

CHAPTER 8 - VEGETATION

Contents

8.1 INTRODUCTION / 86

8.2 METHODS & DATA RECORDED / 88

Sampling / 88
Presence, Density, Frequency / 88
Physiognomy and Structure / 89
Phenology / 89
Dispersal / 89
Soil Properties and Edaphic Features / 90
Layout / 90

8.3 GORONGOSA MOUNTAIN / 90

Aquatic Herb Communities / 91 Bogs and Vleis / 92 Rockfaces / 92 Grassland / 94 Upland Savanna / 96 Scrub-Thicket / 98 Thicket / 98 Forest / 100

8.4 MIDLANDS / 104

Aquatic Herb Communities / 104
Rock faces / 104
Scrub Savanna / 104
Tree Savanna / 105
Scrub-Thicket / 107
Thicket / 107
Forest / 109
Environmental Factors / 109
Phenology / 109
Succession / 112

8.5 RIFT VALLEY / 114

Aquatic Herb Communities / 114
Floodplain Grassland / 115
Scrub Savanna / 119
Tree Savanna / 119
Scrub-Thicket / 123
Thicket / 123

8.6 CHERINGOMA PLATEAU AND COAST / 131

8.7 PLANT COMMUNITY RELATIONSHIPS / 131

Grassland Communities / 131
Woody Communities / 131
Summary of Community Relationships between each physiographic unit / 132

REFERENCES / 132

CHAPTER 8 - VEGETATION

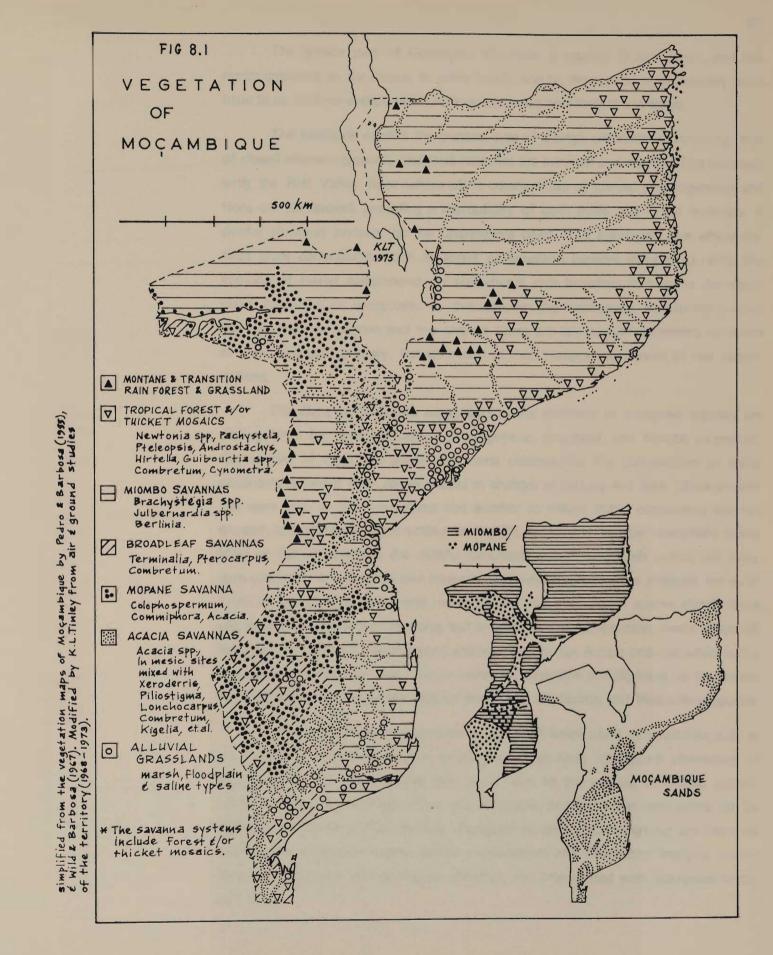
8.1 INTRODUCTION

The vegetation of the Gorongosa ecosystem and the transect across the Cheringoma Plateau to the sea comprises a stepped sequence of moist and dry formations related to the physiography and climate. Mountain rain forest and arid saline grasslands of the Rift floor are juxtaposed within a distance of 22 km. Rain forest covers the greater part of the Gorongosa massif with montane grassland patches and heath on the summits. The Midlands support moist, closed *Brachystegia* (miombo) savannas; the Cheringoma cuesta a mosaic of moist, closed miombo savanna, extensive groundwater forests and dambos. Separating the two miombo areas is the Rift Valley trough with a mosaic of mesic savannas, dry forest, thickets and floodplain grasslands.

The major biomes represented are: Moist Savanna, Forest and the Aquatic Biomes, and to a lesser extent, Afrotemperate, Arid Savanna, and the Marine littoral (terms after Tinley 1975, Fig 3). In the phytochorological terms of Monod (1957) the plant formations belong chiefly to the Angola-Zambezian Domain of the Sudano-Angolan Region (comprising chiefly the *Brachystegia* system), the Eastern Forest Domain of the Guineo-Congolian Region, the Montane Region, and are in close proximity to the Southern Subgroup (BI. Bb) of the arid Sahellian Type in the Zambeze Valley and Gazaland. Unfortunately the more recent phytochorological treatments of Africa by White (1965, 1971) and Chapman & White (1971) have made a fundamental error in combining the southern Sudanian and Sahelian sub-types as one phyto-region, ie. equivalent to grouping the Moist and Arid Savanna Biomes as one biotic and climoedaphic system.

The vegetation map of Africa (AETFAT/UNESCO 1959) at a scale of 1:10 million shows five types in the Gorongosa — Cheringoma transect: montane (No 3), forest savanna mosaic on the coast (No 9), *Brachystegia* woodland (No 18), undifferentiated dry types (No 20) in the Rift Valley, and mangroves (M). The 1:2 million vegetation map of Mocambique by Pedro & Barbosa (1955) and the 1:2,5 million vegetation map of the Flora Zambeziaca Area by Wild & Barbosa (1967) show 14 vegetation types. A number of this complexity of types are, however, merely a change of species dominants, or aspects of the same formation, and the present author has simplified these by means of air and ground studies to produce a more accurate depiction of spatial relations and boundaries of the major vegetation types in Mocambique (and Map 2 in Smithers & Tello (1976).







In 1965 the botanist José M. de Aguiar Macedo completed a four month survey of the vegetation of both Gorongosa National Park (Macedo 1966) and Gorongosa Mountain (Macedo 1970a, 1970b). Unfortunately a vegetation map with explanatory text was made for the mountain area alone (Macedo 1970b). His preliminary report on the vegetation of the national park contains eleven schematic profiles and sections dealing with conservation especially of the mountain forests.

In the absence of high relief, the normal climatic gradient on the central and southern coasts of Mocambique is in belts parallel to the coastline with the highest rainfall, humidity and damped temperature extremes closest to the land-sea junction. Low rainfall with high extremes and variability occur inland. This sequence superimposed on edaphic controls is responsible for the zoned nature of vegetation in the broad plains region, known as Gazaland, between the Save and Limpopo Rivers. In the Gorongosa — Cheringoma transect a stepped physiographic sequence parallel to the coast has resulted in a stepped or disjunct climo-edaphic sequence with moist formations near the coast, dry to arid formations in the Rift Valley trough, and a repeat of moist formations on the Midlands west of the Rift. The abrupt rise of the isolated Gorongosa massif above the Riftward margin of the Midlands results in the development of orographic rains which provide rain forest conditions on its confines.

The physiognomic terms used here follow Tinley (1975). Attention must be drawn to the persistent misclassification in the literature of the *Brachystegia* (miombo) formation as open forest ("forêt claire") or woodland as opposed to savannas. As the analysis in this section will show, miombo forms the moist end of the savanna or woodled grassland climo-edaphic cline between the equatorial rain forest and the deserts. Botanists seem keen to separate miombo from other savannas apparently on the criterion of their closed canopy habit. However, mopane and certain acacias also show the closed canopy habit over large areas in many situations, and the floral and faunal constituents of miombo are savannoid.

Savanna and veld are duplex systems composed of one or more woody strata, of greater or lesser density, with a nearly continuous grass groundlayer. By contrast, grasslands and forest or thicket are either almost purely herbaceous or woody; they are therefore uniform formations though they show horizontal stratification.

The subject of misapplication of successional terminology has been covered under Process & Response (Chapter 6). However, it should be re-emphasized that the separation of climatic (climax) and edaphic communities is nonsense, as all communities are climo-edaphically controlled whether they are influenced or not by factors such as fire, frost, cultivation or herbivores.

87

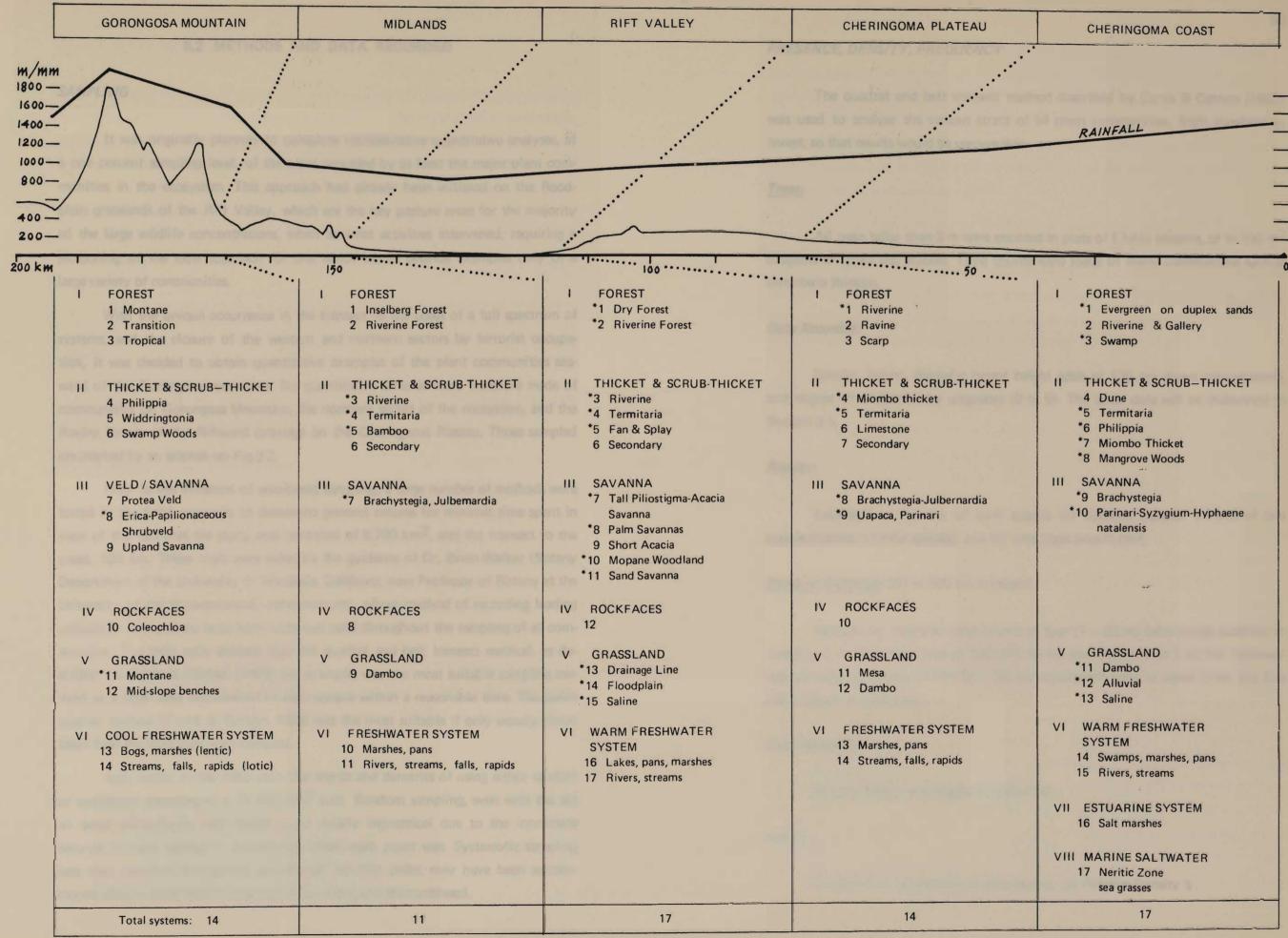
The greater part of Gorongosa Mountain is covered in rain forest, and this meets grassland on the slopes, in valley heads, and on the summit areas abruptly, with little to no ecotone except where rock outcrops support thicket and scrub.

The Midlands exhibit the greatest area of a single unbroken community; that of closed miombo savanna, and thus ecotones are minimal and narrow. This contrasts with the Rift Valley floor where plant communities of diverse physiognomies and flora are juxtaposed, providing a multiplicity of both sharp and broad ecotones. A similar situation pertains on the Cheringoma coast. It is significant that where distinct plant communities such as forest or grassland become reduced to relics, the ecotone of mixed components on transitional soils broadens to become the major plant formation or ecosystem. In this way, on the macroscale, transitional biomes can become new biomes and the original types are left as ever decreasing remnants or they disappear entirely, though many of their components survive in new combinations.

The plant communities recognized in the montane to mangrove transect are distinguished by their contrasting physiognomic, structural, and floristic properties. Composites of these and substrate criteria circumscribe the communities on aerial photographs where they are expressed as changes in texture and tone. These properties were used as controls against one another to ensure that a community was not divided into separate types simply on height, density or canopy spacement alone. Most of the communities are closely correlated with distinct soils and/or soil moisture gradients. It is appreciated however that whilst conspicuous relations are exhibited between communities and climo-edaphic features, not all species distributions are incurred by these factors alone, but are also due to competition, shade, dispersal, fire and biotic influences such grazing and human activities. A clear example, which is due to grazing pressure, and the "hippo lawns" of *Cynodon* and *Digitaria* on the Urema Plains which occur on similar vertisol profiles as tall *Setaria* and *Vetiveria* grasslands.

Due to the close juxtaposition of quite different plant communities, such as dry forest on sand and mopane savanna on clays, from contiguous alternation of alluvio-catena; few communities are "pure" due to the overlap of certain components on ecotonal intrusions. Thus not all species in a particular community can be regarded as typical or characteristic. The plant communities recognized are therefore associations of species having similar requirements and tolerances, implying coincidence of communal and ecological affinities, and interspersed with instrusives or colonists.







8.2 METHODS AND DATA RECORDED

SAMPLING

It was originally planned to complete representative quantitative analyses, at a one percent sampling level, of the areas occupied by at least the major plant communities in the ecosystem. This approach had already been initiated on the flood-plain grasslands of the Rift Valley, which are the key pasture areas for the majority of the large wildlife concentrations, when terrorist activities intervened, requiring a jettisoning of the ideal approach for one which would provide examples only of a large variety of communities.

With the unique occurrence in the transect to the coast of a full spectrum of systems, and the closure of the western and northern sectors by terrorist occupation, it was decided to obtain quantitative examples of the plant communities seaward of the Gorongosa ecosystem. No quantitative samples were therefore made of communities on Gorongosa Mountain, the northern sector of the ecosystem, and the Ravine forests of the Riftward drainage on the Cheringoma Plateau. Those sampled are marked by an asterisk on Fig 8.2.

Prior to the initiation of area-based sampling, a large number of methods were tested in the field, primarily to determine greatest returns for minimal time spent in view of the fact that the study area consisted of 8.700 km², and the transect to the coast, 100 km. These trials were aided by the guidance of Dr. Brian Walker (Botany Department of the University of Rhodesia, Salisbury, now Professor of Botany at the University of the Witwatersrand, Johannesburg), whose method of recording feeding utilization of plants by large herbivores was used throughout the sampling of all communities. The field tests showed that the quadrat and belt transect method, as described by Curtis & Cottam (1962) for example, was the most suitable sampling method as a large area was covered in each sample within a reasonable time. The point quarter method (Curtis & Cottam 1962) was the most suitable if only woody plants taller than the field layer were sampled.

Also tested in the field were the merits and demerits of using either random or systematic sampling in a 12 000 km² area. Random sampling, even with the aid of aerial photographs was found to be totally impractical due to the inordinate amount of time wasted in determining where each point was. Systematic sampling was thus practised throughout, and though the first point may have been subconciously chosen those that followed were inevitable and thus unbiased.

PRESENCE, DENSITY, FREQUENCY

The quadrat and belt transect method described by Curtis & Cottam (1962) was used to analyse the various strata of all plant communities, from grassland to forest, so that results would be comparable.

Trees:

All trees taller than 3 m were counted in plots of 1 ha in savanna, or in 500 m² subplots in forest and thicket. Total counts were made of island communities such as termitaria thickets.

Data Recorded:

Species, height, diameter breast height (dbh at 135 cm above ground level), and degree of utilization by ungulates (0 to 5). The latter data will be elaborated in Section 9.5.

Results:

Expressed as: (a) no. of each species (b) Relative Density % (total of one species/number of total species), and (c) total basal area in cm².

Shrub or Fieldlayer (50 to 300 cm in height):

Sampled by means of total counts in four $(1 \times 25 \text{ m})$ belts across subplots in forest and thicket (total area of 100 m^2). In the savanna plots of 1 ha the fieldlayer was sampled by means of five $(5 \times 20 \text{ m})$ equidistant belts in dense cover and five $(10 \times 20 \text{ m})$ in open cover.

Data Recorded:

Species, height, and degree of utilization.

Results:

Expressed as: (a) number of each species, (b) Relarive Density %.

88



Grass or Herbaceous Stratum:

Sampled by a minimum of 10 (1 m²) quadrats per 300 m² subplot in forest or thicket, and by 30(1 m²) quadrats per hectare at 20 m intervals in savanna and grassland. In relatively homogenous grasslands 15 (1 m²) quadrats were used in one hectare or half hectare plots. Where two well-defined layers occur within this stratum, two sets of readings were made, eg. scrub invasion within a taller grass sward, or tall weeds in short grassland.

Data Recorded:

Species, dominants (in cover-abundance), height and degree of utilization.

Results:

Expressed as: (a) number of quadrats of occurrence, (b) Relative Frequency % (out of total number of occurrences).

PHYSIOGNOMY AND STRUCTURE

Physiognomy and structure were recorded by means of profile diagrams drawn to scale along belt transects (Davis & Richards (1933), using measuring poles for horizontal distance between individual trees, and for the height of lower storey components. Canopy tree heights were measured by triangulation and cross-checked against windthrown or elephant — felled trees. Belt transect were 5×60 m in forest and 10×60 m (up to 200 m) in savannas and across ecotones.

Bisects of thicket were 5 or 10 m wide and for scrub-thicket (eg. fynbos) 1 or 2 m in width. Sample size was adjusted to the density of cover. In addition, visual estimates were made to construct cover-stratification diagrams as shown in Cain & Castro (1959: 223).

PHENOLOGY

Over a period of three to four years the phenophases of woody plants were recorded on the Midlands and in the Rift Valley, and to a lesser extent on the Cheringoma Plateau. The phenology of the highest summit grassland, and its associated forbs, on Gorongosa Mountain was made once a month over a two year period. Phenophases recorded for woody plants included: mature leaf (ml) leaf fall (lf), bare

89

(ba), new leaf (nl), flowering (fl) fruiting (fr). The occurrence of different stages on separate trees, or on the same plants, is indicated in the tables by the concurrence of symbols in a month. A minimum of five specimens of each species in a particular phase was required for recording a positive occurrence. Rare or inconspicuous species would have been underscored. Although these data were noted whenever I was in the field, road traverses of 100 km were made once a month, latitudinally across the ecosystem as far as the Cheringoma divide.

No data was collected on the following aspects; (1) the number of species in different phenophases per unit area, (2) quantitative records on similar species in different situations, and (3) the pollinators. Phenological data will be included under the plant communities of each physiographic feature and then compared under a separate heading. Plant foods and cover availability for animals through the annual cycle is the complementary aspect of plant phenophases.

DISPERSAL

To obtain even a rudimentary understanding of the interrelations and dynamics of succession and evolutionary tendencies in the development of ecosystems, a knowledge of the part played by dispersal agents in different plant communities is fundamental.

Methods of dispersal of a large number of plant species were observed but many others have had to be arbitrarily designated according to their seed morphologic characteristics. Thus all drupe, berry, and arillate seeds are designated as animal dispersed, plumed or winged seeds and pods as wind dispersed, and those with explosive dehiscing pods or capsules as active ballists. It is appreciated, however, that many of these are polychorous, being disseminated by several methods according to circumstances. Where this is known all agents will be included without attempting to determine the most important agent. Examples of polychory include the wind blown pods of *Colophospermum mopane* which are also carried by sheet and rill wash during rains and deposited on ebb lines along microrelief features. They can also be dispersed by animals such as elephant. The succulent tree-euphorbias have explosive capsules which can throw the seeds several meters from the mother plant. These seeds are furthermore avidly eaten by doves and voided from perches resulting in these species becoming major components of thicket clumps. Acanthaceae which have explosive capsules are in addition dispersed by birds once the seeds have been thrown, and are also found germinating in buffalo dung. Other species with berries may have to rely on wind dissemination once the berries have dried out. With these limitations in mind the woody plant components have been used in an attempt



to characterize various plant communities. The data are illustrated in comparative compound diagrams showing percent occurrence of dispersal types, and the importance of such methods in each community, by adding the relative density or frequency of the species involved, where these have been determined. The dispersal classes have been determined from personal observation and guidance from published data and the books by Ridley (1930) and Van der Pijl (1972). The classes are noted by capital letters in brackets after each species and are open to additions or corrections by other workers: Z = animal dispersed (zoochory), V = by weight (barochory), Y = water (hydrochory), W = wind (anemochory), X = by explosive dehiscence and seeds thrown (active autochory or active ballists). A question mark after any of the symbols means that the case is uncertain.

The succeeding chapters will show the salient part played by the various dispersal types in coaction with the animal components in influencing succession and landscape evolution.

SOIL PROPERTIES AND EDAPHIC FEATURES

Soil pits and auger samples were made in every plant community and quantitatively analysed by the Soil Science Department, University of Pretoria for pH (H20), salinity R (Ohms) and percent effervescence of free carbonates CaCO3 (using dilute HCI).

LAYOUT

Due to the influence of contiguous surfaces on succession and system interactions, and the influence of adjacent communities on the floristic relations of a community, the vegetation of each physiographic feature are dealt with together, following the same procedure used in previous chapters. Within each feature, however, communities with similar physiognomy are placed together in order of relative complexity, from herbaceous communities to forest. The subheadings used within each physiognomic group include:

- (a) physiognomy, structure, composition, (b) dispersal, (c) phenology/availability, (d) environmental factors, (e) succession.
- A final section will synthesize the chapter by means of comparative analyses and floristic relationships of the communities.

90

8.3 GORONGOSA MOUNTAIN

With its greater axis longitudinal, the oval form of Gorongosa Mountain rises steeply from the Midlands between 400 & 500 m to over 1 800 m. This presents two major faces to the elements, a northern and western xerocline comprising equator-facing rainshadow (lee) slopes, and a southern and eastern mesocline of poleward-facing and rainward (windward) slopes. A NE—SW diagonal marks the transition from one to the other. This has resulted in aspect and altitudinal assymetry of the rain forest lower margin; from 500 m on the mesocline to the 1 200 m contour on the xerocline, where the lower margins extend down stream gorges linking with the riverine strips of the Midlands and Rift Valley. Dry savannas, more typical of the valleys and drier areas of the miombo system occur in the xerocline, with thickets on colluvium or talus materials of mixed composition. The mesocline savanna and thickets meet the lower margins of the rain forest usually abruptly, accentuated by past and present shifting cultivation. The upland savannas on the mesocline comprise the moister end of the miombo system and thus contain species typical of skeletal soils plus others found nowhere else in the region.

