a decrease in yield from burnt as compared with unburnt pastures (West 1965) although Dauhenmire (1968) presents much conflicting evidence. A common case is fire reducing individual plant size (eg. height and leaf area) but an increase in tillering resulting in normal rates of production. Weigert and Evans (1970) consider that the measurement of peak standing crop gives an artificially low value for total production due to the continual break down and loss of matter in annual swards. This fact and the unknown amount of grazing by small rodents and insects will have depressed estimates of plant biomass given in this chapter. Bourliere and Hadley (1970) present evidence suggesting a +25% correction factor may compensate for these losses.

4.54. Plant Nutrient Content.

There are a great many papers published on the nutrient content of East and Central African forage grasses but very few have readily comparable data for growth stage, season, plant components or species or ecological types, (eg. Stent 1933;

Bredon and Horrell 1962; Bredon and Wilson, 1963; Dougall, 1963; Dougall et al 1964; Naik 1967; Lawton 1967; Field 1968; Long, Thornton and Marshall 1969; and Taerum 1970).

It is readily agreed that plant species is of little importance in determining plant nutrient content; plant component and growth stage of much more importance, (French 1959; Worden, Sellers and Tribe, 1963). In the African context an ecological division into annual and perennial classes or tall and short grasses or sour or sweet veld can be useful in assigning grazing values. However, while the same plant part of two species may have identical nutrient contents the physical properties of the grass, such as needle or broad leaf, leaf stem ratio, spiky awns etc. may affect palatability. Chemical properties such as aromatic leaves and other secondary plant compounds may also affect palatability.

Tables 4.9 and 4.10 illustrate the differences between stem and leaf fractions in protein content and table 4.9 shows the effect of clipping in maintaining higher protein values. These tables also serve to show the very low levels of protein available in dry season forage in African range land. Table 4.11 shows the similarity in nutrient content between the same growth stages of different grass species of the same ecological type.

The mineral content of several grass samples is given in table 4.12. Levels of calcium, magnesium and copper fall within recommended feeding levels for domestic ruminants as detailed by Maynard and Loosli (1971) and Davis and Skidmore (1966). Phosphorus values are low in comparison with reccomended levels (Naik, 1965; Davis and Skidmore, 1966). Appendix 5 discusses the question of mineral content of forage and animal tissue and points out that forage phosphorus values are low enough to cause deficiency diseases in cattle and that wildebeest blood phosphorus levels would be fatal in cattle. Russell (1961) mentions that in soils of high sodium content, plant phosphorus uptake is reduced, this could well be the case here, see chapter 2.2.

4.55. Fire Effects on Forage Nutritive Values.

Like most aspects of tropical fire ecology (Phillips 1965), the question of the value of the fire induced flush is a source of controversy (West 1965; Daubenmire 1968). The miombo woodland perennial grasses show this characteristic property of dry season post burn flush. The cause of the flush has been variously attributed to increased temperatures, high ash mineral input, increased microbial activity and dew reaching the growing points. One more plausible theory is that the flush is due to the removal of dead litter and senescent stems and leaves which otherwise have an inhibitory effect on the apical meristem, Mes 1958; Daubenmire 1968).

A slightly similar but more recent theory is that removal of senescent tissue releases the plant from hydrostatic tension allowing scarce nutrients and water to be used for new growth, (Agnew. 1974, pers. comm,). This theory fits with evidence from grass cutting (e.g. the mowing of road side verges in the dry season) which also stimulates fresh growth in the dry season, but without removing dead litter or stem bases.

As is shown in figure 4.5 the protein content of the post burn flush is extremely high, occasionally reaching over 20%. Such growth has a higher protein content than the green growth of unburnt leaf at the start of the rains, (this study, and Mes 1958). Using a policy of small patch work burns in the early and middle dry season it is possible to provide a continuous supply of high protein forage for grazing animals. Despite a low yield at this season the low grazing intensities in the woodlands prevent excessive damage on these burnt areas. As the dry season progresses the new growth on upper slopes begins to wilt and only those grasses with access to shallow water tables continue growth.

West (1965) and others, eg. Staples (1945) consider the practice of early burning to be detrimental to the grass cover, and that individual grass plants suffer from loss of "physiological vigour". I suppose that their term "physiological vigour" is analagous to "competitive ability". Such authors advocate a late burn, just after the first rain. Figure 4.6 gives a diagrammatic picture of the effects of early and late burns on the grass and its nutrient cycle. It is apparent that too late a burn will destroy new growth formed with the root stock nutrient reserves. An early burnt plant is subject to wilting which if prolonged can also harm to the plant. Daubenmire (1968) and Phillips (1965) consider that the prolonged dry season, low annual rainfall, and chance of dry cold season post burn frost are important damaging factors for early burning in Rhodesia, the area of West's and Staples' work. They consider, however, that in the higher rainfall areas of Zambia and Tanzania an early burn can be preferable to a late burn.

An overall discussion of fire effects, including vegetation change, effects on grass production and animal feeding and distribution patterns is left until chapter 9 when a burning policy is put forward.