The rainshadow effect caused by the mountain mass is most marked at the base, and immediately west of the mountain just outside the ecosystem limits. Here, savanna species typical of the hot low-lying Rift Valley are mixed with miombo or alternate on the mosaic of sands and clays; the latter supporting the valley species. On the mesocline, forest is rapidly confined to riverine situations below the 500 m contour and the tall miombo, not yet disturbed by cultivation, contains a woody field-layer in its grass stratum of forest margin and understorey species.

While only the highest summits above about 1700 m can be defined as montane, some of the thicket constituents and protea of this zone also occur on the lower forest margins and stream slopes of the mesoclines between 800 and 900 m. The summit grasslands are entirely separated from those of the lowlands by rainforest except at one small site on a west-facing spur immediately adjacent to Gogogo, the highest peak. Only on this one narrow spur can veld fires from the Midlands occasionally ascend and ignite the highest summit grassland. Otherwise summit grassland are burnt by tribal hunters or possibly by lightning induced fires.

Gorongosa Mountain is unique in that the greater part is covered by rainforest and the least proportion by grass or treeveld, the converse of most African mountains. If areas modified by shifting cultivation on the footslopes are avoided, a

PLATE 15 SUMMIT & SLOPE ASPECTS OF GORONGOSA MOUNTAIN



(A) Gogogo summit area with the highest point on the mountain on the left (1863 m alt.). Depicting montane grassland with montane thicket around the base of rock outcrops. Cyathea tree-fern in the foreground. Zombue summit discernable below fern fronds.



(B) Gogogo summit under orographic cloud (guti drizzle) with montane grassland and scattered *Protea gazensis* shrubs.



(C) The 100 m high Murombodzi Falls on the southern slopes of the mountain. A perennial tributary of the Nhandare River flanked by riverine high forest.



(D) Rock outcrop communities — arborescent *Strelitzia nicolai* clumps, and the pedestalled sedge *Coleochloa setifera*, with hair-like foliage on otherwise bare rockfaces.



large series of profile transects can be obtained showing altitudinal and aspect gradients of moisture, physiognomy and species replacement. The main path to the highest summit area of Gogogo enters the lower margin of rainforest on the mesocline at about the 800 m contour where tall, large-boled trees form a canopy between 25 and 30 m. As one ascends the spur in the cool shade of the understorey the canopy level gradually becomes lower and other tree species appear which are mixed with those most common on the highest forest margins. The montane forest of the highest parts rarely exceeds 10 m in height and the canopy leaves appear smaller than those of the lowland forest below. The midslopes are thus a transition zone of mixed forest flora and fauna, the bird components being the most conspicuous. The upper montane forest is generally festooned with *Usnea* lichens and epiphytic orchids and ferns, indicating the zone wreathed longest by cloud.

The exit from montane forest to the summit grasslands is generally abrupt or through a margin of heaths and cedars. Where the change from forest to grassland is sudden the impact on the observer is greatest; from humid cool shade with the scent of leaf litter and the sounds of bird calls to crisp clear air infused with the faint aromatic perfume of everlastings and a riot of flowering forbs amongst the grasses. From the dark humidity of the forest one comes out into a chill wind in bright sunshine, with mist creeping over nearby peaks and breathtaking vistas of the lowlands and distant mountains. Such an experience is at once a balm and a rejuvenation to the whole being for any who live in the adjacent oppressive steaming heat of the coast lowlands.

From the Gogogo summit plateau on clear days the towering peak of Mhanda Inselberg and beyond to the west the Inyanga Mountains of Rhodesia can be viewed, the archipelago of inselbergs towards Tete in the northwest, and the Chimaninani end of the Great Escarpment in the southwest. To the southeast the Urema Lake and surrounding flood plain grasslands on the Rift floor are distinct, and in the northeast the isolated Morrumbala massif at the junction of the Chire and Zambeze Rivers.

91

AQUATIC HERB COMMUNITIES

Open water

The submerged rooted and floating aquatics of the cool lotic or lentic waters on the mountain are unrecorded, but contain a number of species in common with the bog community described below. Herbaceous species on stream margins in the upper reaches, attaining 100 cm in height, include: *Aeschynomene* sp., *Cyperaceae*, *Dissotis* sp., *Melastomastrum* sp., *Restio* sp., *Rhynchospora rugosa* and ferns (Macedo 1970a). A single seasonal tarn or pan occurs on a flat plateau interfluve grassland in the central part of the mountain east of Zombue summit just above the 1600 m contour.



TABLE 8.1

Acid bog herb communities of mountain summits & coast high watertable sands

GORONG	OSA MT. SUMMIT	СН	ERINGOMA COAST
Peat moss	Sphagnum sp.		
Club moss	Lycopodium carolinianum		Lycopodium carolinianum
Grasses	Agrostis continuata	+	Andropogon eucomis
+	Andropogon eucomis	+	Ischaemum arcuatum
	Coelachne africana		Oxyrhachis gracillina
+	Ischaemum arcuatum		Panicum dregeanum
	Sacciolepis luciae		Panicum parvifolium
			Panicum subalbidum
Sedges	Bulbostylis densa		Bulbostylis contexta
	Costularia natalensis		Bulbostylis pilosa
	Cyperus holostigma		Cyperus tenax
	Cyperus leptocladus		Fimbristylis dichotoma
	Ficinia filiformis		Fuirena umbellata
	Fimbristylis hygrophila		Kyllinga pauciflora
	Fuirena stricta		Rhynchospora candida
	Pycreus macranthus	+	Rhynchospora rugosa
+	Rhynchospora rugosa		Rhynchospora triflora
	Scirpus fluitans		
Yellow-eye			
grass	Xyris sp. (KLT 2223, 2293)		Xyris straminea
Pipewort	Eriocaulon sonderanum		Eriocaulon subulatum
Rush	Juncus Iomatophyllus		Juncus kraussii (or J. maritimus)
Forbs	Anagallis gracilipes	+	Drosera burkeana
	Cynorkis anacamptoides		Drosera indica
	Cyrtanthus tuckii		Gentianaceae (KLT 2917)
	Dierama pendulum		Lapeirousia erythrantha
+	Drosera burkeana		Lindernia sp. (KLT 2913)
	Helichrysum adenocarpum		Lobelia erinus
	Laurembergia repens		Mesanthemum africanum
	Lobelia intertexta		Platycoryne pervillei
	Senecio auriculatissimus		Polygala capillaris
	Senecio inornatus		Sauvagesia erecta
	Utricularia appendiculata	+	Utricularia livida
+	Utricularea livida		Utricularia subulata

+ = species in common

Proportional Composition

Mountain Sumit Bog		Coastal Bog				
Mosses	2	1				
Grasses	5	6				
Sedges	10	9				
Sedge-like herbs	3	3				
Forbs	12	12				

TABLE 8.2

Reproductive periods of bog and view herbs on the Gogogo summit plateau of Gorongosa Mountain (1700–1830 m).

(recorded from 1969 to 1972)

		J	А	S	0	N	D	J	F	M	А	M J
Poaceae	Agrostis continuata									+	4	
	Andropogon eucomis							+	+	+		
	Coelachne africana									+		
	Ischaemum arcuatum					+	+	+	+	+	1	14
	Sacciolepis luciae									+	+	
Cyperaceae	Bulbostylis densa									+		
	Costularia natalensis						+	+	+	+	+	
	Cyperus holostigma										+	
	C. leptocladus						+	+				
	Ficinia filiformis						+	+				
	Fimbristylis hygrophila					+	+	+	+	+	+	
	Fuirena stricta										+	+
	Pycreus macranthus						+	+				
	Rhynchospsora rugosa						+	+	+	+	+	
	Scirpus fluitans						+	+	+	+	+	+
Xyridaceae	Xyris sp. (KLT 2223, 2293)				+	+	+	+	+	+	+	
Eriocaulaceae	Eriocaulon sonderanum						+	+	+	+		
Juncaceae	Juncus Iomatophyllus				+	+						
Orchidaceae	Cynorkis anacamptoides									+		
Amaryllidaceae	Cyrtanthus tuckii			+	+	+						
Haloragaceae	Laurembergia repens									+	+	
Primulaceae	Anagallis gracilipes						+	+	+			
Lentibulariaceae	Utricularia appendiculata									+	+	
	U. livida									+	+	
	Genlisea hispidula						+	+	+	+		
Campanulaceae	Lobelia intertexta	+	+	+	+	+	+	+	+	+	+	+ +
Compositae	Helichrysum adenocarpum									+	+	
	Senecio auriculatissimus	+	+	+	+	+	+					
	S. inornatus								+	+		

2 2 3 5 7 14 14 11 20 16 4 1 (99 total occurrences)



BOGS & VLEIS

Around valley heads and on stream margins in the summit grasslands, are springs and oozes which support perennial low herbaceous bog communities, generally less than 50 cm in height. Some are peat bogs dominated by patches of *Sphagnum* moss, mixed with sundews and many small mat-forming herbs of rhizomatous, stoloniferous and tufted growth form. The more seasonal bogs support pure patches of the 150 cm tall pedestalled sedge *Costularia natalensis*. The bogs are extremely acid (pH 4) and are closely related floristically in species, or species equivalents, to the acid coastal bogs on high watertable podsolic sands. Their compositional proportions of mosses, grasses, sedges, cyperoids and forbs are also very similar. Sedges and small forbs predominate in each. For this reason the components of the montane and lowland bogs are listed together for comparative purposes (Table 8.2). No saline waters are known to occur on the mountain.

Phenology

The majority of the bog and vlei components on the highest summit area of the mountain show a midsummer and autumnal peak in flowering. Some species such as *Lobelia intertexta*, which also occurs in the adjacent grasslands, flowers throughout the year. The spread of the reproductive period of bog herbs may differ annually, depending on the incidence of precipitation, frost, and fire. In two years of monthly visits to the Gogogo summit area, the red fire lily *Cyrtanthus tuckii* was only recorded once, in a consecutive period of three months, following a fire which had burnt off both grassland and vlei areas.

Environmental factors

Fires are not an annual event on all the summit grassland and vleis of the mountain. Some areas are only burnt once in two or three years. If the Gogogo summit area escapes early or midwinter fire started by tribal hunters, fire from the lowlands only reaches past the narrow spur late in the dry season (September or October) or is extinguished by orographic rain before it ascends as far as the uppermost slopes.

Frost occurs at night during the midwinter months on flat and concave terrain of the grasslands, but no data is available on frequency or intensity. At the same altitude in the Inyanga Highlands, 100 km west of Gorongosa, frosts are recorded in June and July only (Rhodes Estate records).

92

Succession

Natural headward erosion by migrating nickpoints of streams, or more usually by pipe erosion and the development of sink holes, indicated by lone or clumpted tree ferns *Cyathea dregei*, result in the slow elimination of bog and vlei areas. The process is slow due to the coherence of the peaty soils bound by a dense root mat. Thus vlei areas remain as perched systems on either side of deep narrow streams which originated as subsoil drainage. This substrate sequence results in a plant succession which shows the following stages on the mountain: bog (perennial) — vlei (seasonal) — riverine suffrutex stage — shrub stage — forest. The sequence can go from vlei directly to donga erosion, which is then invaded by woody forest components. Similar gradual or more rapid successions are shown in the development of herb vlei to swamp forest.

ROCKFACES

Communities

The rounded granite rockfaces are covered in radial lines of pure stands of the pedestalled sedge *Coleochloa setifera* which attains 100 cm in height and has hair-like foliage. In greater or lesser abundances, either on the pedestals themselves or in mats, are associated lichens, ferns, orchids, *Aloe arborescens, Crassula argyrophylla, Hypoxis spp, Vallozia sp,* and others. A cycad, *Encephalartos* sp., is reported from rock outcrops on the northern rim of the mountain near Inhantete summit.

Phenology

The flowering of three components were recorded: *Aloe arborescens* (April to July), *Coleochloa setifera* (January to March) and *Crassula argyrophylla* (October to November). The aloe also occurs as a component of montane thicket and as an epiphyte on tree trunks of the forest margins.

Environmental factors

In some sites *Coleochloa* is sufficiently dense to be burnt off by veld fires, otherwise rockfaces are never burnt. Most outcrops occur in exposed sites and are excessively drained and experience a contrasting sequence of precipitation from mist, direct high insolation, and strong wind.



TABLE 8.3

Flowering periods of montane grassland components on the Gogogo summit area of Gorongosa Mountain (1700–1840m) (recorded from 1969 to 1972)

		JASOND JF MAM	J
Poaceae	Agrostis continuata		
1 Gaucac	Andropogon eucomis	+ +	
	Andropogon schirensis	+ + + +	
	Andropogon flabellifer	+ +	
	Aristida recta	terror to the total to partners, I	
	Digitaria apiculata	+ + + + + + +	
	Elionurus argenteus	+ + + + + +	
	Eragrostis racemosa	and the second s	
	Eragrostis volkensii	+ + + + + + +	
	Eulalia villosa	+ + + + + + +	
	Festuca abyssinica	+ + + + + + + +	+
	Festuca costata	+ + +	
	Koeleria capensis	+ + +	
	Loudetia simplex	+ + + +	
	Merxmuellera davyi	+ + + +	
	Microchloa caffra	+ +	
	Monocymbium ceresiiforme	C> 1700 tm l tm l t	
	Panicum ecklonii	+ + +	
	Panicum inaequilatum	+ + + + + + + + +	
	Rhynchelytrum rhodesianum	+ +	
	Setaria anceps	+ + + + + + + + + + + + + + + + + + + +	
	Setaria sphacelata	the good from more of the	
	Sporobolus mauritianus		
Cunavasasa	Sporobolus subtilis	+ + + +	
Cyperaceae	Bulbostylis schoenoides Bulbostylis macra	+ +	
	Pycreus macranthus		
	Schoenoxiphium sp. (KLT 2289)	+ +	
Commelinaceae	Commelina africana	+	
001111110111100000	Commelina diffusa	+	
	Cyanotis barbata	+	
Liliaceae	Albuca kirkii	+ and the transfer of the tran	
	Aloe rhodesiana	+ + + +	
	Dipcadi longifolium	softens, with an everant	
	Kniphofia linearifolia	+	
	Ledebouria revoluta	+ + + +	
	Urginea nyasae	+	
Amaryllidaceae	Cyrtanthus sp. (KLT 2201)		
Hypoxidaceae	Hypoxis dregei	+ +	
Iridaceae	Gladiolus sp.	+ +	
	Dierama pendulum	+ + + + + +	
Orahidaaaa	Moraea spathulata		
Orchidaceae	Satyrium neglectum Satyrium chlorocorys		
Proteaceae	Protea gazensis		
Santalaceae	Thesium scabridulum	+ + +	
	Thesium sp. (KLT 2526)	The order of the second	
Caryophyllaceae	Silene burchellii	+ +	
Ranunculaceae	Knowltonia transvaalensis		
Crassulaceae	Crassula alsinoides	+	
Papilionoideae	Aeschynomene nodulosa	+	
	Argyrolobium rupestre	+	
	Crotalaria gazensis	- Carrier of the contract +	
	Eriosema buchananii	+ + + +	
	Eriosema burkei	+ +	
	Eriosema lebrunii	+ +	
	Indigofera cecilii	+ + + + + + + + + + + + + + + + + + + +	
	Indigofera setiflora	+ +	4
	Kotschya scaberrima Lotus wildii	1 + + +	'
	Rhynchosia clivorum	+ +	
	Vigna nervosa	+	

TABLE 8.3 (continued)

			J	Α	S	0	N	D	J	F	M	Α	М	J
Geraniaceae	Geranium incanum		+					+	+	+	+	+	+	+
Polygalaceae	Polygala ohlendorfiana			+				+	+	+	+	+	+	+
Apiaceae	Alepidea longifolia					+								
	Pimpinella sp. (KLT 2076, 2101)										+	+	+	
Gentianaceae	Sebaea leiostyla		+	+							+	+	+	
Lamiaceae	Acrocephalus chirindensis										+	+		
Scrophulariaceae	Alectra sessiliflora											+		
	Nemesis montana										+			
	Sopubia mannii										+	+		
	Sutera carvalhoi		+									+	+	+
Dipsacaceae	Scabiosa austroafricana							+	+	+	+			
Campanulaceae	Cyphia mazoensis											+		
	Lobelia chamaedry folia					+						+		
	Lobelia intertexta			+	+	+			+			+		
	Wahlenbergia virgata					+	+	+	4					
Compositae	Athrixia rosmarinifolia					+								
	Conyza subscaposa			+	+	+								
	Gerbera ambigua					+	+	+	+					
	Senecio erubescens							+	+					
	Senecio swynnertonii			+				+	+					
	Tolpis capensis			+					+	+	+			
	Vernonia natalensis							+	+					
	Helichrysum adenocarpum											+		
	Helichrysum buchananii											+	+	
	Helichrysum cephaloideum										+			
	Helichrysum gazense		+	+									+	+
	Helichrysum odoratissimum		+											
	Helichrysum nitens				+	+	+							
	Helichrysum nudifolium					+	+	+	+					
	Helichrysum pilosellum								+					
	Helichrysum setosum											+		
	total occurrences		10	15	8	31	17	30	44	18	35	36	10	6 (260)
		%	4	6	3	12	7	12	17	7	13	14	4	2



Succession

The isolated tufts of *Coleochloa*, whilst not initiating the confluence of root mats, allow such a process to take place. The more horizontal rockfaces become completely covered by root mats and dense shrub stages of succession occur, comprising most of the species described under Montane Thicket. On steeper faces the plant mass can exceed the angle of repose and slumping occurs in patches. In isolated sites the sequence is: herb mats — suffrutex and shrubs — scrub thicket — gravity slide — bare rock — repeat of sequence. No sites were found where the woody cover had attained a forest dimension.

GRASSLAND

The mountain grasslands comprise three main types: montane (> 1700 m) and submontane (1400-1600 m) treated together, and upland (800-1400 m). The last occurs as pure swards, only on the benches of the southwest slopes of the mountain, elsewhere the slopes are wooded to a greater or lesser degree and form part of the moist extreme of miombo savanna.

Montane grassland

The montane grassland of the Gogogo summit plateau above the 1700 m contour is composed of a dense sward of tufted perennial grass species, with an average height of 40 cm in the vegetative state and 80 cm when in inflorescence. The striking feature which separates montane grassland from all the lowland types, except the dambo or high watertable grasslands on sands, is the abundance of associated forbs and suffrutices. The large tussocks of *Merxmuellera davyi* (ex. *Danthonia davyi*) also contribute to the distinctiveness of montane grassland physiognomy. The most important grasses in the Gogogo summit area are *Andropogon schirensis*, *Eragrostis volkensii*, *Festuca abyssinica*, *F. costata* and *Merxmuellera davyi*. The most important associated forbs are composites (*Helichrysum* species) and papilionaceous legumes.

Macedo (1970a, 1970b) reports that the grasslands at a lower level, between 1400 and 1600 m on rounded relief of the valley heads in the centre of the mountain, are dominated by *Monocymbium ceresiiforme* and *Loudetia simplex*.

94

Twenty four grass species and sixty nine forb species representing twenty three families were collected over a two year period at monthly intervals from the Gogogo summit grassland. Of the latter, composites made up 23%, and papilionaceous legumes 17% of the total. Nine of the sixteen composites were *Helichrysum* species. The montane grass-forb association can therefore be defined as *Festuca — Helichrysum — Pailionoideae* grassland the total list of ninety three species appears under the following section Table 8.7).

It is significant that high grass species diversity per unit area, and rich forb and suffrutex floras, are associated only with acid leached grasslands as exemplified by montane, upland and moist savanna (eg. miombo), and high watertable (podsolized) sands in lower rainfall and coastal situations. This contrasts with the low grass species diversity per unit area, and relatively poor forb flora of grasslands on heavier acid or alkaline base saturated soils.



Phenology

Conspicuous mass flowering of one or several species at different times of the annual cycle is a feature of montane grassland. The succession of aspect dominance on Gogogo summit comprises:

Compositae: Liliaceae: Helichrysum nitens Urginea nyasae

OCTOBER

Poaceae:

Festuca costata

JANUARY

Poaceae: Liliaceae: Andropogon schirensis

Knipphofia linearifolia

MARCH

Orchidaceae: Compositae: Satyrium neglectum Helichrysum cephaloideum

Compositae:

Helichrysum buchananii

APRIL - MAY

Greatest mass flowering of four species occurred around the time of the autumnal equinox in March. In the lower grassland in the centre of the mountain, both grass dominants *Monocymbium* and *Loudetia* showed aspect dominance in the late summer and early autumn.

Flowers of some species such as *Geranium incanum* are to be found in almost every month of the year except when veld fires have occurred. Sedge components of the grassland are all in full inflorescence in midsummer, and the grasses and composites show a trimodal peak at the time of the equinoxes and summer soltice, ie. October (vernal), December — January, (aestival) and April (autumnal). The papilionoids also show three peaks, in July (hibernal), January and April. Forbs that flower only during the winter season include *Helichrysum gazense*, *Helichrysum odoratissimum*, *Kotschya scaberrima*, *Sebaea leiostyla* and *Sutera carvalhoi*. The three main peaks coincide closely with the two radiation peaks near the equinoxes, caused by high cloud cover values over the intervening summer period, and with the summer solstice at the peak of the rains and with daylength. A lesser August peak is caused by the occurrence of fire in the late winter.

The effect of veld fires in stimulating the unseasonal or earlier flush of grass-land and savanna is well known in Africa (eg. Phillips 1965, West 1965, and their bibliographies). However, fire-induced flush of grasses only occurs where there is sufficient soil moisture; in the arid savannas of Botswana and South West Africa grasslands may remain bare for several months after fire until the advent of the first rains (Tinley 1966). Out of phase, early flowering of certain grass and forb components was recorded in Agust 1971 after a fire at the end of July had burnt the greater part of the Gogogo summit area. Flowering specimens confined solely to the burnt areas included the

grasses Andropogon flabellifer, Elionurus argentens, Koeleria capensis, Michrochloa caffra, Rhynchelytrum rhodesianum, and the forbs Indigofera cecilii, Polygala chlendorfiana and Tolpis capensis. Senecio swynnertonii however was flowering equally abundantly in both burnt and unburnt grassland at the same time (Table 8.3).

Bayer (1955) suggests that fire stimulates early flowering in grassland components by heating up the ground, which simulates the increase of soil temperature in the spring. Bayer points out too, that a large proportion of spring aspect forbs have underground storage organs or have greater ability to obtain moisture and are thus independent of the first rains on which the grass components generally rely. Due to these features and contrasting seasonal influences, the response of vernal and autumnal forbs is quite different; the former are stimulated by fire and the latter are generally suppressed. Bayer concludes that the whole behaviour of the spring aspect plants points to the antiquity of lightning fires as a normal periodic event in the ecology of grasslands (see also Komarek 1964, 1965). Lemon (1968) describes the increase of vigour after fire of certain grassland forbs on the Nyika Plateau in Malawi.

Environmental factors

No climatic data is available from the summit grassland areas, thus the frequency intensity of features such as precipitation fog, drought, and frost are unknown. The summit areas are subject to frequent orographic fog and drizzle (*guti*) throughout the year, especially in spring, summer and autumn, occurring on more than 14 days per month, and least in May (8 days), as judged by data from the Great Escarpment on the frontier (Fig 4.12). The increased cloudiness and humidity, resulting in decreased light intensity and temperature is strikingly expressed by the abundance of ephiphytes on the crowns and trunks of the montane forest trees near the summit. Judging by the Inyanga records, frosts can be expected in the summit grasslands in June and July.

Fire occurrence has been dealt with above in relation to bog and viei communities. The influence of fire on flowering of both grasses and the associated spring aspect forbs has been noted above.

Intensity of fire is directly dependent on the distribution of precipitation in any one year. The mountain summits are generally at their driest in September and hot fires can then extend from the grasslands into the forest margins and through montane thicket. The only clear evidence that veld fires are reducing forests on their margins in the entire transect is in the summit areas of Gorongosa Mountain. It seems contradictory that fire in relatively short grasslands in a humid regime should have devastating ef-

95



Environmental factors

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fect on forest, when in the dry lowlands fire in medium to tall (3—4 m) grasslands has little or no retarding effect on the long term configuration of existing forests, or in suppressing thicket and forest extension on the coast. The disproportional impact of fire may be more closely tied to the soil moisture balance regimes in the different sites rather than abundance of grass fuel or severity of the dry season. This aspect seems to have been little studied in the detailed longterm investigations on fire in various parts of Africa, and thus the whole subject remains an open question.

Succession

Over most of the summit areas montane grasslands and forest meet abruptly without any ecotonal shrub margin. In the heads of the valleys in the central part of the mountain, grassland is replacing forest as fires burn back their edges. On valley slopes a scrub zone, of varying width comprising mainly bracken *Pteridium aquilinum* and *Smilax kraussiana*, separates pure grassland from the riverine forest strips. In this scrub, forest precursors such as *Trema orientalis*, *Maesa lanceolata*, *Harungana madagascariesis*, *Dombeya burgessiae* and tall ginger plants *Zingerberaceae* are to be found.

In the summit areas where boulder outcrops occur, tall thickets of pure or mixed *Philippia benguellensis* and *Widdringtonia nodiflora* are interposed between the grassland and forest, and these are burnt out at intervals long enough to allow regeneration to a canopy height of 10 m.

The progressive and retrogressive succession of these zones appear to vacillate with the occurrence of consecutive years of either high rainfall or drought, the devastation by fire being greatest in the latter. The ending surfaces are generally being invaded by forest or scrubthicket seral to forest, and grassland is extending on the stable rounded topography.

Upland grassland

On the southwest slopes of the mountain, dense swards of tufted perennial grasslands cover bench plateaux between the 800 and 950m contours. These are generally taller than the montane grassland, averaging 80 cm in height in the vegetative state. Main components include *Loudetia superba*, *Themeda triandra*, *Trachypogon spicatus* and *Tristachya hispida*. On forest margins *Cymbopogon validus* becomes dominant and on savanna margins *Hyparrhenia filipendula H. tamba*, *H. variabilis*, *Panicum maximum* and other species common to the miombo. In most sites on latosols or on old cultivation sites the grasses *Pennisetum purpureum* and *Melinus* sp. form extensive dense clumps up to 4 m in height.

The pure bench grasslands occur on what appear to be soils which are excessively waterlogged after the occurrence of rains and which subsequently become extremely dry. They are avoided by subsistence cultivators. On the slopes of the Nhandare River the benchlands have been broken up by mass slumping which indicates a deeply weathered profile on the gabbro geology.

96

Veld fires burn these grasslands almost every year except when well distributed rains occur. At one time a thriving beef ranch was maintained on the southwest slopes of the mountain and one of the most important pasture grasses was *Cymbopogon validus*. Under heavy grazing this tufted species, which attains 3 m in height, assumed a prostrate growth form and became more vegetatively productive.

Succession

These grasslands are climax cover on the bench plateaux, with tension zones against forest or thicket in moist sites on valley slopes and streambanks, and against savanna in stoney sites and areas of old cultivation and overgrazing. Slopes and small scarp areas which may have supported forest in the past, and could be re-invaded by forest under a regime of fire protection, are indicated by the bracken fern *Pteridium aquilinum* with a mixture of *Smilax kraussiana*, *Vernonia* spp., and low scrub with isolated savanna trees such as *Dalbergia nitidula*.

UPLAND SAVANNA

Upland savanna is an altitudinal tailing off of the surrounding Midland miombo and mixed acacia and broadleaf savannas of the valleys, up the sides of the mountain. The former on the mesoclines, and the latter, which relate to the Rift Valley vegetation, extend up the xeroclines. At the same time the uplands have woody savanna species which are found nowhere else in the ecosystem and are confined to the mesocline slopes. These include:

Acacia karoo Cussonia spicata Dalbergia nitidula Erythrina lysistemon Faurea sp. Syzygium cordatum

The savanna of the uplands is typically comprised of pure species savanna patches of even age, separated by grassland or mixed in a mosaic with the thickets. Its appearance is thus quite different to the continuous even spacement (except where



cleared for cultivation) of the surrounding Midland miombo. Although the mesocline and xerocline upland savannas are clearly different in species composition, at each extreme they overlap on transitional aspects and slopes of the mountain, ie. on a single spur, mesocline species occur on the poleward aspect and xerocline species on the equatorward face.

Mesocline Savanna

A patchwork of wooded grasslands, generally single layered, up to 12 m in height but generally shorter, of evergreen and deciduous species. Woody components include:

Acacia karoo (W? Z) Albizia adianthifolia (W) Brachystegia glaucescens (ex B. tamarindoides) (X)

Ficus vogelii (Z) Heteropyxis natalensis (W) Parinari curatellifolia (Z)

Cussonia spicata (Z) Dalbergia nitidula (W) Erythrina lysistemon (Z) Faurea sp (W) Pericopsis angolensis (W) Strychnos spinosa (Z) Syzygium cordatum (Z)

The grass stratum comprises most of the species noted for the upland grasslands. Extensive lists are given by Macedo (1970b) for this aspect in his Complex 16.

Xerocline savanna

Open to closed canopied tree stratum attaining 10 m in height and dominated by broadleaf combretaceous species such as:

Combretum fragrans (W) C. molle (W) C. zeyheri (W) Terminalia mollis (W) T. sambesiaca (W) T. sericea (W)

other tree species include:

Afzelia cuanzenis (Z)
Burkea africana (W)
Diplorynchus condylocarpon (W)
Kirkia acuminata (W)
Lonchocarpus bussei (W)
L. capassa (W)
Markhamia obtusifolia (W)
Peltophorum africanum (W)

Sterculia quinqueloba (Z)
Stereosperum kunthianum (W)
Piliostigma thonningii (Z)
Pterocarpus angolensis (W)
P. brenanii (W)
P. rotundifolia (W)
Sclerocarya caffra (Z)
Xeroderris stuhlmannii (W)

97

Pure woodland patches of *Millettia stuhlmannii* (X) with a closed canopy occur on sandy colluvium. This and the xerocline savanna merge into tall thicket areas, especially on the pediments and lower talus slopes of the mountain. Most species are strongly deciduous. Macedo (1970b) gives extensive lists of similar species in different combinations for the communities he recognizes on the xerocline. The grass stratum is relatively sparse compared with the mesocline slopes and is composed of:

Andropogon gayanus Digitaria spp. Heteropogon contortus Hyparrhenia spp.
Pogonarthria squarrosa
Themeda triandra

and interspersed with tall (3-4 m) patches of *Beckeropsis unisetta* and *Rottboellia* exaltata.

Dispersal

On the mesocline are 7 (50%) occurrences of animal dispersed fruits, 6 (43%) by wind and 1 (7%) is an active ballist. Nearly equal importance of wind and animal dispersed species pertains on the mesocline. By contrast 18 (78%) on the xerocline are wind dispersed plus 4 (17%) animal dispersed and 1 (4%) explosively dehiscent (Fig 8.3).

Environmental factors

The upland savannas are burnt out annually, but the intensity and reach of fire depends on the density of the grass stratum. The closed canopy patches forming woodlands are often devoid of a grass understorey and fire may burn through the leaf litter at most, otherwise they remain as unburnt patches. The upland savanna and grasslands, unlike the thicket and forest patches with which they mosaic, are relatively undisturbed by shifting cultivation as the forested soils with their high humus content are preferred by tribal cultivators.

Succession

The savanna and grass areas appear to be in quasi-equilibrium and show no active scrub encroachment or reduction of area except where local overstocking or past cultivation has disturbed the soils, resulting in the spread of low dense scrub. In the absence of such disturbance, separation of forest, savanna and grassland is determined chiefly by edaphic factors.



SCRUB-THICKET

The largest areas of scrub-thicket occur at intervals on the lower slopes of the mountain which have long been subjected to shifting cultivation and annual veld fires. Small patches of scrub-thicket occur in the montane zone but as these usually form the field layer to trees taller than 4 m they are treated with the next physiognomic group.

On the southern and eastern slopes of the mountain the full spectrum from bracken to tall thicket occurs as a mosaic on different age cultivation fallows. Dense scrub-thicket with a closed canopy at about 3 m height occurs on the lower margins of rainforest mostly on old cultivation sites. This cover is composed of a large variety of woody forest, savanna, thicket and alien species recombined from the original cover and the juxtaposed communities.

Components include:

SCRUB

Acacia karroo (W? Z)
A. polycantha (W Z)
Albizia adianthifolia (W)
Annona senegalensis (Z)
Antidesma venosum (Z)
Bauhenia petersiana (X)
Bridelia micrantha (Z)
Brachylaena rotundata (W)
Cassia petersiana (Z?)
Dombeya burgessiae (W)
Entada abyssinica (W)

Harungana madagascariensis (Z)
Heteromorpha trifoliata (W)
Lobelia johnsonii (W?)
Maesa lanceloata (Z)
Mussaenda arcuata (Z)
Securidaca longipendunculata (W)
Strychnos spinosa (Z)
Trema orientalis (Z)
Vernonia sp (W)
Vitexpayos (Z)

CLIMBERS AND SCANDENTS

Bauhenia galpinii (X)
Clematis sp (W)
Combretum paniculatum (W)
Friesodielsia obovata (Z)
Landolphia sp (Z)

Lantana camara (Z)
Macuna coriacea (X?)
Rhoicissus tridentata (Z)
Rubus sp (Z)
Smilax kraussiana (Z)

HERBS

Afromomum sp Dissotis sp Leonotis leonurus Pteridium aquilinum

GRASSES

Cymbopogon validus Imperata cylindrica Melinus sp. Panicum maximum Pennisetum purpureum Setaria chevalieri 98

This thicket grades into riverine forest in the valleys where *Filicium decipiens*, *Halleria lucida*, *Oreobambos buchwaldii* (bamboo) and *Trichocladus ellipticus* are important constituents. Lone or clumped forest canopy remnants such as *Chlorophora excelsa* and *Newtonia buchananii* are left as islands in riverine and talus slope sites. Many other constituents are listed by Macedo (1970a, 1970b).

Dispersal

Of the 26 woody species listed there are 18 (55%) occurrences of animal dispersed fruits, 12 (36%) wind dispersed and 3 (9%) explosively dispersed (active ballists).

Environmental factors

As these scrub-thickets abut on grasslands they are burnt out by veld fires during exceptionally dry periods, but otherwise largely escape annual fire.

Succession

Scrub-thicket is seral to forest through a thicket stage on the mesocline slopes of the mountain, and to thicket on the xeroclines.

THICKET

Two main kinds of thicket occur on the mountain: montane thicket in the summit areas and tall pediment thickets adjoining riverine zones on the xerocline.

Montane Thicket

The thicket areas on the summit occur in patches with a canopy varying in height from 4 to 10 m, chiefly on torfields or around the base of the domed granite outcrops. The irregular shaped patches are either interposed between the upper limits of montane forest and the summit grasslands, or occur as separate features related to the outcrop areas. The canopy spacement varies greatly from closed clumps to scattered tree specimens linked by a tangled scrub thicket fieldlayer of shrubs and suffrutices. Two canopy components, the cedar *Widdringtonia nodiflora* and the arborescent fynbos *Philippia benguelensis*, form pure even-sized stands of mature trees attaining 10 m in height.

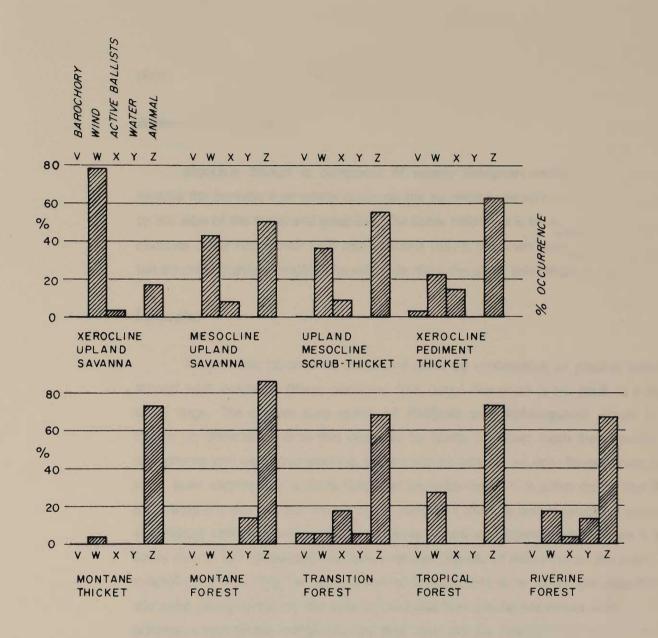


FIG. 8.3 COMPARATIVE OCCURRENCE OF DISPERSAL TYPES IN

WOODY COMPONENTS OF SAVANNA, THICKET AND FOREST

ON GORONGOSA MOUNTAIN (PRIMA FACIE DATA)



On the numerous air traverses made by the author in a light aircraft over the mountain only one area of tall pole-stands (plantation-like) of *Widdringtonia* was encountered; in the central area of the mountain immediately below the isolated tarn mentioned in the Aquatic Communities. This cedar woodland appears to be closer to 20 m in height. The pure thickets of *Philippia* too are clearly discernible from forest on air photographs or from an aircraft due to their contrasting extremely fine leaf texture. The only other woody species associated with the nearly pure thickets of *Philippia* is *Myrica pilulifera* which is similarly associated with the otherwise pure scrub-thickets of coast fynbos *Philippia simii* on the Cheringoma cuesta.

Montane thicket is composed of some forest species, those from forest margins, rock outcrops and its own non-forest constituents.

Components include:

TREES

Buddleia salviifolia (W)
Cassine papillosa (Z)
Curtisia dentata (Z)
Halleria lucida (Z)
Kiggelaria africana (Z)
Maesa lanceolata (Z)
Maytenus acuminata (Z)
Myrica pilulifera (Z)

Nuxia congesta (W)
Philippia benguensis (W)
Pittosporum viridiflorum (Z)
Rhamnus prinoides (Z)
Rhus chirindensis (Z)
Strelitzia nicolai (Z)
Widdringtonia nodiflora (W)

SHRUBS AND SUFFRUTICES

Aloe arborescens
Anthospermum ammanioides
A. vallicola
Cliffortia nitidula
Hypericum revolutum
Indigofera lyallii

Myrsine africana
Philippia hexandra
Plectranthus sp (KLT 2420)
Polygala virgata
Stoebe vulgaris
Tephrosia grandibracteata

In some areas *Indigofera Iyallii* forms pure scrub-thicket patches up to 3 m in height on the margins of thicket or forest. The 7 m tall, banana-like *Strelitzia nicolai* is an important component of coast dune forest from the Eastern Cape through Natal to the Mocambique coast south of Inhaca Island. It is absent north of Inhaca but reappears again as a montane species in the Great Escarpment mountains of the Rhodesian-Mocambique frontier. Gorongosa appears to be its northernmost distribution limit.

Dispersal

Eleven (73%) of the thicket free components have animal (mainly bird) dispersed fruits, 4 (27%) are wind dispersed, passive ballists (Fig 8.3).

Environmental factors

Montane thicket is composed of mostly evergreen species but during dry months the periodic fires which occur on the summits burn into or through this cover to the edge of the forest and grassland. The dense fieldlayer is the main fuel, but where clumped cedar occur their high resin content results in crown fires. *Philippia* patches too are more highly susceptible to veld fires than the other thicket cover.

Succession

Thicket can be seral to forest and grow by coalescence of patches initiated around rock outcrops. Where damaging fires occur the cover is set back to a dense scrub stage. The mature pure stands of Philippia and Widdringtonia appear to be climax on different soils to that occupied by forest. However, both these species are heliophytes and vigourous seedling, sapling and polestands are only found where there is an open understorey; a dense fieldlayer excludes them. It is often stated that Widdringtonia is a dry "forest" but in many mountain areas as on Gorongosa it occurs in the highest rainfall cloud zone. The dryness or lack of understory luxuriance is probably due to soil factors and the fallen needles. Stands of casuarina on the coast, for example, are also "dry" in comparison to the adjacent dune forest, yet they receive the same precipitation. In the sites where these two species are mixed with the components noted above, indications are that they will be overtaken by maturation of thicket and remain as canopy relics, only able to become re-established on the margins or after fire has opened up the fieldlayer. It is the latter which may be responsible for the even-aged appearance of many Widdringtonia stands; simultaneous colonization of newly opened substrates. Succession in this cover is therefore progressive, retrogressive or homeostatic depending on circumstances.

Pediment Thicket

Mostly deciduous with some evergreen species forming a closed canopy at about 20 m. Consists of a mixture from rainforest, dry forest, riverine, termitaria, and savanna systems. The tall thickets in valleys of the xerocline slopes and pediments



merge with riverine and shorter thicket types of the adjoining Midlands. Components, as derived from Macedo (1970b Complex No. 16) include:

TREES (mid to upper layers)

Acacia nigrescens (W? Z) A. sieberana (Z) Afzelia cuanzensis (Z) Albizia glaberrima (W) A. versicolor (W) Burkea africana (W) Bauhenia petersiana (X) B. tomentosa (X) Cassia abbreviata (Z) Celtis sp. (Z) Cleistanthus schlechteri (X Z?) Combretum fragans (W) C. imberbe (W) Cordyla africana (Z) Diospyros mespiliformis (Z) Euphorbia sp (X, Z)

Ficus 3 spp (Z)
Flacourtia indica (Z)
Kigelia africana (V, Z)
Lannea stuhlmannii (Z)
Lecaniodiscus fraxinifolius (Z)
Millettia stuhlmannii (X)
Pterocarpus rotundifolia (W)
Sclerocarya caffra (Z)
Shrebera tricoclada (W)
Sterculia appendiculata (Z)
Strychnos madagascariensis (Z)
S. potatorum (Z)
Tamarindus indica (Z)
Trichilia emetica (Z)
Ziziphus mucronata (Z)

Dispersal

Of 37 dispersal type occurrences, 23 (62%) are by animals, 8 (22%) by wind, 5 (14%) by explosive dehiscence, and 1 (3%) by weight (barochory).

Environmental factors

Although most of the riverine and pediment thickets of the xeocline are undisturbed by man, some on the western basal slopes may have originated on old cultivation sites. Veldfires generally die out when encountering thicket, singeing the margins and extending a short way into the understorey in parts. Although the majority of components are deciduous many are tardily or only slightly deciduous, depending on the distribution and amount of rainfall in any year. Midsummer droughts cause unseasonal leaf fall in some, followed by a new flush in February and March.

Succession

No data was personally gathered on the xerocline thickets. Macedo (1970b) only notes upperstorey species, thus sapling dominance and the seral tendency is unknown. However, most of the thickets appear to be in a climo-edaphic equilibrium and are only seral to forest where moisture conditions allow, such as streambanks and valley heads.

100

FOREST

Above the 600 m contour, which separates Gorongosa Mountain from the surrounding Midlands, 50% (300 km²) of the mountain is covered in rain forest, 7% (40 km²) is summit grassland and the remainder 43% (260 km². mostly on the flanks) is savanna. Due probably to its relatively low altitude, a clear zonation, as is apparent on the volcanic mountains of the eastern Congo for example, can only be found on Gorongosa Mountain where forest occurs as an unbroken cover from near the base to the summits. In such situations it is possible to separate the tall lowland tropical zone, a middle transitional zone with mixed species composition, and an upper montane (or Afrotemperate zone) of shorter less luxuriant forest with an abundance of epiphytes, and summit grasslands with everlastings and the tree heaths.

Lebrun (1935) working in the eastern Congo was the first to designate what he called Transition Forest, consisting of a mixture of species from the montane and tropical formations. Chapman & White (1970) refer to this zone as submontane in Malawi, however in many sectors a greater tropical influence is apparent and it is then correctly subtropical! It is thus more realistic to maintain Lebrun's term. The width of these zones depends on moisture conditions in different aspects and the interfingering of ravines and spurs. Tropical species occur to much higher altitudes in the ravine sites.

On Gorongosa Mountain the altitudinal limits to the three zones are similar to that given for the eastern Congo by Lebrun (1934): Tropical below c. 1200 m, Transition 1200 — 1600 m, and Montane (Afrotemperate) above 1600 m. Macedo (1970a, 1970b) recognized similar altitudinal limits for the montane and tropical forests on Gorongosa Mountain. On lower isolated mountains such as Morrumbala, at the junction of the Chire and Zambeze Rivers, montane and tropical species are codominant in the canopy at the heads of gulleys at about the 1000 m contour. A similar situation exists on the inselbergs and fore-ranges near the Frontier Great Escarpment. The greater part of the forest area of Gorongosa Mountain is probably occupied by Transition Forest as exemplified by *Podocarpus milanjianus* (Afrotemperate) and *Newtonia buchananii* (Tropical) occurring as canopy dominants side by side. Chapman & White (1970) recognize the canopy tree *Chrysophyllum gorungosanum* as the indicator for their submontane (Transition) Forest. Transition Forest can thus be expected to be floristically richer than the zones above and below it.

As there is continued debate by workers on the status and affinities of these mountain forests, one fundamental factor, which becomes obvious as soon as explained, requires emphasis. Over the whole of eastern Africa, from the Cape to Ethiopia, forest is confined to three main sites: scarps, ravines and the land-sea junction.



The important point about mountain masses of any dimension is their orographic rain regime and this islanding of high rainfall zones results in an overlay of rain forest conditions with altitudinal effects. At the same time a converse situation exists where typical montane genera such as Podocarpus, Philippia, Ilex, Rapanea and Myrica occur in high rainfall lowland sites on podsalized high watertable sands. On the Mocambique Coast montane components occur in swamp forest, on the margins of dambos, and in tropical evergreen forest on leached duplex sands. On the continental plateau away from montane sites, *Podocarpus* and *Philippia* are associated with dambo swamp forests (mushitu) in northern Zambia (Lawton 1963). Like river valleys and rock outcrops, termite hills are important two-way stepping stone links for forest and/or arid or desertic elements. Thus even for an apparently conservative system such as montane forest which is essentially similar throughout Africa south of the Sahara, the interplay of geomorphic succession and biogeographic recombinations act as species filters and provide forest components a diversity of refuge sites, homeostatic habitats or initial sites for expansion in which thickets of all kinds play a fundamental role.

Montane Forest

The uppermost temperate forest zone, generally above the 1600 m contour, is composed of mostly evergreen trees forming a closed canopy at 10 to 15 m; in some areas shorter, whilst in gullies emergents may attain 25 m. The soils are either deeply weathered, acid fersiallitics developed on fine grained granite, or lithosols. In contrast to the lower tropical zone, the subordinate small tree layers are poorly developed as is the shrub or sapling layer; instead dense societies of acanthaceous herbs, labiates and balsams occur in patches where the tree canopy is sparce. Rocks and canopy branches are festooned with epiphytic mosses, club-mosses, ferns and orchids with *Usnea* lichen hanging from exposed canopy branches. The canopy trees typically include:

Aphloia theifomis (Z)
Curtisia dentata (Y, Z?)
Ilex mitis (Z)
Kiggelaria africana (Z)
Maytenus acuminata (Z)
Ocotea kenyensis (Z)

Pittosporum viridiflorum (Z?) Podocarpus milanjianus (Z Y) Rapanea melanophloeos (Z) Schefflera abyssinica (Z) Syzygium musukuense (Z) Xymalos monospora (Z?)

Soft-leaved herbs of the forest floor include *Impatiens cecillii*, *I. sylvicola*, *Isoglossa milanjensis*, *Plectranthus* sp. and *Salvia* sp. A first collection of ferns totalling 70 species was made from the southwest slope and Gogogo summit area of the mountain by Schelpe (1966).

Tropical Forest

Newtonia buchananii are major canopy trees but lower down the forest grades into a more tropical array of species similar to those occurring on the Cheringoma coast and the escarpments of the Midlands, including the area below the Chimanimani massif. (Dutton & Dutton 1973). This lowland forest contains many equatorial rain forest species hence the phytogeographic designation of oriental, or eastern, forest domain of the Guinea—Congolian Region (Mond 1957).

The canopy is between 20 and 30 m in height with emergents attaining 35 m especially in gullies and ravines. The trees are a mixture of evergreen and deciduous species with plank buttresses or fluted trunks, and large leaved (mesophyll and macrophyll) physiognomy interspersed with a dominance of bipinnate, mimosa-like (nanophyll), leaflets (eg. *Newtonia*) or microphyll and micro-mesophyll leaflets of caesalpiniaceous (eg. *Erythrophloeum*) canopy trees. The predominance of micro-mesophyll leaf size in the equatorial rain forest is due to the abundance of caesalpiniaceous canopy trees.

The larger areas of the lower tropical forest zone is now confined to the V-shaped patches which follow the rivers which debouch from the steep ravines of the mountain's mesocline slopes. Elsewhere it has been badly damaged by shifting cultivation and only single or clumped canopy relics remain on the talus slopes.

Thus species composition is now chiefly an overlay of rain forest and riverine components. The subordinate tree layers are well defined and the field or sapling layer, up to 3 m in height, is dense. Large stemmed lianes which attain the canopy are a conspicuous feature. Typical upper stratum trees include:

Anthocleista grandiflora (Z?)
Blighia unijugata (Z)
Bombax rhodognaphalon (W? Z?)
Celtis gomphophylla (Z)
Chlorophora excelsa (Z)

Eryghrophleum suaveolens (Z?) Newtonia buchananii (W) Pachystela brevipes (Z) Pteleopsis myrtifolia (W) Syzygium guineense (Z)

The tropical forest zone occurs, in addition to riverine zones to which it is now largely confined, on fersiallitic and colluvial soils derived from gabbro or granite, or a mixture of both basic and acid talus, or on lithosols, (these include Fernandes' 1968a) types Vb, Lb, Cvb, Cbv).



Transition Forest

Influenced by the temperate zone from above and the tropical zone from below, the bulk of the mountain is covered in Transition Forest which shows the full spectrum of features from both zones in height, physiognomy and understorey features including: undercanopy thickets composed of species such as *Dracaena fragrans* or *Trichocladus ellipticus*, density of climbers, epiphytes and herb societies on an altitudinal transect. Shorter and stag-headed canopy is typical on the crests of the spurs, and the tallest forest trees are usually associated with the gullies and ravines. Similar soils are occupied by Transition Forest as those noted for the tropical zone, and it extends in its upper limits onto ferallitic soils derived from micropegmatite granite.

Median to upper canopy strata trees include:

Apodytes dimidiata (Z?) Bersama abyssinica (Z) Calodendrum capense (Y, Z?) Cassipourea congoensis (Z) Chrysophyllum gorongosanum (Z) Cola greenwayi (Z) Craibia brevicaudata (X) Croton sylvaticus (Z?) (X?) Cryptocarya liebertiana (Z) Drypetes gerrardii (Z) Ekebergia capensis (Z) Fagara sp (X) Ficus kirkii (Z) Filicium decipiens (Z?) Garcinia milanjiensis (Z) G. volkensii (Z) Homalium dentatum (W? Z?)

Linociera battiscombei (Z) Macaranga capensis (X?) Neoboutonia african (X, Z?) Newtonia buchananii (W) Olea capensis (Z, Y) Phyllanthus discoideus (X, Z?) Rauvolfia caffra (Z?) Sapium ellipticum (Z?) Schefflera umbellifera (Z) Strombosia scheffleri (Z) Strychnos mellodora (Z) S. usambarensis (Z) Tabernaemontana angolensis (V, Z?) T. ventricosa (V, Z?) Trichocladus ellipticus (X) Voacanga thousarsii (Z)

The small tree layer or fieldlayer, generally below 5 m in height but up to 10 m on the lower slopes, includes:

Achyrospermum laterale
Aidia micrantha
Alchornea laxiflora
Allophylus chaunostachys
Argomuellera macrophylla
Aulacalyx diervilleoides
Coffea ligustroides
Cremaspora triflora
Dovyalis macrocalyx

Dracaena fragrans
Erythrococca polyandra
Ochna oconnorii
Pauridiantha symplocoides
Phyllanthus inflatus
Psychotria zombamontana
Tannodia swynnertoni
Tarenna pavettoides

102

In the low 1 m high shrub layer, *Mostuea brunonis* is dominant in large sectors of the lower slope forest.

The forest species lists, especially that of the small tree layer, has been aided in large part by the collections of Mr. Tom Müller of the Salisbury Herbarium.

Ravine & Riverine Forest

Macedo (1970a, 1970b) lists many tree species for the ravine riverine zones throughout the mountain area. These are composed of many rain forest and thicket species as well as those more generally confined to, or typical of, streambanks. Some of the components include:

Albizia glaberrima (W)
Adina microcephala (W)
Anthocleista grandiflora (Z?)
Bersama abyssinica (Z)
Blighia unijugata (Z?)
Bombax rhodognaphalon (W? Z?)
Bridelia micrantha (Z)
Chlorophora excelsa (Z)
Craibia brevicaudata (X)
Ekebergia capensis (Z)
Erythrophleum suaveolens (Z?)
Filicium decipiens (Z?)
Ficus capensis (Z Y)
Halleria lucida (Z Y)
Harungana madagascariensis (Z)

Khaya nyassica (W)
Millettia stuhlmannii (X)
Newtonia buchananii (W)
Pandanus sp (Y, Z?)
 (prob. P. livingstonianus)
Parkia filicoidea (Z)
Raffia sp (Y, Z)
Rauvofia caffra (Z?)
Sapium ellipticum (Z?)
Syzygium guineense (Z)
Treculia africana (Y? Z)
Trichilia sp (Z)
Trichocladus ellipticus (X)

The giant canopy liana *Entada pursaetha* with long pendant pods, one, to one and a half metres long, is abundant in riverine forest and its stems frequently attain 50 cm (dbh).

Dispersal

As the agents of dispersal of many species is uncertain only the broadest comparisons can be drawn (Fig 8.3).

In montane forest, of 14 occurrences, 12 (86%) are animal dispersed and 2 (14%) are also water dispersed according to Phillips (1931). Tropical forest with 11 occurrences has 8 (73%) animal dispersed species and 3 (27%) wind disseminated. Of 41 occurrences in Transition Forest 28 (68%) are animal dispersed, 7 (17%) are active ballists, 2 (5%) by wind, 2 by water and 2 by weight (barochorous). Riverine forest trees comprise 20 (67%) animal dispersed out of 30 occurrences, 5 (17%) wind, at least 4 (13%) by water and 1 (3%) an explosively dispersed species. It is probable that



many more, including the winged components, are disseminated by water. Despite the uncertainties the overwhelming majority of trees are animal dispersed. As no quantitative data on density or frequency of these species is available it is unfortunately impossible to obtain an importance value from the two percentages which would probably show, for example, a high value for wind dispersal in the tropical zone due to the abundance of *Newtonia buchananii*, as well as in riverine forest where *Adina microcephala* and *Khaya nyasica* predominate. Active ballists are common in Transition Forest and relatively unrepresented in the zones above and below it.

Phenology

The few data noted on forest components on the mountain show a prevalence of flowering from August to December and a main fruiting period from February to June with a peak in autumn.

Environmental factors

Most of these features have been dealt with in the sections on grassland and thicket. It need only be reiterated that the montane forest margin is the only one in the entire system where progressive retreat due to fire is conspicuous (possibly associated with alteration in soil moisture balance). Elsewhere forest is badly damaged only by human activities of shifting cultivation and timber extraction.

Succession

The balance between grassland, thicket and forest in the summit areas has been dealt with above. On the xerocline lower slopes, savanna, thicket and forest appear to be in a homeostatic balance with soil moisture regimes of the different land facets; forest being confined almost exclusively to valley head and riverine sites. It is on the lower mesocline slopes where active forest extension (secondary thicket) is occurring on old cultivated areas left fallow. From the time the field is abandoned, the following progressive sequence occurs: (a) herb and suffrutex weeds with woody scrub formed by forest margin species as well as coppices of some original forest components, (b) scrub-thicket (c) thicket (mixed savanna and forest species) (d) forest. However, where dense stands of elephant grass *Pennisetum purpureum* occur as the secondary cover, this appears to hold back (inhibit) the succession to forest, as is clearly shown in other moist areas such as the eastern Congo sector of the equatorial zone (pers. data). On the mesocline the most important components in the scrub and

103

thicket stages toward forest are *Bridelia micrantha*, *Harungana madagascariens* and *Trema orientalis*. *Harungana* is also important in the moist coast forests of the Cheringoma cuesta, and *Bridelia* is a canopy dominant in the secondary thickets of the Lake Kivu area of the eastern Congo.



8.4 MIDLANDS

The deeply dissected hill country of the Midlands, with rounded to flat interfluves, is covered in tall closed miombo savanna of homogeneous appearance (the homogeneity is due primarily to the predominance of microphyll sized (15 x 15 mm area) leaflets which make up the canopy cover). This sea of miombo is uninterrupted except by a few inselbergs of various dimensions and gaps where dambo remnants occur. A change in canopy texture is discernable where dendritic strips of streambank trees and forest occur. These strips are most conspicuous at the end of the dry season when the tardily deciduous miombo canopy has dropped its leaves. The miombo upper canopy averages between 18 and 20 m in height, contrasting with that nearer the Frontier Escarpment which is half this height, and its duplex structure is completed by a median to tall continuous grass stratum which is burnt annually.

As the greater part of the Midlands is formed by metamorphic crystalline granite-gneiss the soils are predominantly skeletal (pg) sandy or stony and overdrained, except on interfluve crests where they are deeper. However, where basic rocks intrude, deeply weathered latosols occur which have an improved soil moisture balance. The small dambo areas are sandy with an impervious gley subsoil (Pgh). Although termite hills occur in the miombo, they are seldom covered by dense thicket as their soils are generally poor in clay and are thus droughty.

Miombo occurs in the isohyet range from 900 mm to 2 000 mm in the Midlands and Gorongosa Mountain area within the ecosystem. A strongly seasonal hot wet period occurs from November to April and a six month dry season from May to October. Midsummer droughts occur periodically and interrupt the phenophase cycles.

The hill miombo of the Midlands is related to that in Rhodesia, Malawi and parts of Zambia and has a different appearance and successional status, although they are floristically similar, to dambo miombo as exemplified by the Cheringoma cuesta and the Zambeze-Congo watershed.

The most striking seasonal features of miombo in Mocambique is the contrast between in the lush midsummer situation, when the sounds of massed cicades and the liquid whistles of the migrant European Oriole predominate, and the bleak silent grey sea of trunks and blackened ground after fire in the dry season.

Visual experience in the miombo savanna woodlands is wholly introvert due to the tall closed canopy which excludes the sky and long vistas. Except when hot

fires have singed the canopy, the spectacular synchronous flush of red leaves in the pre-rain spring, noted on the Interior Continental Plateau in Rhodesia, is not a feature of the Coastal or lowland miombo.

Of the fifteen communities mentioned below only the inselberg communities assume local prominence; the remainder are small and patchy, or narrow and linear in the case of riverine sites. Closed tree savanna covers more than ninety percent of the Midlands.

AQUATIC HERB COMMUNITIES

Except for the waters which rise on Gorongosa Mountain most of the stream and river network in the Midlands is seasonal. In rocky perennial streams the submerged aquatic *Hydrostachys* sp. is common, and on the banks and islands emergents include tall reeds *Phragmites mauritianus* fronted by floating mats of *Echinochloa pyramidalis* along the water's edge.

No data is available on the vegetation of the seasonal pans and views which occur on the relic dambo floors of the Midlands.

ROCKFACES

The herb constituents of rockfaces in the Midlands are related to those on Gorongosa Mountain but with the absence of the dominant sedge *Coleochloa setifera*. Components include:

Aloe chabaudii Aloe chryptopoda Crassula spp. Euphorbia spp. Myrothamnus flabellifolia Orchidaceae Vallozia sp.

Root mats are formed on gently sloping faces in which scattered small trees take root. The rock fig *Ficus soldanella* is characteristic of even the smallest outcrops of rock in the miombo.

SCRUB SAVANNA

In the Midlands, scrub savanna is confined to areas of secondary growth on old cultivation sites, subject to annual fires, and is essentially a developmental stage to tree savanna, as opposed to thicket, due to the established grass stratum. Thus the woody scandents and climbers typical of scrub-thicket are absent and the scrub is comprised of components from all strata of tree savanna.



TREE SAVANNA

Tall closed canopied tree savanna or savanna woodland covers the greater part of the Midlands. The height of miombo canopy trees changes at the two ends of the moisture-altitudinal gradient becoming shorter in the drier zones and in the wetter uplands. Although a large number of upperstorey tree species occur, it is the predominance of the genera *Brachystegia* and *Julbernadia* which give the miombo its characteristic small leaved uniformity. The canopy trees are mostly compound leaved, bipinnate, deciduous species. The benign hydrothermal regime of Central Mocambique, from combined maritime and orographic influences, appears to be responsible for individual rather than synchronous leaf phases exhibited by miombo canopy trees, and the facultative deciduousness in some species such as *Brachystegia spiciformis* which varies with site and the amount of precipitation in a season.

The number of distinguishable layers in savanna, in addition to the basic duplex combination of woody plants and grass strata, depends on various permutations of life form height classes and the degree of suppression or competition imposed by the upper canopy layer. Other contributary factors include the frequency and intensity of environmental factors such as frost, fire, utilization by herbivores and edaphic influences.

In the miombo of the study area, four strata are defined by height classes and characterised by species usually confined to them. These are: (A) canopy and emergent trees, (B) medium Tree Layer (C) small tree layer, and (D) grass or herbaceous stratum. In some areas stratum (A) is in the height interval 16 to 28 m and in others 13 to 23 m. However, in upland areas, best exemplified in Rhodesia, the miombo is much shorter and the A and B strata are merged so that a species such as *Diplorhynchus condylocarpon* has equal status to the *Brachystegia* species in size and abundance. At the other end of the profile the grass stratum is clearly separated from the small tree layer when it is of median height up to 2 m. In many areas however where *Hyparrhenia* species predominate, the grass stratum is between 3 and 4 m in height and effectively submerges the small tree layer.

In scarp and hilltop areas subject to orographic fog the emergent canopy trees, in particular *Brachystegia spiciformis*, have their canopy branches and upper bole festooned with an abundance of epiphytic orchids and ferns, comprising some six species of each. Herbaceous scandents and climbers are common in the grass stratum and lianes are relatively rare, but are responsible for initiating thicket clumps where deeper soils occur. Thorny components are rare except in secondary growth on old cultivation sites where *Acacia polyacantha* may assume local temporary dominance.

A special woody life form associated with miombo is the bamboo *Oxytenanthera* abyssinica which occurs in clumps and forms societies in the median tree layer (Fig 8.14). Succulence is totally absent in the tree strata and is exhibited solely by some herbs of the grass stratum.

Physiognomy and structure is illustrated by a profile diagram drawn in the field, which shows the crown and growth form characteristics (Fig. 8.14). Most upper tree strata species exhibit the savanna "sun" growth form with umbrella-shaped crowns and crown branches diverging midway up the bole. An exception is *Xylopia parviflora* which has a more typical forest or "shade" growth form with straight clean bole and small rounded crown. The small tree and shrub layer typically have deformed shapes due to damage by fire and wild ungulates.

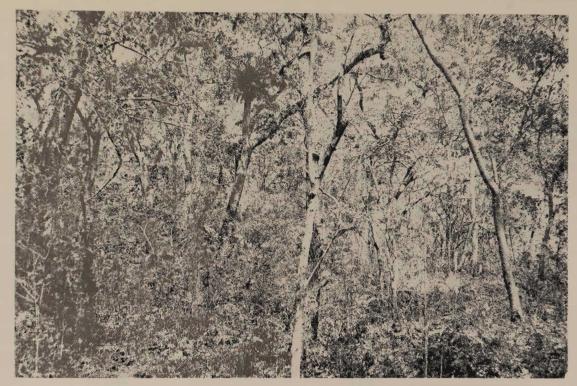
Three quantitative examples of tall closed miombo savanna are given from the Midlands area west of the Rift Valley (Table 8.4 /Fig 8.14). These show the variable dominance of several species in all strata depending on the selective influences such as substrate, dispersal, fire and human activities. The species occurrence in the several woody layers also shows the presence of stratal indicators, or characteristic species, and the major contribution of canopy species at different stages of growth.

In the canopy or upper tree layer one of the following species is dominant or codominant in the three highest densities, *Brachystegia boehmii*, *B. spiciformis*, *Erythrophloeum africanum*, *Julbernadia globiflora* and *Pterocarpus angolensis*. In the northwest of the ecosystem *Brachystegia glaucescens* is the sole dominant, patchily, over large areas. *Brachystegia glaucescens*, *Julbernadia globiflora* and *Ricinodendron rautananii* tend to form pure species societies within the miombo system. Locally *Burkea africana*, *Monotes spp.*, and *Pericopsis angolensis* can assume high density. In the subordinate tree layers, *Diplorhynchus condylocarpon* is by far the most abundant and characteristic species throughout the central Mocambique Midlands. Local midstratum dominance is also shown by combretaceous, *Combretum* and *Terminalia* species *Pterocarpus* species or *Pseudolachnostylis maprouneafolia*.

No quantitative data is available for the grass stratum, but mosaic dominance occurs of tall *Hyparrhenia* spp., *Heteropogon melanoleuca, Andropogon gayanus* and *Bekeropsis uniseta* with median height swards of *oudetia superba, Digitaria milanjiana, Panicum maximum, Schizachyrium sanguinem* and *Themeda triandra*. The miombo grass stratum contains a rich herbaceous, suffrutex and dwarf shrub flora, examples of which are listed in Table 8.4. Geophytes and other annuals, especially ginger plants *Zingiberaceae*, are conspicuous in post fire flush and flowering in spring.



PLATE 16 ASPECTS OF THE MIOMBO ECOSYSTEM



(A) Closed canopied miombo woodland on white duplex sands with a dense fieldlayer of thicket and forest saplings interspersed with a sparse grass cover. The epiphyte is a staghorn fern Platycerium peltatum.



(C) 'Dambo miombo'. Sandy high waterable drainage line grasslands and termitaria thicket islands fringed by miombo woodland and forest mosaic (dry season aspect).



(B) Closed canopied miombo savanna woodland on sandy latosols with a continuous but light grass stratum. Other areas have a dense grass layer 2 m in height. Typical of Midlands and red sands of coast plateau.



(D) Dambo and miombo margin after a veld fire. Note widely spaced grass tufts typical on sand substrates.



TABLE 8.4

Analysis of woody strata in 1 hectare of miombo savanna woodland on the Midlands

(A)	CANOPY & EMERGENTS > 13-23m.	No. of trees	Total basal area cm ²
	Julbernardia globiflora	29	545 199
	Erythrophleum africanum	26	579 764
	Brachystegia boehmii	19	321 826
	Burkea africana	15	344 335
	Brachystegia spiciformis	9	191 742
	Sterculia quinqueloba	5 2 2 2 2	15 843
	Ricinodendron rautanenii	2	34 650
	Pseudolachnostylis maprouneifolia	2	3 218
	Combretum zeyheri	2	2 044
	Shrebera tricoclada		1 521
	Xeroderris stuhlmannii	1	707
	Pericopsis angolensis	1	1 018
	Sclerocarya caffra	1	2 828 314
	Amblygonocarpus andongensis		2 045 009
V 100 M T	14 spp.	115	2 043 003
(B)	MEDIUM TREE LAYER > 7-13m	1000	or reign one
	Diplorhynchus condylocarpon	19	155 591
	Pseudolachnostylis maprouneifolia	11	23 245
*	Erythrophleum africanum	10	38 375
44	Brachystegia boehmii	6	8 015
*	Julbernardia globiflora	5	5 413
	Sclerocarya caffra	5	7 701
- 14-	Xylopia parviflora	5 5 3 2 2	5 677
	Amblygonocarpus andongensis	2	1 964
伊	Strychnos madagascariensis		856
- 16-	Ricinodendron rautanenii Xeroderris stuhlmanii	1	1 591 491
		1	201
*	Hymenocardia acida Burkea africana	4	133
*	Brachystegia spiciformis	1	314
*	Sterculia quinqueloba	1	707
	Crossopterix febrifuga	1 100	177
	Swartzia madagascariensis	- Impoperrable	133
	17 spp.	71	250 584
(0)			
(C)	SMALL TREE LAYER 2—7m	34	106 984
*	Diplorhynchus condylocarpon Erythrophleum africanum	12	12 276
	Xeromphis obovata	11	8 828
	Byrsocarpus orientalis	6	3 423
*	Psuedolachnostylis maprouneifolia	4	1 521
*	Julbernardia globiflora	3	531
*	Brachystegia boehmii	3	1 135
*	Sclerocarya caffra	4 3 3 3 2 2 2 2	755
	Holarrhena pubescens	3	616
*	Brachystegia spiciformis	2	177
*	Millettia stuhlmannii	2	416
*	Xeroderris stuhlmannii	2	707
	Flacourtia indica	2	314

Table 8.4 (continued)

Hymenocardia acida	1	50
Ziziphus mauritiana	1	79
Amblygonocarpus andongensis	1	79
Combretum zeyheri	1	177
Lannea discolor	1	177
Piliostigma thonningii	1	20
Kigelia africana	1	20
Strychnos spinosa	1	20
Crossopterix febrifuga	1	79
Commiphora serrata	1	50
Ximenia caffra ·	1	20
"Eugenia" sp.	1	20
	- Agazerrania	
25 spp.	99	138 474
		-3 +-47 11 -3
Grand total		
in 1 ha 35 spp.	285	2 434 067

^{* =} potential canopy components.





In sites where deeper soil pockets occur, small thicket patches may be initiated around the boles of canopy trees by woody climbers, particularly *Artabotrys brachy-petalus* and *Friesodielsia obovata* which are animal dispersed species.

Dispersal

The three main woody strata of tall miombo savanna are clearly characterised by the predominance of particular modes of seed dispersal. Wind and animal dispersed types have the highest occurrence in all strata, but the addition of density data for each type immediately gives their real importance in each strata (Fig 8.4).

Although wind and animal dispersed types considerably exceed those with exploding legume pods which throw their seeds (active ballists) this group contains the *Brachystegia* and *Julbernadia* dominants which have the highest density. By contrast animal dispersed components of the canopy have a low density.

In the median tree layer wind dispersal has the highest importance value due to the abundance of *Diplorhynchus condylocarpon* and *Combretaceae* in occurence and density. Active ballists are rare apart from the abundance of canopy species present in this stratum. Animal dispersed types have the highest occurrence and density in the small tree and shrub layer (Fig 8.4).

SCRUB THICKET

Primary scrub-thicket occurs in discontinuous patches, related to deeper pockets of soil in the miombo chiefly on the crests of interfluves, occasional patches around the basis of tree boles, and amongst rock outcrops. The interstage growth of bamboo *Oxytenanthera abyssinica* thicket also forms a low impenetrable scrub. These will be dealt with in the following section.

By far the greatest extent of continuous scrub-thicket with a canopy at 3 to 4 m is secondary regrowth on fallow areas left by the rotation of shifting cultivation. The largest areas occur in the Midland sector of latosols immediately south of Gorongosa Mountain. Scrub-thicket is only continuous as a mosaic alternating with scrubsavanna. Scrub-thicket components include:

Scrub

Acacia polyacantha
Acacia seyal
Annona senegalensis
Antidesma venosum
Combretum fragrans
C. molle
C. zeyheri
Dalbergia melanoxylon
Entada abyssinica

Scandents Climbers

Asparagus spp. Bauhenia galpinii Dalbergia arbutifolia Dalbergia lactea

Grasses

Pennisetum purpureum

Harrisonia abyssinica
Julbernadia globiflora
Lippia javanica
Markhamia obtusifolia
Piliostigma thonningii
Securidaca longipendunculata
Strychnos madagascariensis

S. spinosa

Vangueria infausta
Vernonia spp.
Vitex payos
Lantana camara
Macuna coriacea
Smilax kraussiana

Rottboelia exaltata

Scrub-thicket rarely grows beyond 5 m before being cleared again for cultivation, or is opened up by annual fires thus forming a savanna with scrub patches.

THICKET

Four main types of thicket occur as island patches within miombo savanna, these are: (a) thicket on deep sand pockets, (b) termitaria thickets, (c) bamboo thickets on rock outcrops. That which occurs on termitaria in sandy lithosols is the most poorly developed due to the excessive drainage, and only a few trees typical of bottom-land clays occur together with miombo tree species on the termite hills. In the heavier latosols termitaria thickets are better developed and in many areas are covered by a pure stand of bamboo *Oxytenanthera abyssinica*. Only on the margins of the relic dambos are there well developed termitaria thickets similar to those in the Rift Valley and on the Cheringoma Cuesta.

(a) Thicket on deep sand pockets

These thickets are composed of a mixed assemblage of woody plants derived from moist forest, dry forest, termitaria, rock outcrops, and bottomland savanna as well as from the miombo fieldlayer itself. Climbers and scandents are abundant and these roof in a closed canopy between 6 and 8 m. Above this rise emergents such as *Pteleopsis myrtifolia* and *Erythrophleum sauveolens* to 15 or 20 m. The density of climbers in the canopy at 6 to 8 m is such that a dense tangle is formed which re-



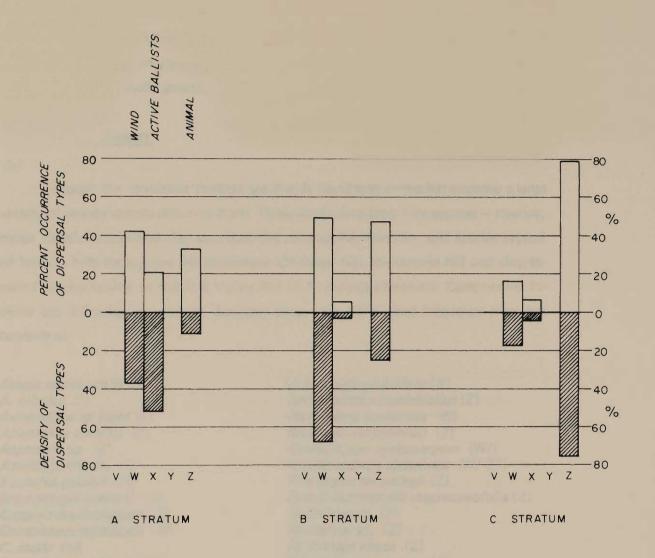


FIG. 8.4 COMPARATIVE IMPORTANCE OF DISPERSAL TYPES

(OCCURRENCE PLUS DENSITY) IN THREE WOODY STRATA

OF CLOSED <u>BRACHYSTEGIA</u> (MIOMBO) SAVANNA ON THE

MIDLANDS SECTION OF THE GORONGOSA ECOSYSTEM

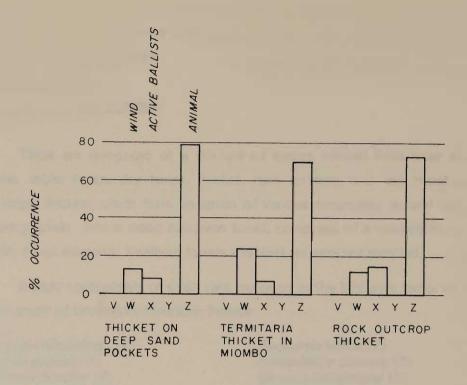


FIG. 8.5 PREDOMINANCE OF ANIMAL-DISPERSED WOODY

SPECIES IN VARIOUS KINDS OF THICKET

OCCURRING IN MIOMBO



plicates the undercanopy thickets formed in some forests, and enables forest understorey birds, such as the terrestrial bulbul *Phyllastrephus terrestris*, to use the canopy as a "dislocated" feeding zone. An example of this thicket type is illustrated by a profile bisect in which the components are listed (Fig 8.14). The thicket fieldlayer is dominated by small Rubiaceous trees such as *Polysphaeria lanceolata* and *Canthium crassum* which occur in riverine and other moist forests, and patches of *Oplismenus*, *Olyra* and *Panicum* shade grasses.

(b) Termitaria Thickets

Though the termitaria thickets are poorly developed in the hill miombo a large variety of woody species occur on them. These are derived from five sources — riverine, moist forest, bottomland clay savannas, the surrounding miombo, and species typical of termite hills throughout the ecosystem. Of these, 60% are termite hill and clay savanna species typical of the Rift Valley and arid savannas elsewhere. Components include the following (an asterisk denoting those with the highest frequency from ten termitaria):

Acacia nigrescens W Z) A. nilotica (Z) Annonaceae sp indet (Z) *Allophylus alnifolia (Z) *Asparagus sp. (Z) Azanza garckeana (Z) Bauhenia galpinii (X) Brachystegia boehmii (X) Capparis erythrocarpos (Z) Combretum hereoensis (W) C. molle (W) Commiphora schimperi (Z) Cordia pilosissima (Z) Dalbergia boehmii (W) Dalbergia melanoxylon (WZ) Dichrostachys cinerea (Z) *Diospyros mespiliformis (Z) *Diplorhynchus condylocarpon (W) *Ehretia amoena (Z)

*Julbernadia globiflora (X) Lecaniodiscus fraxinifolius (Z) Markhamia acuminata (W) Maytenus senegalensis (Z) Ormocarpum trichocarpum (W?) Oxytenanthera abyssinica (W? Z?) Piliostigma thonningii (Z) Pseudolachnostylis maprouneafolia (Z) Rhoicissus sp (Z) Rubiaceae sp. (Z) Securinega virosa (Z) Sterculia quinqueloba (Z) Steganotaenia araliacea (W) Synaptolepsis kirkii (Z) Tamarindus indica (Z) Trichilia emetica (Z) *Xeroderris stuhlmannii (W) Ximenia caffra (Z) Ziziphus mucronata (Z) Ziziphus pubescens (Z)

(c) Bamboo Thicket

*Flacourtia indica (Z)

*Friesodielsia obovata (Z) Grewia lepidopetala (Z)

Dense pure societies of solid-stemmed bamboo *Oxytenanthera abyssinica* thicket occur on the heavier soils in the Midlands, including sandy loams and latosois

108

usually on valley slopes of higher rainfall (> 1200 mm) miombo. In the high water-table sands of the Cheringoma Coast, bamboo is confined almost entirely to the heavier soils of termite hills, and extends into lower rainfall miombo on termite hills, deep soil pockets and streambank sites. An example of bamboo clumps forming the mid and lower stratum of miombo is shown in Fig 8.14. *Oxytenanthera* is deciduous and has a periodic gregarious flowering and seeding after which it dies. New growth is from seed, and the vigorous vegetative shoots put out every rainy season results in the formation of large clumps.

(d) Thickets on rock outcrops

These are composed of a mixture of species derived from seven sources — riverine, moist forest, dry forest, thicket, rock surfaces, arid, and moist savannas. The larger thickets, which form an apron of various dimensions around the base of inselbergs, grade into a mesic evergreen forest, composed of a mixture of rain forest and dry forest elements. Inselberg forests and thickets were not sampled.

Woody components of small rock outcrops in the Midlands sector of the ecosystem south of Gorongosa Mountain include:

Allophylus alinifolius (Z)
Bauhenia galpinii (X)
Berchemia discolor (Z)
Bersama abyssinica (Z)
Cleistochlamys kirkii (X Z)
Cleistanthus schlechteri (X' Z)
Combretum apiculatum (W)
Diospyros senensis (Z)
Erythoxylon emarginatum (Z)
Euphorbia sp. (X, Z)
Ficus ingens (Z)
Ficus soldanella (Z)

Flacourtia indica (Z)
Friesodielsia obovata (Z)
Garcinia livingstonei (Z)
Kirkia acuminata (W)
Lannea stuhlmannii (Z)
Oncoba spinosa (Z)
Pseudocassine transvaalensis (Z)
Strychnos potatorum (Z)
Terminalia sansibarica (W)
Xylotheca tettensis (Z)
Zizyphhus mucronata (Z)

Dispersal

Dispersal in all thicket types in the miombo system is predominantly zoochorous (Fig 8.5). An exhaustive listing of species may change the relative importance of those dispersed by wind and explosive dehiscence (active ballists), but would likely only reinforce the predominance of animal dispersed types especially in the higher rainfall zones where forest elements are commoner constituents.

An important element in the compsition of almost every type of thicket community is the presence of widespread thicket forming species. The majority are animal dispersed (particularly by birds and primates) and are related to two basic features in



an environment: (1) perches, and (2) water-based sites. In the first group are any prominences including trees, termite hills, rock outcrops, stumps and human artifacts such as fence posts, walls, gates, buildings etc. The second includes streambanks, the periphery of open waters, ravines and dongas, springs and fountains. The implications of these in landscape evolution and the interrelations of communities will be dealt with in a later section (9.9).

FOREST

Forest in the hill miombo system is confined to sites with high soil moisture, including streambanks, alluvial fans, escarpments, ravines, and the basal pediments of inselbergs. The forests are thus patchy and isolated or linear, linked by the narrow line of riverine trees in miombo which widen on meander and talus deposits on incised streams, or by a stepping stone archipelago-like series of small thicket islands, described above, which occur to a greater or lesser degree in different situations.

Immediately to the west of Gorongosa Mountain, on the interfluve between the Nhandue and Vunduzi Rivers are dry forest remnants on relic duplex sands, and below them on sands of alluviated valleys, now incised, is dry forest in riverine situations. The evolution of this landscape and ecosystem cycle is reconstructed in Chapter 6.2 (Fig. 6.2).

The riverine strips traversing miombo are narrow lines of tall trees which widen in areas with islanded or marginal alluvial deposits. Where the deposits are predominantly sandy, dry forest or its elements form the more extensive cover and the true riverine tree species form a single line confined to the actual riverbanks.

The two most abundant riverine trees in the Midlands are *Adina microcephala* and *Khaya nyasica* which are wind (and water?) dispersed. For extensive lists of riverine components reference should be made to Macedo (1970b: 8.12, 11.4). Commoner components include the following:

Canopy trees:

Adina microcaphala (W)
Albizia glaberrima (W)
Blighia unijugata (Z)
Bombax rhodognaphalon (W)
Diospyros mespiliformis (Z)
Ekebergia capensis (Z)
Erythrophleum suaveolens (Z?)
Ficus capensis (Z)

Garcinia livingstonei (Z)
Khaya nyasica (W)
Millettia stuhlmannii (X)
Newtonia buchananii (W)
Parkia filicoidea (Z)
Sterculia appendiculata (Z)
Syzygium guineense (Z)

109

Small trees:

Antidesma venosum (Z) Bersama abyssinica (Z) Bridelia micrantha (Z) Dracaena reflexa (Z) Mimusops fruticosa (Z)

Nuxia oppositifolia (W) Phoenix reclinata (Z) Rothmannia manganjae (Z) Tricalysia nyassae (Z) Turraea nilotica (Z)

Herbs:

Brillantaisia pubescens

Climbers:

Entada pursaetha

Rhoicissus spp.

In drier valleys in the miombo, trees such as Acacia robusta, Diospyros fruticosa, Diospyros mespiliformis, Cordyla africana, Lonchocarpus capassa, Tamarindus indica, and Xanthocercus zambesiaca are typical of the riverine strips.

Dispersal

As little is known about the composition of escarpment and inselberg forests, the following remarks are confined to the riverine cover. Although two wind (and water?) dispersed trees, *Adina* and *Khaya* are the most abundant riverine species, more than 60% of the total woody species listed by Macedo (1970b) have animal dispersed diaspores, which is similar to the *prima facie* analysis given for the riverine forest on the mountain (Fig. 8.3). In drier valleys the relative importance of animal dispersal types remains predominant, as proved by the data from the Rift Valley.

ENVIRONMENTAL FACTORS

The Midland miombo savanna and its subordinate inclusions of thicket and forest patches experience: a bimodal radiation regime with peaks in November and March due to the screening effect of heavy cloud during the rains; a unimodal five month summer rains period from November to March followed by a seven month dry period from April to October, and no frost in the winter dry season. The two major climatic phases can be divided into four seasons by hydrothermal indices (Fig 4.13):

- (1) Spring torrid period (August to October)
- (2) Summer sweltering period (November to February)
- (3) Autumnal hot-drying period (March and April)
- (4) Winter cool-dry/humid period (May to July).



Due to orographic, or nocturnal katabatic fog, and heavy guttation and dew formation in the autumn and midwinter period, the cool season is dry by day and humid at night. Of the 93 rain days per year, 68 (73%) occur between November and April. Five months receive more than 100 mm (perhumid) rainfall on the long term. Variability of rainfall is only 26% as compared to the adjacent Rift Valley which has a regime nearly three times more variable. A feature of the regional climate expressed most drastically in areas of lower rainfall, are midsummer drought in January, or February and March. A rapid means of determining drought periods apart from the conspicuous leaf discolouration of the vegetation, is by the use of De Martonne's index of Aridity (I = $^{P/T}$ + 10) described under Climate (Ch. 4). Midsummer droughts are defined by indices between 1 and 2,5 or by a period of more than two weeks with less than 15 mm rainfall. The greatest temperature range occurs in the prerain spring (August to October) and the least in autumn.

Closely related to these wetting and drying phases and intervention of midsummer droughts, is the occurrence of annual fire in the miombo savanna. Today,
mostly due to human agency, annual fires sweep through the miombo savanna, burning
for weeks or months according to density of grass fuel, wind and its ability to cross
the riverine strips. Fire intensity is greatest late in the dry season, singeing the upper
canopy trees to nearly 15 m where a tall 3 to 4 m *Hyparrhenia* grass stratum occurs.
Fires occurring earlier in the dry season, including those which may be initiated as
early as March or April following midsummer droughts, typically burn in a mosaic and
are of low intensity, many dying out at night when heavy guttation occurs. Such areas
can be burnt again in the late dry season. The predominance of fire scars on trees, on
the leeward side (NW) of the prevailing trade winds due to the longer duration of fire
out of the wind, and the differential susceptability of trees more than 3 m in height
to fire. *Erythrophleum africanum* was by far the most scarred, and 20% (57/284) of
all trees in 1 ha were fire scarred.

The densest settlement of tribal cultivators in the Midlands sector within the ecosystem is in the area south and east of the Gorongosa Mountain. Shifting cultivation of two to three years on one site followed by a fallow period of up to 15 or 20 years is practised on the poor sandy lithosols (Pg), and semi-permanent cultivation of about 10 years with a short fallow period on the red latosols (Vb). This introduces a mosaic pattern into the landscape, many sites at different stages of regressive or progressive succession.

No domestic stock are kept, due to the presence of tsetse fly and nagana, and the large wild herbivore populations in the miombo are extremely low with periodic short influxes from the Rift Valley related to post-fire flush of grasses, maturation of indigenous fruits such as marulla *Sclerocarya caffra*, or tribal food crops of maize and sorghum (Ch. 9).

PHENOLOGY

Foliage phenophases

Except where late season fires have destroyed the leaves of the median and upper canopy, the spring aspect to the miombo in the maritime continental margin shows a mosaic of phases. A species, such as *Brachystegia spiciformis*, can be in full mature leaf and pod in one site, and nearby, the same species is bare or in new scarlet leaf flush. The mosaic pattern in spring, autumn and winter is clearly conspicuous from a low flying aircraft.

Where tall grasses have enabled the flames to reach into the middle or upper canopy, singeing if not burning tree leaves, an earlier and more synchronised new leaf flush and flowering occurs at the end of July and early August. However, in the Midlands this synchronism, which is typical of the miombo on the continental interior plateau subjected to frost, is lost in the autumn and winter dry season when, as there is no frost to trigger leaf fall, there is a differential leaf fall of species and individuals in response to soil moisture depletion. In Salisbury the first frost month is June and a month earlier in the centre of the subcontinent in northern Botswana and the Caprivi.

The phenogram for miombo savanna trees in the Midland physiographic unit shows a gradation of leaf phenophases into four seasons, and a bimodal flowering regime in the equinoxes (Fig 8.6). The first new leaves on trees appear in early August or July, if triggered by fire, and the most leafless period is over September when the lowest Aridity Index (0,8) occurs. However, trees bare of leaves occur as early as April when *Pterocarpus angolensis* and *Ricinodendron* are the first to show leaf discolouration and leaf fall. The same two species were the first to react to low night temperatures in northeast South West Africa in May 1966, despite late main rains (pers. obs.). These species are also the first indicators of midsummer drought conditions, when their leaves turn yellow and fall if rainless conditions persist, resulting in a new flush of leaves and flowering if wet conditions return in March or April.

Superimposed on these climo-edaphic controls are the effects of leaf defoliating caterpillars on *Burkea africana*, *Erythrophleum africanum*, or *Sclerocarya caffra* in November causing a new leaf flush (and flowering in some) in January. Certain of the caterpillars, like the mopane "worm", are highly prized as food by tribal people.



Reproductive Phenophases

Lack of experimental or quantitative correlations between climatic and edaphic factors allows for only an interpretation for the flowering peaks by way of the coincident relationships between climo-edaphic parameters and reproductive peaks. For example, quantitative correlations from the northern tropics in West Africa showed that flowering was closely related not only to the incidence of rain in two woody species studied, but also to the temperature drop associated with rainfall (Rees 1964a, 1964b). Rees (1964b: 16) concludes that if these relationships are true "flowering would occur in response to either a low minimum temperature (in the absence of rain) or a rapid temperature-drop, almost invariably associated with heavy rain in the wet season or a rainstorm in the dry season".

Reproduction in the tree layers

The most striking feature of reproduction in miombo trees in the Midlands are bimodal phenophases coincident with the bimodal radiation and insolation peaks about the time of the equinoxes (Fig 8.6). The radiation and heat peaks just before and after the summer rains is due to the screening effect of a dense cloud cover blanket during the rains (see Ch. 4 Climate). However, the equinoctial peaks may also result from solsticial triggers, particularly as midwinter fires simulate the ground warming which begins about a month after the winter solstice (mid July) (also the time when many passerines in the area begin their reproductive period. Judging by Bonsma's (1940) monthly chemical analysis of browse foods this bimodality may, however, be in response to endogenous mobilization of nutrients in spring and again in autumn when fruits are being formed.

A subtle phenomenon, first noted commonly in the Rift Valley savannas and emphasized by the discovery of marulla fruit in elephant dung at the "wrong" time of the year, is the bimodal flowering exhibited by individual trees of certain species.

Individual bimodal flowering is very often, but not always, coincident with the equinoctial periods. Tree species in the miombo which exhibit this phenomenon are *Milletia stuhlmannii* (Aug.—Nov./Feb.—Mar.), *Sclerocarya caffra* (Sept./Apr.), *Piliostigma thonningii* (Dec./Apr.—May.) and *Heteropyxis natalensis* (Nov./Mar.). All except the last species occur outside the miombo system as well, on the Rift Valley plains and in riverine sites. Trees suspected of flowering twice include *Brachystegia spiciformis*, *Albizia versicolor* and *Xeroderris stuhlmannii*.

This bimodal flowering is not to be confused with the dropping of opened flowers (due to their failing to set, insect damage or other reasons) and renewed flowering in close sequence within consecutive months. This sequence is shown by individual trees of conspicuous flowering genera such as *Acacia*, *Cassia* and *Pterocarpus* and noted during extremely dry summer periods interspersed with short heavy falls of rain.

The importance of sap rise and bark characteristics in different seasons determines the resource use of certain miombo canopy trees by man and elephant. *Brachystegia boehmii*, *B. spiciformis* and *Julbernardia globiflora* trunk bark is stripped off by tribal bee-keepers to construct hives, and elephant strip and eat the bark of *B. boehmii*, in the dry season and leave other miombo species relatively unscathed. Of these species, only the first strips cleanly off the bole throughout the year; the bark of the other two species adheres to the wood and can only be stripped cleanly in midsummer. There is thus a strong selective preference for *Brachystegia boehmii* by man and beast.

Herb layer

No quantitative phenological data on the herbaceous layer in miombo was recorded. Generally the herbaceous layer comes into full flush soon after the first rains in November, and the flowering of grasses, particularly, occurs in November and December. However, in many areas fire induces a pre-rain vegetative flush from August to October and it is at this time that suffrutices and geophytes are conspicuous, such as members of the *Zingiberaceae* with large brightly coloured flowers. However, other geophytes such as a purple-flowered *Afromomum* sp. and *Haemanthus multiflorus* are only abundant in November. Many of the forbs flower mainly in the late summer and autumn; examples include *Aerva leucura*, *Agathisanthemum bojori*, *Borreria scabra*, *Cassia mimosoides*, *Celosia trigyna*, *Cissus bathyrhakodes*, *Cleome monophylla*, *Crotalaria virgulata*, *Desmodium gangeticum*, *D. velutimun*, *Melochia corchorifolia*, *Vernonia cinerea*, *Vigna unguiculata* and *Wormskoldia longependunculate*. It is likely, however, that the flush and flowering of herb layer components is most closely tied to the annual variations in rain occurrence, particularly the differential effect of July rains on burnt and unburnt areas.

Maximum growth of the grasses appear to be reached in February, but taller components such as *Hyparrhenia* spp. attain their maximum in the autumn. It is significant that only two tall grass feeders, Lichtenstein's hartebeest and sable, remain in the miombo throughout the annual cycle; most of the other large wild herbivores are visitors from the Rift Valley, mainly in the pre-rain spring when the miombo herb layer has flushed due to fire or unseasonal rain. In the autumn the herbivores visit the few



dambo areas of the miombo. Otherwise the mature coarse grass stratum of miombo remains relatively untouched by wild ungulates. Hopkins (1968) notes that in the herb stratum of Nigerian miombo, maximum dry weight is reached and growth ceases two months *before* cessation of the rains.

In summary, Midland miombo phenophases divide the annual cycle into five seasons similar to those recognised by Boaler (1966) and Malaisse (1972). These are:

- (1) Pre-rain woody spring, leafless-flowering period (mid Aug. to Oct.)
- (2) First rains herbaceous spring (November).
- (3) Main summer rains, mature foliage period (Dec. to mid March.)
- (4) Autumnal drying and fruit maturation period (mid March to mid May).
- (5) Mild winter dry season, leaf fall and fruit dispersal period (mid May to mid Aug.).

SUCCESSION

Geoecological succession and landscape evolution in the Midlands is dealt with in Chapter 6 and Fig 6.2, , in which the role of the miombo savanna system is traced from the relic Plio-Pleistocene surfaces that survive on flat interfluves, to the present deeply dissected hill miombo predominant over the greater part of the Midlands in central Mocambique, and indeed over most of northern Mocambique as well.

As shown by the moist savanna symbols in the block diagram—sequences (Fig 6.2), miombo forms an interzone between forest and the dry clay savannas of bottomlands. Eating-back of the plains and interfluve areas as well as the bottomland dambo surfaces, allowed the extension of miombo in both directions. On the Midlands in the north of the ecosystem, where duplex sands are being actively eroded, the leached clays exhumed from beneath the sand is invaded by nearly pure scrub or pole stands of *Julbernardia globiflora*. The evidence from this marginal area of the Midlands indicates that the floristically poorer and drier climo-edaphic end of the miombo spectrum undergoes little, or very slow, further development from its *Julbernardia* dominance unless further sands are added to the soil profile, either from above by colluvial sheetwash processes, or possibly in the longer term by eluviation of the exposed sandy clays, which would alter the soil moisture balance to the mesic.

In hill miombo the island thickets, which occur either on deep soil pockets, on termitaria, or around tree bases, are not actively invading the surrounding greater extent of miombo savanna. The differential leaf fall of the same miombo canopy trees

112

under the same rainfall regime, but on different substrates and land facets of the same hillslope, indicate not only that many of the species are facultatively deciduous but also that soil moisture balance underlies both deciduousness and the role of forest/thicket extension.

Fire is naturally a major factor in suppressing the extension and establishment of forest/thicket precursors particularly if there are fierce burns in the late dry season. However, evidence from the Midland and Cheringoma evolutionary sequences (Figs 6.2 & 6.5), which will be referred to more fully below, indicates that the efficacy of fire is not only dependant on which part of dry season it occurs in, or the abundance of grass fuel, but also on the fundamental factor of soil moisture balance. If forest/thicket occurs on the mesic to xeric (droughty) side, their extension appears to be more easily destroyed by fire as their components would be in disequilibrium with the substrate. But if the soil moisture balance is above the mesic, then a dense grass sward of 3 to 4 m height producing extremely fierce fires in the late dry season, is insufficient to eliminate even the small tree-base thickets. Examples of this occur in the Rift Valley savannas where a permanent watertable exists at 7 to 10 m in depth. West (1965: 10-11, 23-24) reports on the quite different responses to fire of *Acacia* savanna on compact skeletal latosols and adjacent Burkea-Terminalia savanna on deep sands under an identical rainfall regime, due apparently to the contrasting soil moisture status of the two soils. Trapnell (1959: 165) admits that "a good deal (of forest invasion of miombo) probably depends on local soil-moisture conditions".

Burning experiments laid down in the miombo of northern Zambia in 1934 were studied and described by Trapnell (1959) who distinguished three main categories according to their response to fire: (a) fire tender or semi-tolerant, (b) semi-tolerant to tolerant, and (c) tolerant. The Ndola area is dambo miombo plainsland which has quite a different soil moisture balance to hill miombo, and is therefore closely equivalent to that on the Cheringoma cuesta in Gorongosa.

The *Brachystegia* and *Julbernardia* dominants became extinct in the plots burnt annually in the late dry season in Zambia (Trapnell 1959) but under Rhodesian conditions, where fires were apparently less fierce, these dominants were highly fire tolerant (West 1965: 14–15). In the *Pterocarpus – Dialium – Baikiaea* "filtered-out miombo" in northern South West Africa and the Caprivi, no changes could be discerned after 10 years of burning experiments due to the wide spacing of the tufted grass stratum on Kalahari sands resulting in light fires during any part of the dry season.

A feature of miombo savanna is the mosaic formed by the grassland understorey, changing in height and density in different areas and sites. The experimental



evidence sited above indicates therefore that the changes in relative dominance of tree species in different areas may be selected by different intensity of fires as well as by substrate characteristics. The quantitative data from the Midlands show clearly mosaic dominance and recruitment of canopy trees in different areas, but these data are unfortunately not correlated with characteristics of the grass stratum.

In one quantitative sample from the Midland miombo in Gorongosa, 20% (57 out of 284 trees > 3 m in height) of the trees in 1 ha were scarred by fire. Although *Julbernardia* and *Erythrophleum* were nearly equally predominant in the sample, *Erythrophleum* trees were scarred by fire more than double than the next species (*Julbernardia, Brachystegia boehmii* and *Diplorhynchus*) although it is classified as fire tolerant by the Ndola experiments. The Ndola experiments showed clearly that the fire-tender to semi-tolerant species, in particular the *Brachystegia* and *Julbernardia* canopy dominants, increased under an early burning regime (late autum — early winter) and in the protected plots.

Miombo trees are heliophytes and where all stages of forest invasion of miombo is found on the Cheringoma Plateau, the miombo is shaded out and becomes extinct except for relic emergent canopy trees such as *Brachystegia spiciformis*. Within the dispersal radius of these relics, rare straggling saplings of the same species can be found where openings occur in the forest/thicket understory.

The great miombo system has been regarded as a fire-subclimax but Trapnell (1959: 167) concludes from the evidence of the burning experiments, "that there is no present justification for regarding the ordinary woodland as fire induced type *except* in respect of its understorey and small tree and shrub components". Fanshawe (1971), forest ecologist in Zambia, maintains that miombo is secondary, occurring after the destruction of dry evergreen forest by fire. This conclusion appears to be accepted by Malaisse (1977) working in the southern Congo. Aubreville (1947, 1949b) and Walter (1971, 1973) look upon most if not all of the miombo system as moist anthropogenic savannas.

In the absence of human influences miombo would have been burnt periodically by lightning induced fires in the late dry season — first rains period, resulting in extremely fierce fires which however would have been extinguised in a mosaic pattern by the occurrence of thunderstorm rain. With the advent of cultivator man, these late dry season fires would have become an annual event as fields are prepared from September onward (vide Ch. 7). Both these sources of fire, and shading, militate against the evolution of fire-tender heliophytic *Brachystegia* and *Julbernardia* as canopy dominants across vast expanses of the African Continent, and against the evolu-

113

tion of its unique faunal associates. Thus the only fire regime which would play a fundamental part in the evolution and maintenance of miombo would be those which occurred early in the dry season.

The only possible source of fire early in the dry season over the millenia is from man; honey hunters who rob hives in the main miombo honey season between April and June, and from fires made by game hunters to attract wild ungulates to unseasonal new grass flush. It is no accident that most of the bee-keeping tribal people in Africa are those associated with the miombo whose canopy dominants are renowned honey trees. The main honey flow is related to the gregarious flowering of either or both *Julbernardia globiflora* and *J. paniculata*. Another honey flow occurs in midsummer after flowering of the several *Brachystegia* tree species, but honey gathering at this time does not result in extensive fires. In the equatorial rain forest there is a definate honey season from June to July which is the highlight of the annual cycle for the hunter-gatherer Mbuti pygmies in the Ituri Fores (1° N) (Turnbull 1963: 46–51),

It is worth speculating that the co-relations of man, honey and fire may extend to his antiquity, one million or more years ago, and from this, early dry season fires would have favourably selected for *Brachystegia* and *Julbernardia* predominance and thus the enhancement of a prolific honey tree resource, a coactive evolutionary relationship.

Interpretation of the evidence depicted by the contrasting hill and dambo type miombo systems and their soil characteristics indicate that over vast areas miombo is climax, or in dynamic equilibrium with climo-edaphic determinants and the fire factor, the damaging effect of which is modified by the soil moisture balance of different soils and land facets.



8.5 RIFT VALLEY

The central feature of the Urema Trough is the lake surrounded by extensive open floodplain grassland which extend 30 km northwards. On calm, clear days Gorongosa Mountain is reflected in the Urema Lake, and below it the three Bunga Inselbergs and the sides of the Rift are conspicuous. The floodplains disappear into mirages to the north and terminate abruptly against tree lines of savanna, thicket or forest on alluvial fans entering from the valley sides. The wooded cover occurs in distinct mosaic of clumped and linear patterns related to the alternation of alluvio-catena soils.

This heterogenity is enhanced by the abundance of large island-thickets on termite hills which, archipelago-like, overlay all communities — distinct from, but part of the larger ecosystems. These dark-foilaged thickets, like those in discontinuous patches and strips along watercourses, are particularly conspicuous in the dry season.

The seasonal extremes experienced in the Rift Valley are even more striking than in the miombo. The steaming summer is oppressively hot, with vast flooded shallows under floating pastures and flowering water-lilies, lushly foilaged trees, bird and frog choruses, barbel and turtles in the rain flooded savannas far from permanent water. The impression is one of overwhelming verdant growth set off against a sky dominated by giant cumulo-nimbus thunderstorms releasing heavy curtains of rain over the plains and Gorongosa Mountain.

In contrast the dry season has brown grasslands, leafless savanna trees, a total absence of surface water, except in the main rivers and lake, and hard-baked ground. Grasslands on base saturated soils turn a golden-brown, reminiscent of the margins of the Etosha and Makarikari salt lakes. The dry season tones are often transformed to a blackened landscape by fire, leaving the island thickets on termitaria and forest patches singed but otherwise unscathed. In the dry season a dense haze of smoke closes off the far vistas, and valley fog is a feature of the early mornings. The essence of the Rift Valley ambient is superbly captured in the writings of Vaughan-Kirby and Vasse, quoted in the frontis.

AQUATIC HERB COMMUNITIES

Two distinct aquatic systems occur on the Rift floor. One system consists of the seasonal rain-filled pans which are linked temporarily, if at all, during heavy down-pours of rain. The deeper of these pans retain water until about June. The second is made up of both a seasonal flood and ebb regime, typified by the floodplains, and perennial waters of streams, the lake and oxbow lagoons. The hygrophilous commu-

nities of the seasonal pans most closely resemble those of the floodplains. A full gradation of overlapping aquatic community types occur from briefly inundated habitats to permanent waters. The herbaceous constituents include:

(a) Submerged aquatics:

Ceratophyllum demersum Lagarosiphon spp. Ottelia exserta Potamogeton spp. Najas interrupta

(b) Floating aquatics:

Azolla nilotica Eichhornia crassipes Lemna spp. Pistia stratiotes Wolffia spp. Trapa natans

(c) Rooted aquatics with floating aerial parts

Herbs:

Alternanthera sessilis Ipomoea aquatica Ludwigia stolonifera Marsilia minuta Neptunia oleracea

Nymphaea capensis

N. caerulea

Nymphoides indica Utricularia stellaris

Grasses:

Echinochloa pyramidalis Echinochloa stagnina Oryza longistaminata

Paspalidium obtusifolium Vossia cuspidata

(d) Emergent aquatics:

Aeschynomene indica Cyperus digitatus Cyperus papyrus Sesbania mossambicensis Sesbania Sesban Phragmites mauritianus Typha sp.

The reedbeds occur in streambank sites and in the more permanent backwaters. Only one area of papyrus occurs within the ecosystem sector of the Rift floor, in the southeast at the foot of the Cheringoma slopes between the Mutsambire and Musapasso streams.

Mudflat communities

These are dense ephemoral herb societies which germinate on the mudflats left by the receding floodwaters. Attaining between 20 to 50 cm in height, these plants are at the height of their reproductive phases between June and September. Some constituents of this species-rich community are heavily grazed by wild ungualtes whilst others are ignored. Typical components include:



PLATE 17 FIRE PATTERNS, MEANDER SCROLLS, SAVANNA PANS & CLUMP THICKETS ON THE RIFT FLOOR



(A) Edaphic control of the passage of fire by short grasslands on saline clays and on overdrained ecotones (between convex and low surfaces) which act as firebreaks, depicted by the linear fire-limit in the middle distance.



(C) Knobthorn Acacia nigrescens savanna and clump thickets with an abundance of rain-filled pans (3/ha) developed mostly on eroded termite hill sites. Clump thickets on termite hills and around tree-bases.



(B) Alternating slacks and ridges of a meander scroll sequence on the Pungue River east of Chitengo Camp. Accentuated by the contrasting physiognomies of grassland in the slacks and savanna and thicket clumps on the rises.



(D) Thicket of baobab Adansonia digitata, Acacia welwitschii, Albizia brevifolia and Euphorbia halipedicola, on convex sandy clay bar deposit surrounded by seasonally waterlogged grassland on vertisol clays.



Grasses:

Crypsis schoenoides

Sodges:

Diandrochloa pusilla (on sand)

Sedges:

Cyperus alopecuroides Cyperus esculenta

Cyperus digitata Mariscus hemisphaericus

Herbs:

Altenanthera sessilis Amaranthes graecizans Ambrosia maritima Basilicum polystachyon Bergia mossambicensis Caperonia serrata Chrozophora plicata Coldenia procumbens Euphorbia minutiflora Glinus lotoides G. oppositifolius Gnaphalium hispida Gomphrena celosiodes
Gyrodoma hispida
Heliotropium indicum
H. ovalifolium
Ludwigia stolonifera
Melochia corchorifolia
Phyllanthus niruri
Polygonum plebium
Rorippa micrantha
Sphæranthus gazensis
Sphenoclea zeylanica

Suffrutices:

Aeschynomene indica Sesbania mossambicensis Sesbania sesban

Woody shrub

Mimosa pigra

TABLE 8.5

Composition of Sporobolus kentrophyllus saline grassland from 30 m² quadrats

	No. Quads	Rel. Freq %
Sporobolus kentrophyllus	29	41
Mariscus hemisphaericus	22	31
Sporobolus ioclados	11	16
Eriochloa fatmensis	3	4
Chloris mossambicensis	1	1
Crotalaria sp.	1	1
Echinochloa sp. nr. haploclada	1	1
Tephrosia pumila	1	1
Trianthema salsoloides	1	1

9 spp. (5 grasses, 1 sedge, 3 forbs)

Depth cm.	Texture	s pH	OIL PROFILE Salinity (R)	CaCo ₃	Colour (Munsell)
0-4 4-25	SdLm SdCl	6,4 7,3	1480 70	5–10%	Black (10yr 2/1 Brownish black (2,5 Y 3/1
25-100	CI(G)	7,6	70	10%	Greyish olive (5 Y 4/2)

70

The mimosa is a favoured browse food and only attains shrub growth form during inundations; the remainder of the time it assumes a prostrate growth form in response to heavy utilization by herbivores.

FLOODPLAIN GRASSLANDS

Typically, these perennial hygrophilous grasslands exhibit a mosaic of dominance made conspicuous by their different heights and stratification. Basically there are short, medium, and tall grasslands. In the first category are the *Sporobolus* communities on saline soils, and the microperennial lawns of *Cynodon dactylon* and *Digitaria swazilandensis*, whose leaves are generally below 15 cm in height with inflorescences reaching to 30 cm. The second is characterized by *Panicum coloratum*, *Eriochloa stapfiana* and *Setaria* species which attain 100 cm in height. Tall grasslands are those formed by dense, nearly pure swards of *Vetiveria nigritana* which have an average height of 220 cm. In some areas assoiciations of elephant grass *Pennisetum purpureum*, *Hyparrhenia* species and a giant form of *Panicum maximum* attain in 3 to 4 m in height.

Structurally the median to tall grasslands are quite different to the short swards. The latter comprise only a single layer of grasses, sedges and forbs. Many of these constituents including the *Cynodon* and *Digitaria* dominants form a subordinante stratum within and between the tufts of the median to tall grasses. Due to the low gradient, floodplain grasslands merge almost imperceptibly into savanna grasslands characterised by their overlay of woody tree and shrub strata. All depressions in the savannas are merely remnants of former floodplain grassland extensions.

Short grassland

Saline Grassland

The simplest grass community is that dominated almost exclusively by **Sporo-** bolus kentrophyllus on highly saline clays capped by 3 to 5 cm of sand. Analysis in a one hectare sample showed the following relationships.

Where a surface sandy loam soil of 15 to 20 cm depth overlies sodic clays the above grass community merges into another, which is dominated by the halophyte *Sporobolus ioclados* and which has a richer mixture of savanna and floodplain species. Analysis in a one hectare area showed the following relationships:



Table 8.6 Composition of Sporobolus ioclados saline grassland from 30 m² quadrats.

	No. Quad.	Rel. Freq %
Sporobolus ioclados ¹ Tephrosia pumila Fimbristylis hispidula Digitaria milanjiana ¹ Urochloa mosambicensis ¹ Mariscus hemisphaericus Echinochloa sp. nr. haploclada Cassia mimosoides Cienfugosia hildebrandtii Panicum coloratum ¹ Setaria eylesii ¹ Barleria spinulosa	30 27 23 19 14 14 12 12 11 8 8	15 14 12 10 7 7 6 6 6 4 4
Duosperma quadrangulare Dichrostachys cinerea Digitaria swazilandensis Eriochloa fatmensis E. stapfiana Panicum sp. (KLT 2573) Sporobolus kentrophyllus Stylochiton sp.	4 3 1 1 1 1 1 1	2 2 1 1 1 1 1

20 spp.

(11 grasses¹, 2 sedges, 4 forbs, 2 suffrutices,

1 woody)

SOIL PROFILE

197

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Depth cm	Texture	рН	Salinity(R)*	CaCo ₃	Colour (Munsell)
0–6	CILm	7,4	780		Brownish black (10 YR 2/2)
6–25 25–100	CI CI(G)	7,6 7,5	140 70	NAME OF TAXABLE PARTY.	" (10 YR 3/1) Greyish olive (5 Y 5/2)
* < 250 = 9	saline				

Microperennial lawn grassland

The greater part of the flood plains surrounding the Urema Lake on the south and northwest sides is covered by short 10 cm high stoloniferous grassland of Cynodon and Digitaria swazilandensis. Similar grasslands occur again on the Macoreia Plains north of the lake. These grasslands which are a major pasture for medium and short grass grazers are inundated shallowly to a greater or lesser extent every year. In years of low floods they are dependent on direct rainfall and show rapid changes in flush or drying out (see section 9.4).

Analyses of a 20 km² area of these grasslands south of the Urema Lake and its Sungue arm showed the following relationships.

Table 8.7

Composition of microperennial Cynodon—Digitaria lawn grasslands of the southern Urema Plains derived from 30 m² quadrats in 18 hectare sites (total of 540 m² quadrats).

Cynodon dactylon1 474 20 Euphorbia minutiflora1 270 11 Digitaria swazilandensis 244 10 Echinochloa stagnina1 241 10 Mariscus hemisphaericus2 179 7 Vossia cuspidata1 124 5 Alternanthera sessilis 99 4 Paspalidium obtusifolium1 84 3 Eriochloa fatmensis1 80 3 Echinochloa sp. nr. haploclada1 66 3 Panicum sp. (KLT. 1873) 57 2 Gomphrena celosioides 49 2 Rorippa micrantha 49 2 Tephrosia pumila 48 2 Corchorus olitorius 40 2 Coldenia procumbens 35 1 Eichhornia crassipes 33 1 Ambrosia maritima 33 1 Sida alba 28 1 Phyllanthus niruri 25 1 Heliotropium ovalifolium 21 1	Herb Layer	No. Quad.	Rel. Freq. %
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2428

45 spp. (12 grasses¹, 2 sedges², 30 forbs and suffrutices, 1 woody)



Woody Plants*	Total No.	Rel. Density % (18000m ²
Mimosa pigra	1016	95
Acacia xanthophloea	28	3
Hyphaene benguellensis	25	2
Acacia albida	3	0,3
4 spp.	1072	
AND A STREET OF THE STREET		

(* = only sapling stages represented)

SOIL PROFILE						
Depth cm	Texture	рН	R(Ohms)	CaCO3	Colour (Munsell)	
0-12	CILm	5,8	470	-	Black (10 YR 2/1)	
12–18	CI	5,9	220	-	Brownish black (10 YR 2/2)	
18-50	CILm	6,4	120	and the same of th	" (2,5 Y 3/2)	
60	CILm (G)	7,0	70		Olive brown (2,5 Y 4/3)	

These short grasslands merge into medium to tall grass communities which are waterlogged for longer periods, and which thus occur either in the lower parts and depressions on the plains or in maldrained areas of perched floodplains at a higher contour.

Medium height grasslands

The two examples of saline grasslands noted above (Tables 8.5, 8.6) are the xeric end of a microrelief catena on base staturated alluvium. These and the *Cynodon – Digitaria* (Table 8.7) grasslands merge gradually or abruptly with the two following grass communities which occur on a mosaic of waterlogged black vertisol clays of quite different texture and consistence. In the less moist parts and on sandy clays are *Setaria eylesii* (or *S. holstii*, or *S. woodii*) swards, alternating with *Echinochloa stagnina* on granular clay loams.

The **Setaria** grassland type has a mean height of 100 cm and contains a subordinate short grass and forb layer below. An example showed the following composition:

TABLE 8.8

Setaria floodplain grassland analysed from 30 m² quadrats across one hectare (Road 5 area).

	No. Quad.	Rel. Freq. %
Setaria eylesii ¹	28	22
Mariscus hemisphaericus	28	22
Echinochloa sp. nr. haploclada 1	23	18
Chloris mossambicensis ¹	9	7
Vernonia kirkii	9	7
Sporobolus kentrophyllus ¹	7	5
Cienfugosia hildebrandtii	6	5
Panicum coloratum ¹	5	4
Sesbania sesban	4	3
Eriochloa stapfiana 1	2	2
Barleria spinulosa	2	2
Phyllanthus niruri	2	2
Enicostema hyssopifolium	1	1
Commelina sp.	1	1
Echinochloa stagnina 1	1	1
Asparagus sp	1	1

SOIL PROFILE

Depth cm	Texture	рН	R(Ohms)	CaCO3	Colour (Munsell)
0-4	SdCI	5,9	420		Black (10 YR 2/1)
4-30	CI	7,2	180		Olive
00 50	CIVCI	7.0	70	E 0.	black (5 Y 3/1) " (5 Y 3/2)
30-50	CI(G)	7,3	70	5%	(3 1 3/2)

The shorter 40 cm tall *Echinochloa stagnina* grassland either occurs as a mosaic with *Setaria* or forms extensive areas where it is singly dominant. An example is given in Table 8.9.

TABLE 8.9

Echinochloa stagnina marsh grassland analysed from 30 m²
quadrats across 1 hectare (Road 5 area).

	No. Quad.	Rel. Freq. %
Echinochloa stagnina ¹	29	31
Panicum coloratum ¹	27	28
Mariscus hemisphaericus	19	20
Vernonia kirkii	5	5
Cienfugosia hildebrandtii	4	4
Enicostema hyssopifolium	3	3
Barleria spinulosa	2	2
Setaria eylesii ¹	2	2
Eriochloa stapfiana 1	1	1
Ischaemum afrum 1	1	1
Sesbania sesban	1	1

11 spp. (5 grasses 1,) 1 sedge, 5 forbs and suffrutices)

16 spp. (7 grasses¹, 1 sedge,

8 forbs and suffrutices)

94

129



Table 8.9 (continued)

		0012	MOTILE		
Depth cm	Texture	рН	R(Ohms)	CaCO ₃	Colour (Munsell)
0-4	CILm	5,6	810	_	Brownish black (5 YR 2/1)
4–25 35–50	CI CI(G)	6,4 6,8	320 100	- 14,0	" (2,5 Y 3/1) " (2,5 Y 3/2)

SOIL PROFILE

In all the above tables the presence of *Cienfugosia hildebrandtii* or *Duosperme quadrangulare*, which are vigorous suffrutices with large basal parts, are indicative of the drying-out trend in the hygrophilous grasslands. In areas of gilgai microrelief these species occur on the higher rims separating each microbasin; sites which are later invaded by mopane *Colophospermum mopane*, or acacias such as *A. borleae* and *A. polycantha*. In the microperrenial grassland, fever trees and palm are the most vigorous invaders of the savanna front. Sandy patches are colonized by winterthorn *Acacia albida*, or dry forest precursors.

Tall grassland

Tall floodplain grassland is characterised by the *Vetiveria nigritana* community which attains an average height of 225 cm. This community occurs on similar soils to those on which *Echinochloa stagnina* is found, but under a more seasonally waterlogged condition. An example from half a hectare area is given in Table 8.10 The double layered structure in *Vetiveria* grassland is well developed and the lower storey grasses are grazed the most by ungulates, whilst the rank *Vetiveria* and *Ischaemum* are largely ignored until they produce a new regrowth flush after fire. The lower grass layer is of soft-leaved species; *Digitaria swazilandensis*, *Panicum coloratum*, *Eriochloa stapfiana*, and *Echinochloa stagnina*.

These various floodplain grasslands merge with those of the savannas and are repeated throughout the savannas wherever appropriate substrates occur. On the Rift floor alluvia, tall grass habitats are not confined to riverine sites but occur as a mosaic with medium and short grass habitats through the savannas; hence animals usually associated with the tall grass zone of riverbanks are widespread.

TABLE 8.10

Vetiveria nigritana grassland analysed from 30 m²
quadrats in a 0,5 ha sample (Road 5 area).

Plants	No. Quad.	Rel. Freq. %
Vetiveria nigritana	30	28
Ischaemum afrum ¹	29	27
Bothriochloa glabra ¹	14	13
Mariscus hemisphaericus	14	13
Digitaria swazilandensis ¹	3	3
Panicum coloratum 1	3	3
Cassia mimosoides	2	2
Echinochloa stagnina ¹	2	2
Eriochloa stapfiana ¹	2	2
Phyllanthus niruri	2	2
Vernonia kirkii	2	2
Heteropogon contortus ¹	1	1
Hyparrhenia rufa ¹	1	1
Panicum maximum ¹	1	1
Paspalum scrobiculatum ¹	1	1
Rhynchosia sublobata	1	1
Tephrosia pumila	1	1

17 spp. (11 grasses¹, 1 sedge, 5 forbs)

109

SOIL PROFILE

Depth cm	Texture	рН	R(Ohms)	CaCO ₃	Colour (Munsell)
0-10	CILm	6,3	1100		Black (7,5 YR1,7/1)
10-60	CI	6,2	580		Brownish
					black (10 YR 2/2)
70	CI(G)	7,1	150	5%	" (2,5 Y 3/1)

Environmental Factors

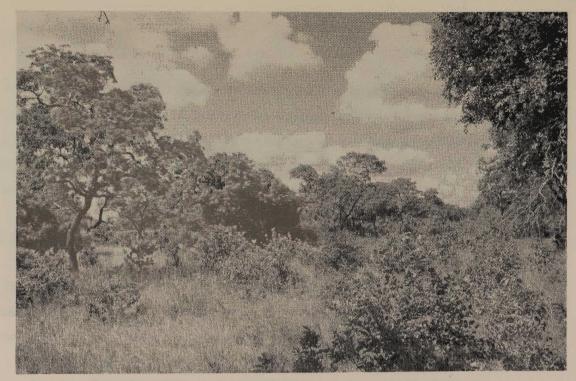
The lawn grasslands, *Setaria* and *Echinochloa* communities, are all inundated to a greater or lesser extent every year. In wet years they are flooded by rising river and lake waters as well as from direct rainfall and local runoff. Under these circumstances waterlogged conditions endure for about 3 to 4 months between December and March. In dry years flooding is temporary and fluctuates with the incidence of rain.

The highly saline *Sporobolus* grass communities occur on the upper parts of microrelief and are waterlogged for shorter periods than the hygrophilous grasslands.

Annual fires burn all the floodplain grasslands except the *Cynodon-Digitaria* lawn community. This grassland and the *Echinochloa-Vossia* community bear the brunt of year-round heavy grazing pressure by the wild ungulates.



PLATE 18 RIFT VALLEY SAVANNA COMMUNITIES



(A) Sand savanna of Burkea africana, Terminalia sericea trees and Hyperthelia dissoluta grass stratum.



(B) Clay savanna of *Hyphaene benguellensis* palms on saline vertisols with 1 to 2 m high *Setaria eylesii* grass stratum (3 m measuring rod in middle distance). Typical two aged structure with adult palms (first slack invaders) and palm shrub stratum kept short by elephant browsing. Dark tree is *Trichilia emetica* on a termite hill.



(C) Clay savanna of mopane *Colophospermum mopane* on calcareous vertisols, with *Aloe marlothii* fieldlayer. Dambo grassland in foreground (autumn aspect).



(D) Fever tree Acacia xanthophloea marginal floodplain woodland. Note quasi-even-aged structure of canopy trees, treeless median layer and mixed weed and grass groundlayer with a few palms (autumn aspect.).



Succession

A grassland and grazing succession occurs on the floodplains which is sensitive to fluctuations in environmental factors such as flooding, drying, drought and fire. These aspects are dealt with in the following chapter (Section 9.4). Successional replacement of grasslands by woody communities is described at the end of the Rift Valley section.

SCRUB SAVANNA

The largest continuous area of scrub savanna is formed by pure stands of *Acacia borleae* on gilgai vertisols of the Nhamisangu floodplain in the north, and by palm *Hyphaene benguellensis* in the south. The *Acacia borleae* cover is between 1 and 2 m in height with a variable density. In parts of the Macoreia Plains this species is mixed with short *Acacia polycantha*. The scrub growth form of the palm *Hyphaene benquellensis*, which otherwise attains up to 20 m in height, is maintained by heavy elephant browsing utilization. The spacing in this community varies from widely separated clumps to dense continuous areas of scrub-thicket 3 to 4 m in height. These species, in common with *Acacia xanthophloea*, are actively invading floodplain areas that are dryingout, and characteristically form pure species communities, but also occur in close mosaic where soils alternate on alluvio-catenas.

Below Bunga Inselberg, on either side of the Vundudzi River, and in the Chitengo area near the Pungue River, large patches of scrub savanna occur on old cultivation sites of some 20 years standing. Areas cultivated in the past on the Rift floor are shown in Fig 7.2. The chief scrub constituents here are *Combretum fragans*, *Lonchocarpus capassa* and to a lesser extent *Piliostigma thonningii*. Heavy browsing by elephant and annual fire have contributed to maintaining their scrub growth form.

In the north, adjacent to the Lunga drainage, is an isolated area of pure *Acacia* nilotica scrub savanna on sheet-eroded sandy clays with a short sparse grass stratum.

TREE SAVANNA

The tree savannas of the Rift Valley are diverse physiognomically and floristically due to the association of fine leaved (nanophyll) thorn trees with broad leaved (mesophyll) species, and large leaved (megaphyll) palms. Diversity is multiplied by the mosaic occurrence of mixed species associations alternating with communities dominated by only one or two species.

119

The grass stratum of the savannas is equally diverse in physiognomy and species associations. The grasses occur in a mosaic pattern and also form communities dominated over large areas by a few species. Clumped dispersal is thus exhibited by all layers in the savannas.

The appearance of the Rift savannas is characterized by tall trees up to 20 m in height with umbrella-shaped canopies, interspersed with the distinctive growth forms of baobabs and islands of large termitaria thicket clumps.

The spacement of the wooded grasslands varies between an open tree savanna and closed canopied savanna woodlands. Six major tree savanna communities occur on the Rift floor in changing species associations related to soil and moisture gradient changes. The main communities are:

- (1) Mixed savanna (Acacia, Albizia, Lonchocarpus, Piliostigma, Sclerocarva)
- (2) Marginal floodplain woodland (Acacia albida, Acacia xanthophloea)
- (3) Knobthorn savanna (Acacia nigrescens)
- (4) Sand savanna (Burkea africana, Terminalia sericea)
- (5) Mopane savanna (*Colophospermum mopane*)
- (6) Palm savanna (*Hyphaene benguellensis*, *Borassus aethiopica*)

As many of these communities occur in closely juxtaposed mosaics due to the close alternation of different soils and their ecotones, it has been possible to sample two or three different kinds within a one hectare sample area. Analysis of three examples includes: (1) a fever tree, winterthorn and palm mosaic association, (2) mopane savanna woodland, (3) an *Acacia nigrescens* — *Burkea africana* mosaic association.

Marginal Floodplain Woodland

The fever tree and winterthorn woodlands grow typically in quasi-even-aged stands of various heights, the youngest occurring on the leading edge invading the floodplain grasslands. The sequence is illustrated by a profile diagram with the fever tree as an example (Fig 8.15). Sandy alluvium in the lower parts of the Urema slack-basin occur in relatively small patches, hence winterthorn will probably decrease relative to the fever tree and palm invasion (increase) of the floodplain. An example of the floristic and dominance relationships in marginal floodplain woodland is given in Table 8.11.

Mopane Savanna Woodland

Like the above species, mopane tends to form pure species stands of various ages. In the centre of the park sector of the Rift Valley two isolated areas of mopane

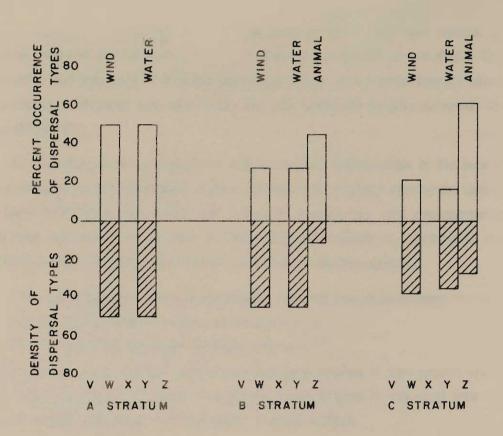


FIG. 8.6 COMPARATIVE IMPORTANCE OF DISPERSAL

TYPES IN THREE WOODY STRATA OF

MOPANE SAVANNA WOODLAND ON THE

THE RIFT VALLEY FLOOR

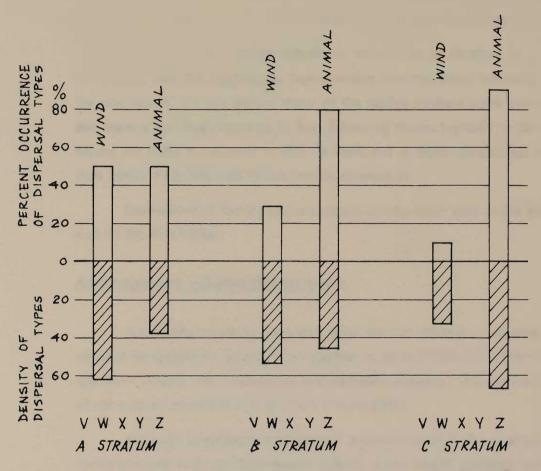


FIG 8.7 COMPARATIVE IMPORTANCE OF DISPERSAL TYPES IN THREE WOODY STRATA OF ACACIA - BURKEA SAVANNA MOSAIC.



occur on sodic calcareous clays. The larger patch measuring 2×7 km (14 km²) occurs in the converging delta area at the head of the Urema Lake, and the other a small area of about 1,5 km² west of the Urema Lake (Road 5 area).

In the north between the Nhandue and Nhamapaza Rivers more extensive areas of mopane occur, mixed with other tree species, on fossil interdistributary slack soils. Even when mixed with other species such as *Dalbergia melanoxylon* and tambootie *Spirostachys africana*, all three species tend to form their own clumps. In Gorongosa, mopane are tall, averaging 15 m, and have a deltoid crown shape. The physiognomy and structure of mopane savanna is shown in a profile diagram where the community alternates with dry forest and vlei grassland on alluvio-catena sequences (Fig 8.18).

An example of the composition and dominance relationships in the several layers of mopane savanna woodland is given from the smaller patch west of the Urema Lake (Table 8.12). The exceptionally high density of mopane per unit area compared to fever tree woodlands, which have a similar canopy spacement, is indicative of the very different crown diameters and intertree distances in the two species.

The large spinescent shrub *Dichrostachys cinerea*, occurs in mopane communities wherever sand overlies the clays as depicted in the sample and associated soil profile. The fieldlayer in the larger mopane area which has a dense canopy cover, is sparse and poorly developed with few species and large patches of bare ground where standing water occurs in the rains. The mature mopane trees in the same area are clumped in related patterns to the microridges of gilgai vertisols.

Dispersal

Mopane is chiefly dispersed by wind and water. Proof of the latter is shown by seedlings germinating along swashlines left after a downpour of rain. The single species dominance in the canopy gives equal importance to these dispersal methods. In the median (B) tree layer and shrub (C) stratum the same importance is maintained due to the predominance of *Dalbergia*, *Aloe* and pole stands of mopane. However, the diversity of zoochorous species increases progressively in the lower woody layers (Fig 8.6).

The whole system is thus overwhelmingly either wind and/or water dispersed. It is possible that anemochory is more important where there is a continuous ground-cover, and hydrochory where sheet wash is operative under sparsely covered or bare ground conditions. The importance of zoochory in the lowest layer is compounded by the development of tree-base thicket initials around many trees.

120

Phenology

The phenophases recorded in mopane savannas will be dealt with in conjunction with other Rift Valley communities. The behaviour of the mopane tree, however, deserves special mention as it is semi-evergreen rather than deciduous in habit.

Leaf fall occurs synchronously in the month of October, the height of the dry season, and the subordinate layers receive maximal direct insolation at this time for one month. At this period many of the sapling mopane come into new leaf and also have a leaf flush response to fire. Flowering occurs typically in January and February (in 1969 it occurred in May as well) but is more conspicuous in some years than others. Fruit dispersal occurs from June onwards.

Environmental factors and succession will be dealt with at the end of the section on the Rift Valley.

Acacia nigrescens — Burkea africana mosaic

Alternating on sandy clays and sands are two tall tree — tall grass savannas dominated by knobthorn on clays and *Burkea* on sands (Table 8.13). The most abundant species in median and shrub layers is *Combretum fragrans*. This species is an indicator of old cultivation areas where it occurs in pure stands.

Although *Urochloa mosambicensis* is predominant in the example analysed, it forms a mosaic with tall *Hyparrhenia rufa* (on clays) and *H. dissoluta* (with *Burkea* on sand) which occur as dominants over large areas.

Some of the sectors where *Combretum fragrans* and *Urochloa mosambicensis* predominate were cultivated in the past (20 to 30 years ago), but other areas were unmodified according to local tribesmen. There is a general association between *Urochloa* grassland and the Chd and Cd soils which are characterised by favourable texture (SdLm and SdCILm) and the highest phosphorus values in the Rift Valley (Appendix 1).

A notable feature of the example analysed is the complete absence of young stages of the two canopy dominants, *Acacia nigrescens* and *Burkea africana*. Elephant are responsible for ring-barking the adults of these two species, resulting in the death of many 20 m high specimens, but their selective influence on the young stages is unrecorded as saplings were unrepresented in the area.



Analysis of marginal floodplain woodland in 1 hectare.

Mixed fever tree, winterthorn and palm community on an alluvio-catena.

		No. Trees in 1 ha	Total basal area cm ²
(A)	CANOPY & MIDSTRATUM > 3-20 m		
	Acacia xanthophloea Acacia albida Hyphaene benguellensis	20 13 4	643.221 476.804
	3 spp.	61	1.120.025
(B)	SHRUBLAYER 0,5-3 m	Total in 500 m ²	Rel. Frequ. %
	Hyphaene benguellensis Acacia xanthophloea Capparis erythrocarpos	14 3 1	78 17
	3 spp.	18	
(C)	GRASS STRATUM	Freq. in 30	Quad.
	Sida alba Digitaria swazilandensis Gomphrena celosioides Tephrosia pumila Eriochloa fatmensis Solanum panduriforme Panicum maximum Tephrosia astragalina Panicum infestum Weed indet. Amaranthus græcizans Phyllanthus niruri Abutilon angulatum Vernonia cinerea	22 17 16 13 13 12 9 8 7 6 5	80% 73 57 53 43 43 40 30 27 23 20 17 13

(less than 4 occurrences omitted)
32 spp. recorded

Analysis of mopane savanna woodland in 1 hectare on sodic calcareous clays (Road 5 area)

	Carterio Ingenia Inc		
(A + B)	CANOPY & MIDSTRATUM > 3-17 m	No trees	Total basal
(A + D)		in 1 ha	area cm²
	Colophospermum mopane (WY)	410	3.214.240
	Dalbergia melanoxylon (WY)	82	409.580
	Aloe marlothii (WY)	18	33.342
	Ziziphus mucronata (Z)	18	16.748
	Trichilia capitata (Z)	1	154
	Sterculia africana (Z)	1	16.520
	Commiphora pyracanthoides (Z)	1	314
	Maerua angolensis (Z)	1	113
	Acacia welwitschii (WY)	1	616
	9 spp	533	3.691.627
(C) S	SHRUB STRATUM 0,5—3 m	Total in 500 m ²	Rel. Freq. %
	Aloe marlothii (WY)	42	37
	Dichrostachys cinerea (Z)	24	21
	Colophospermum mopane (WY)	18	16
	Ehretia amoena (Z)	5	4
	Capparis erythrocarpos (Z)	4	4
	Zygoon graveolens (Z)	4	4
	Combretum mossambicense (W)	4	
	Thilachium africanum (Z)		3
	Ziziphus mucronata (Z)	3 2 2 2	4 3 2 2 2 2
	Manilkara mochisia (Z)	2	2
	Dalbergia melanoxylon (WY)	2	2
	Vepris zambesiaca (Z)	1	1
	Kigelia africana (Z)	1	1
	Canthium setiflorum (Z)	1	1
	Maerua kirkii (Z)	1	1
	15 spp.	114	
(D) G	GRASS STRATUM (30 x 1 m ²)	No. Quad.	Rel. Freq. %
	Urochloa mosambicensis	13	8
	Tephrosia pumila	11	7
	Barleria spiriulosa	10	6
	Coelorhachis/Rytachne (KLT 2586)	9	6
	Setaria sp. nr. holstii	9	6
	Mariscus hemisphaericus	8	6 5 5 5
	Panicum coloratum	8	5
	Jasminum sp.	7	5
	Ruellia patula	7	5
	Enteropogon macrostachy	6	4
	Panicum sp. (KLT 2572)	6	4
	Sporobolus ioclados	6	4
	Dichrostachys cinerea	5	3
	Digitaria milanjiana	5	4 3 3 3
	Heteropogon contortus	5	3

(less than 5 occurrences omitted) 42 spp. recorded



Table 8.12 (continued)

co	III	PR	OF		
3U		PH	UF	11	-

Depth	Texture	рН	Salinity (R)	CaCO ₃	Colour (Munsell)
0-20	Sd	6,4	2650	-1	Black (7,5 YR 2/1)
20-30	Sd	6,4	3350		Brownish
					black (10 YR 3/2)
30-35	ScCILm	6,2	1120		" "
35-50	SdCl	6,2	270	-	Olive
					brown (2,5 Y 4/3)
50-70	ScDI	8,1	130	10%	" "

TABLE 8.13

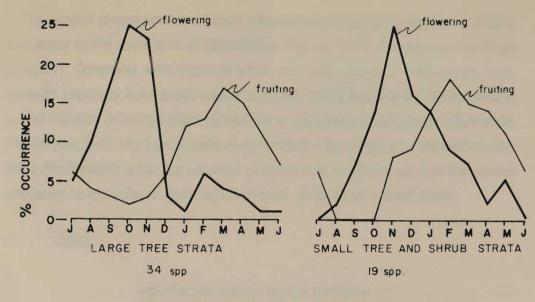
Analysis of Acacia nigrescens — Burkea africana savanna mosaic in 1 ha on a clay-sand alluvio-catena

(A)	CANOPY TREES 10-21 m	Total in 1 ha	Total basal area cm ²
	Burkea africana (W)	17	491.607
	Acacia nigrescens (WZ)	14	355.873
	Piliostigma thonningii (Z)	8	111.673
	Combretum fragrans (W)	7	44.881
	Lonchocarpus capassa (W)	7	64.268
	Xeroderris stuhlmannii (W)	6	56.433
	Sclerocarya caffra (Z)	5	102.963
	Crossopterix febrifuga (Z)	3	12.474
	Kigelia africana (Z)		1.591
	Strychnos madagascariensis (Z) Terminalia sericea (W)	1	1.257
	Terrification Sericed (VV)		1.257
	11 spp.	70	1.244.277
		Total in	Total basal
(B)	MIDSTRATUM TREES 3-10 m	1 ha	area cm ²
	Combretum fragrans (W)	45	385.000
	Cleistochlamys kirkii (Z)	18	21.651
	Crossopterix febrifuga (Z)	3	270
	Kigelia africana (Z)	3 3 2 2	1.521
	Cordia goetzei (Z)	2	255
	Lonchocarpus capassa (W)	2	707
	Antidesma venosum (Z)	1	113
	Cassia abbreviata (Z)	1	79
	Diospyros usambarensis (Z)		79
	Oncoba spinosa (Z)		79
	Piliostigma thonningii (Z) Trichilia capitata (Z)		80 176
	Xeroderris stuhlmannii (W)	1	177
	Ziziphus mucronata (Z)	1	20

Table	8.13 (continued)		
(C)	SHRUBLAYER 0,5—3 m	Total in 500 m ² (5×2	20) 5
	Combretum fragrans (W) Securinega virosa (Z) Dalbergia boehmii (W) Combretum mossambicense (W) Grewia lepidopetala (Z) Harrisonia abyssinica (Z) Tricalysia jasminiflora (Z) Cleistochlamys kirkii (Z) Diospyros usambarensis (Z) Lonchocarpus capassa (W) Phyllanthus reticulatus (Z) Allophylus alnifolius (Z) Annona senegalensis (Z) Antidesma venosum (Z) Crossopterix febrifuga (Z) Deinbollia xanthocarpa (Z) Ehretia amoena (Z) Markhamia obtusifolia (W) Piliostigma thonningii (Z) Stereospermum kunthianum (W) Ziziphus mucronata (Z) Commiphora schimperi (Z) Kigelia africana (Z) Lecaniodiscus fraxinifolius (Z) Maytenus senegalensis (Z) Rubiaceae indet. (Z) Strychnos madagascariensis (Z) Vangueria infausta (Z)	21 11 6 5 5 5 4 3 3 3 3 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2	
	28 spp.	96	
(D)	GRASS STRATUM	Occ. in Rel. 30 quad	Freq.%
	Urochloa mosambicensis Panicum maximum Heteropogon contortus Setaria sp. Acalypha senensis Digitaria milanjiana Hyparrhenia rufa Combretum fragrans Urtica urens Asystasia gangetica Hyperthelia dissoluta Pogonarthria squarrosa	27 23 16 7 6 5 5 4 3 2 2	22 19 13 6 5 4 4 3 2 2 2

³¹ spp. (7 grasses, 11 forbs, 11 woody) (less than 2 occurrences omitted)





REPRODUCTIVE PHENOLOGY

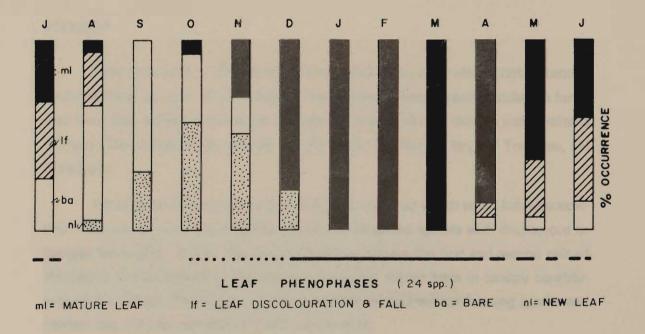
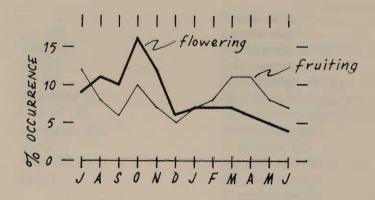
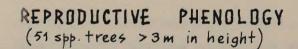
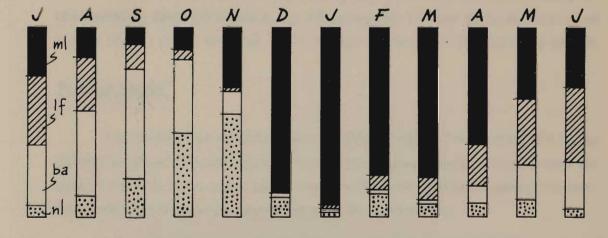


FIG. 8.8 PHENOGRAM FOR MIOMBO SAVANNA TREES
ON THE MIDLANDS SECTOR OF THE GORONGOSA ECOSYSTEM







LEAF PHENOPHASES (51 SPP.)

ml = mature leaf, If = leaf discolouration & fall, ba = bare, nl = new leaf

FIG 8.9 PHENOGRAM FOR RIFT VALLEY SAVANNA TREES





Dispersal-

The parallel predominance of anemochorous and zoochorous species in all strata is due mostly to the abundance of *Combretum fragrans* which reproduces at all three levels (Fig 8.7). Otherwise wind dispersal is the main characteristic of the canopy components, with zoochory increasingly important down to the shrublayer. The increase in density and number of animal dispersed species in the lowest woody layer is due mainly to the frequency of tree-base thicket elements in this savanna type. The sectors with tall, dense *Hyparrhenia* grassland are poor in shrublayer constituents, and the reverse occurs adjacent to trees (perch sites) and in shorter, or sparsely, grassed areas.

SCRUB-THICKET

The only mature scrub-thicket habitat on the Rift floor is that formed by pure stands of *Antidesma venosum* along the Mucombezi riverbanks, and on some of the old Pungue channels in the Dingedinge area. Otherwise, the dense woody cover less than 4 m in height which occurs around tree-bases and on new termite hills marginal to the floodplains, are young stages of the thicket dealt with below.

THICKET

Four main kinds of thicket occur on the Rift floor, all of which contain canopy trees attaining just over 20 m in height. One species, *Sterculia appendiculata*, a forest tree from East Africa, occurs as an emergent to nearly 30 m in riverine and termitaria thickets. The thicket types include: (1) Riverine, (2) Alluvial fan, (3) Tree-base, (4) Termitaria.

All of these thickets have a similar floristic make-up which varies kaleidoscopically from site to site. The majority are animal dispersed species with drupaceous or baccate fruits (Fig. 8.10). The major difference betwen the first and second pair of thickets is the abundance of savanna and floodplain margin trees in canopy constituents of the former. The latter pair are dominated by true thicket-forming species and contain relatively few savanna or forest components.

Those termitaria in dry forest on duplex sands and adjacent to forest naturally have a much higher content of forest species.

Riverine and Alluvial Fan Thicket

Large patches of alluvial fan thicket occur on the fans formed along the edges

of the Urema Trough. These are interspersed with true forest on the duplex sands of splays or aggraded distributaries and linked by disconnected patches of riverine thicket along functional watercourses.

A typical example of the mixed character of alluvial fan thicket is shown by the following partial list from near the Muaredzi — Urema confluence:

Acacia robusta (W? Z?)
A. welwitschii (W)
Adansonia digitata (Z)
Afzelia cuanzensis (Z)
Albizia brevifolia (W)
Berchemia discolor (Z)
Boscia salicifolia (Z)
Cassia abbreviata (Z)
Cleistanthus schlechteri (Z)
Cleistochlamys kirkii (Z)
Commiphora schimperi (Z)
Cordyla africana (Z)
Diospyros senensis (Z)
D. usambarensis (Z)

Drypetes mossambicensis (Z)
Euphorbia halipedicola (X, Z)
Hyphaene benguellensis (Z)
Kigelia africana (Z)
Lannea stuhlmannii (Z)
Markhamia obtusifolia (W)
Sclerocarya caffra (Z)
Spriostachys africana (X, Z)
Strychnos madagascariensis (Z)
Tabernaemontana elegans (Z)
Trichilia capitata (Z)
T. emetica (Z)
Ximenia americana (Z)
Ziziphus mucronata (Z)
Z. pubescens (Z)

Riverine thicket contains a similar assortment but with a greater preponderence of species such as *Ficus sycamorus*, *Diospyros mespiliformis*, *Mimusops fruticosa*, *Trichilia emetica*, *Ekebergia capensis*, and *Khaya nyasica*. In a few parts these and other species form a closed stratified forest community noted in the following section.

Tree-base Thicket

This thicket type is abundant, and a vigorous invader of most of the Rift Valley wooded savannas. The full sequence from animal dispersed seeds in dung around the bases of trees, seedlings, scrub stage to mature coalesced patches are particularly common in the area between the Urema Plains and the Pungue River.

Like termitaria thicket the tree-base type is composed chiefly of animal dispersed seeds which are centrifugally dispersed to perch sites in a habitat. Melton (in press) shows that baboon preferentially defaecate on termite hills in his Uganda study area.

Related to both these perch-based thickets, are those which develop on civet dung middens in open ground. The three thicket types are similar in composition as similar fruits are taken by primates, civet, and birds such as the green pigeon (cf. fruits eaten by baboon and civet). Furter details on this subject is concluded in Chapter 9. The composition of tree-base thickets is indicated by the following table.



TABLE 8.14

Occurrence of animal dispersed thicket initials recorded from the base of 112 savanna canopy trees

	Presence	Rel. Freq.%
Capparis erythrocarpos	46	10
Ziziphus mucronata	37	8
Deinbollia xanthocarpa	33	7
Jasminum sp.	30	7
Trichilia capitata	29	6
Tamarindus indica	24	5
Cleistochlamys kirkii	22	5
Tricalysia jasminiflora	19	4
Lecaniodiscus fraxinifolius	17	4
Ximenia americana	16	3
Thilachium africanum	14	3
Combretum mossambicense	12	3 3 3 2 2 2 2 2 2 2 2 2 2 2
Dalbergia melanoxylon	12	3
Grewia microcarpa	11	2
Landolphia kirkii	11	2
Phyllanthus reticulatus	10	2
Allophylus alnifolius	9	2
Commiphora schimperi	9	2
Ehretia amoena	9	2
Securinega virosa	9 7	2
Diospyros mespiliformis		2
Maclura africana	7	2
Diospyros usambarensis	6	1
Harrisonia abyssinica	6	1
Boscia salicifolia	5	1
Diospyros senensis	5	1
Drypetes mossambicensis	5	
Grewia sulcata	5	
Lonchocarpus capassa	5	Souther (ZI)

66 spp. recorded (less than 1% frequency omitted)

The change in composition and predominance of tree-base thicket constituents in different systems is well exemplified by the following examples from marginal flood-plain woodland, knobthorn and mopane communities.

TABLE 8.15

Variation in the predominant constituents of tree-base thicket initials in different savannas.

FEVER TREE SAVANNA WOODLAND Capparis erythrocarpos Ziziphus mucronata Deinbollia xanthocarpa Tamarindus indica Ximenia americana	Occur. from 34 trees 30 25 21 20 16	
MOPANE SAVANNA WOODLAND Jasminum sp. Asparagus africanus Dalbergia melanoxylon Grewia microcarpa Trichilia capitata	Occur. from 52 trees 29 22 11 10	
KNOBTHORN TREE SAVANNA Lecaniodiscus fraxinifolius Cleistochlamys kirkii Phyllanthus reticulatus Capparis erythrocarpos Securinga virosa	Occur. from 18 trees 12 9 9	

The presence of wind dispersed species such as *Combretum mossambicense Dalbergia melanoxylon* and *Lonchocarpus cappasa* in tree-base thickets indicate either that their seeds are also zoochorous or they are caught up against obstacles such as tree trunks or thickets when blown.

TABLE 8.16

Examples of tree-base thicket frequency in hectare samples from various Rift Valley savanna woodlands.

	Savanna	No, tree- base thickets	No. canopy trees	%
(a) (b)	Acacia xanthoploea (fever tree) Mixed Acacia albida Hyphaene	34	43	79
	benguellensis — A. xanthophloea Mixed Acacia nigrescens — Burkea	28	61	46
(c)	africana Colophospermum mopane	28 55	69 417	41 13



TABLE 8.17

Termitaria thicket woody constituents. Presence of species on 42 termitaria from various habitats on the Rift floor.

	OCCUR.		OCCUR.
Salvadora persica (Z)	24	Securinega virosa (Z)	9
Capparis erythrocarpos (Z)	23	Sterculia appendiculata (Z)	9
Thilachium africanum (Z)	23	Xylotheca tettensis (Z)	9
Trichilia capitata (Z)	23	Commiphora schimperi (Z)	8
Cleistochlamys kirkii (Z)	22	Cordyla africana (Z)	8
Ziziphus mucronata (Z)	16	Diospyros mespiliformis (Z)	8
Allophylus alnifolius (Z)	15	D. senensis (Z)	8
Dalbergia arbutifolia (W, Z)	15	D. usambarensis (Z)	8
Tamarindus indica (Z)	15	Berchemia discolor (Z)	7
Ehretia amoena (Z)	14	Maerua angolensis (Z)	7
Tricalysia jasminiflora (Z)	14	Pavetta catophylla (Z)	7
Afzelia cuanzensis (Z)	13	Strychnos potatorum (Z)	7
Deinbollia xanthocarpa (Z)	13	Azima tetracantha (Z)	6
Lecaniodiscus fraxinifolius (Z)	13	Capparis tomentosa (Z)	6
Combretum mossambicense (W)	13	Cassia abbreviata (Z)	6
Mimusops fruticosa (Z)	12	Diospyros quiloensis (Z)	6
Cassine schlechterana (Z)	11	May tenus senegalensis (Z)	6
Combretum microphyllum (W)	11	Phyllanthus reticulatus (Z)	6
Xanthocercis zambesiaca (Z)	11	Spirostachys africana (X, Z)	
Ximenia americana (Z)	11	Cordia pilosissima (Z)	5
Boscia salicifolia (Z)	10	Euclea schimperi (Z)	5
Phoenix reclinata (Z)	10	Euphorbia ingens (X, Z)	5
Drypetes mossambicensis (Z)	10	Kigelia africana (Z)	5
Harrisonia abyssinica (Z)	9	Lonchocarpus capassa (W)	5
Hyphaene benguellensis (Z)	9	Manilkara mochisia (Z)	5
Lannea stuhlmannii (Z)	9	Sterculia africana (Z)	5
Maclura africana (Z)	9	Cadaba termitaria (Z)	3
Saba floribunda (Z)	9		

55 spp. (182 total woody spp. recorded)

TABLE 8.18

Analysis of strata in a termitaria thicket (Road 3 area). Total area $314 \text{ m}^2 \text{ (} = 3\% \text{ /ha)}$

(A) CANOPY & EMERGENTS > 10-20 m (C) FIELDLAYER 50-300 cm

	No.	RD %		No.	RD %
	314	0		100 m ²	0
Miasysama funtiass	m ²	20	Canada		4.0
Mimusops fruticosa Lannea stuhlmannii	5 4	36 29	Capparis erythrocarpos	33	18
Sterculia appendiculata	3	21	Diospyros mespiliformis	20	11
Lonchocarpus capassa	1	7	Deinbollia xanthocarpa Tricalysia jasminiflora	19 16	10
Dalbergia arbutifolia	1	7	Allophylus alnifolius	10	9 5
Daibergia arbutifolia			Cleistochlamys kirkii	10	5
5 spp.	14		Cassine schlechterana	8	4
о эрр.			Pavetta catophylla	7	4
(B) MEDIUM TREE LAY	FR		Securinega virosa	7	4
>3-10 m	The same		Lecaniodiscus fraxini-	-	
			folius	7	4
Cleistochlamys kirkii	8	25	Trichilia capitata	7	4
Trichilia capitata	8	25	Diospyros senensis	7	4
Diospyros senensis	7	22	Dalbergia arbutifolia	6	
Cordia goetzei	3 2	9	Phyllanthus reticulatus	5	3
Strychnos potatorum		6	Cordia goetzei	4	3 3 2 2
Berchemia discolor	1	3 3 3	Lonchocarpus capassa	3	2
Cassia abbreviata	1	3	Berchemia discolor	2	1
Drypetes mossambicensis	1	3	Xylotheca tetensis	1	1
Tabernaemontana elegans	1	3	Sterculia appendiculata	1	1
	La S		Tamarindus indica	1	1
9 spp.	32		Premna senensis	1	1
			Grewia sulcata	1	1
			Thilachium africanum	1	1
			Trichilia emetica	1	1
			Ehretia amoena	1	1
			Boscia salicifolia	./ 1	1
			Strychnos sp. 'warty fruit Dalbergia boehmii	1	1
			28 spp. 1	82	



Table 8.18 (continued)

(D) GROUNDLAYER (20x1m²=20m²) 10-50 cm

		Rel.		No.	Rel.
	Quads	. Freq.		Quads.	Freq.
Asystasia gangetica	18	14	Abutilon sp.	3	2
Achyranthes aspera	14	11	Securinega virosa	3	2
Saba floribunda	9	7	Diospyros senensis	3	2 2
Jasminum sp.	8	6	Cordia goetzei	2	1
Cleistochlamys kirkii	7	6 5 5	Phyllanthus reticulatus	2	1
Pavetta catophylla	7	5	Tricalysia jasminiflora	2	1
Anisocycla blepharosepula	6	5	Bussea wolfhorstii	1	1
Capparis erythrocarpos	6	5	Capparis sepiaria	1	1 ,
Diospyros mespiliformis	6	5	Sterculia appendiculata	1	1
Dalbergia arbutifolia	5	4 .	Diospyros usambarensis	1	1
Lecaniodiscus fraxinifolius	. 5	4	Tamarindus indica	1	1
Commelina sp.	5	4	Cassine schlechterana	1	1
Pupalia lappacea	4	3	Ceropegia sp.	1	1
Flaggelaria guineensis	4	3	Ipomoea albivenia	1	1
Glycine wightii	4	3	Oplismenus burmannii	1	1
Deinbollia xanthocarpa	4	3	Basilicum polystachyon	1	1
Combretum microphyllum	4	3	Aerva leucura	1	1
Panicum heterostachyum	3	2	, , , , , , , , , , , , , , , , , , , ,		
Tumoum notorostaciny ann			35 spp.	131	

126

Termitaria Thicket

A major component of the Rift Valley savannas and the 'dambo miombo' of the Cheringoma Plateau are the large island-clumps of thicket on termite hills. In some areas termitaria thickets occur at a density of 3 per hectare. Termitaria thickets are physiognomically important in savanna and *tando* areas, and in the dry season their tardier leaf fall makes them particularly conspicuous.

All stages of woody plant community development on termite hills is evident in Rift Valley examples — from bare hills with seeds deposited on them, to trees 25 m in height, and clumps of 20 m in diameter. Most of the woody species are animal dispersed.

The occurrence of woody constituents on 42 termitaria in the Rift Valley are noted in Table 8.17. No species show a high frequency predominance, due to the kaleidoscopically changing composition from one termite hill to another, and the influences of the communities with which they are juxtaposed.

Dispersal

The outstanding feature of all thicket types in the Rift Valley, as elsewhere in the transect, is the predominance of animal dispersed plant species (Fig. 8.10). Thickets are initiated from seeds dispersed by animals, which are perch orientated (eg. primates and birds), or those which preferentially use dung middens (eg. civet) and bare areas (see Section 9.8, 9.9).

Due to their base saturated soils, termite hills show highest frequency of certain species; *Capparaceae* in particular, (Wild 1952). The same species are predominant as tree-base (or other perch site) thicket components, on base-rich substrates. Thus the underlying climo-edaphic control of their distribution is overlain by their preferential use and dispersal by animals.

A single example of the analysis of all strata in one termitaria thicket is given in Table 8.18. Environmental factors, phenology and successional aspects will be dealt with at the end of the Rift Valley section.

FOREST

On the Rift floor only two kinds of forest occur, riverine forest, and dry forest on duplex sands. The former is rare and confined to isolated occurrences, mostly on cut-off meanders. Dry forest also occurs in disjunct patches related to the fan pattern of aggraded fossil distributaries.

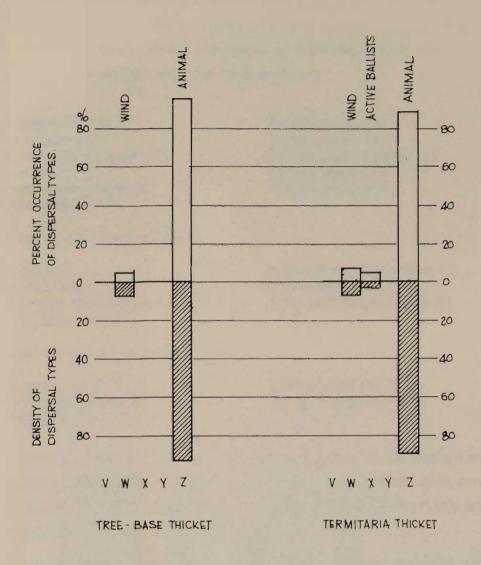


FIG 8.10 COMPARATIVE IMPORTANCE OF DISPERSAL TYPES AMONG WOODY CONSTITUENTS OF CLUMP THICKETS ON THE RIFT FLOOR (UREMA TROUGH).

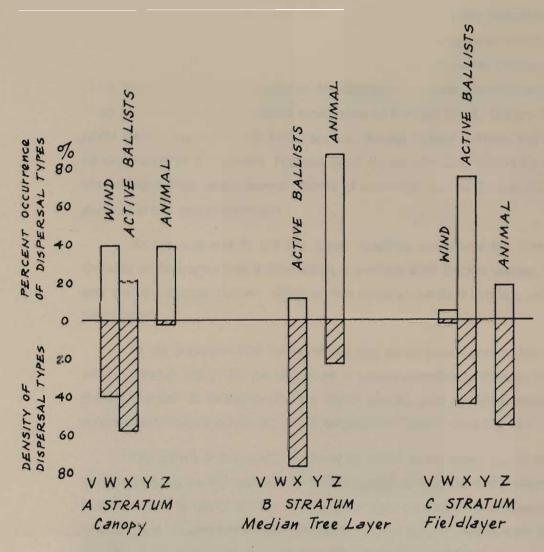


FIG 8.11 COMPARATIVE IMPORTANCE OF DISPERSAL TYPES IN THREE WOODY STRATA OF DRY FOREST.



Riverine Forest

The largest patch occurs on the north bank of the Nhandue one kilometer downstream from Canganatole camp. Here a high canopy and emergent stratum of trees between 22 and 30 m occurs with a sparse median tree layer and a dense patchwork of undercanopy thickets formed by shrubs and scandent acacia. Tall island patches of riverine forest occur on old courses of the Pungue River, east of Chitengo Camp. The most important large riverine trees include:

Albizia glaberrima (W)
Blighia unijugata (Z)
Bombax rhodognaphalon (W?)
Cordyla africana (Z)
Diospyros mespiliformis (Z)
Ekebergia capensis (Z)

Ficus sycamorus (Z)
Khaya nyasica (W)
Sterculia appendiculata (Z)
Syzygium guineense (Z)
Trichilia emetica (Z)

Lowerstory components include:

Cordia goetzei (Z) Diospyros senesis (Z) Erythroxylum emarginatum (Z) Garcinia livingstonei (Z) Lecaniodiscus fraxinifolius (Z) Oncoba spinosa (Z) Tabernaemontana elegans (Z)

Fieldlayer components include:

Acacia schweinfurthii (Z?) Capparis erythrocarpos (Z) Cleistochlamys kirkii (Z) Dalbergia boehmii (W?) Tricalysia jasminiflora (Z)

Riverine forest is evergreen to deciduous, depending on the species dominance in each area. *Sterculia appendiculata* forms nearly pure species stands in some areas and is deciduous early in the dry season. *Diospyros* and *Trichilia* are mostly evergreen and these stand out as dark clumps where they predominate.

Animal dispersed species predominate in all strata, but due to the numerical abundance of *Khaya*, wind dispersal is a feature of the canopy. This is similar to the swamp forests of the Cheringoma coast which are dominated in some areas by the anemochorous (and hydrochorous?) *Adina microcephala*.

Dry Forest

Dry forest is a unique forest formation of the coast sands and Kalahari Sands of south central Africa. Extending from the west coast (Angola and Iower Congo) across the centre of the subcontinent (S. Congo, Zambia, Rhodesia) to the Mocambique Plain and the Tanzania and Kenya coasts. Typically, dry forest occurs in a rain-

fall range between 500 mm and 1 000 mm, on either duplex sands or on fine grained compact sands. The species dominance between the two coasts varies kaleidoscopically, with endemic centres in the west (defined by *Tessmannia camoneana* for example), centre (eg. *Cryptosepalum*, *Baikiaea*) and east coast (eg. *Newtonia hildebrandtii*, *Cynometra* spp., *Guibourtia schliebenii*, *Xylia torreana*, et. al.).

This forest type has up to the present been erroneously included as part of the Eastern Forest Domain of the Guinea-Congolian phytogeographic region (White 1965, 1971). White (*op. cit.*) refers to this as the Usambara—Zululand Domain. In fact both these terms correctly relate only to the Guineo—Congolian elements and forests confined to the orographic or coastal moist areas of the East Coast. The dry forest components are not equatorial rain forest species, though related to them, and should rather be designated as a Southern Tropical Sand Forest Domain. Within its range on the Mocambique Plain alone, several centres of endemism can be defined by woody components in one or other stratum.

At the arid end of the dry forest ecocline, and where this formation meets thickets on base saturated duplex sands, it overlaps with thicket species. At the moist end and on leached duplex sands or fine compact sands it overlaps with rain forest tree species.

In the Southern Rift Valley sector, dry forest occurs only to the Chire Trough (Hall — Martin 1972). On the east coast it occurs sporadically through to the Kenya—Somali frontier. A characteristic dry forest species, such as *Hymenocardia ulmoides*, occurs intermittently across the whole range of the 'Sand Forest Domain'.

Dry forest is structured similarly to other forest types, but in some sites the upper canopy trees are sufficiently widely spaced so that the mid stratum is the effective canopy. The upper canopy trees in such situations are thus emergents. Dry forest is deciduous, to semi-deciduous, depending on the species predominant in the canopy of each patch, and the severity of dry season drought conditions.

In the Urema Trough, dry forests occur in abrupt changes from the surrounding grassland and savanna, due to the generally sharp change between the duplex sand substrate on old distributary courses of fossil alluvial fans, and the other soil types of alluvio-catenas.

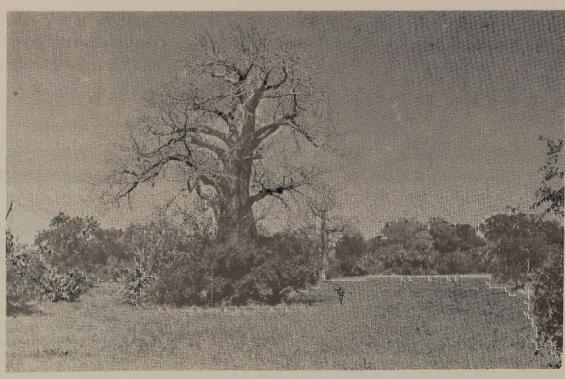
The composition of one dry forest example from the Urema Trough is shown in Table 8.19.

In common with other disjunct communities, each dry forest patch appears to have different species combinations and canopy dominants. This feature is related

PLATE 19 RIFT VALLEY DRY FOREST & TREE-BASE THICKET COMMUNITIES



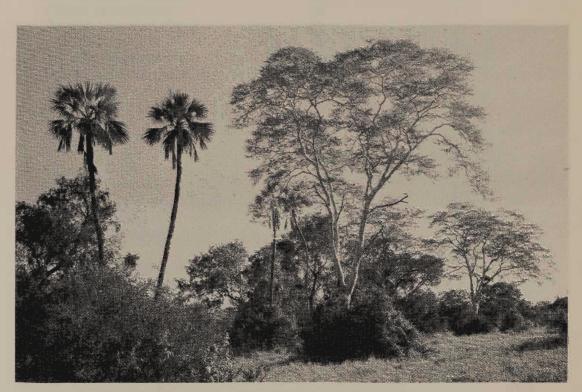
(A) Oblique air view of dry forest confined to aggraded distributary bed of fossil alluvial fan. The relatively sharp margins and narrow ecotone is due to rapid lateral change of duplex forest sands to grassland vertisol clays (slack fines).



(C) Tree-base thicket of zoochorous species around a baobab tree, and dry forest strip in the background. Dimensions of the thicket indicated by lay figures and 3 m measuring rod (mid dry season aspect.).



(B) View across the clay-sand alluviocatena sequence. From mopane and aloe savanna on a convex clay surface in the foreground across a seasonally waterlogged lower dambo surface to the forested duplex sands of the convex surface of an aggraded distributary bed. Note lay figure with 3 m rod.



(D) Tree-base thickets of zoochorous species around palms and fever trees in *Urochloa mosambicensis* grassland on phosphorus-rich sandy loams.



to the clumped dispersion shown by many species within the more extensive dry forest areas. A canopy dominant in one patch can be quite absent from others and so on. Some of the canopy and high midstratum trees not recorded in the hectare sample of the Sangarassa Forest inloude:

Albizia brevifolia (W)	Fernandoa magnifica (W)
Aloe bainesii (W)	Ficus sansibarica (Z)
Balanites maughamii (Z)	Guibourtia conjugata (Z)
Cladostemon kirkii (Z)	Gyrocarpus americanus (W)
Euphorbia halipedicola (X, Z)	Hymenocardia ulmoides (W)
E. lividiflora (X, Z)	Inhambanella henriquesii (Z)
Erythrina livingstoniana (Z)	Paropsia schliebeniana (Z)
Exoecaria bussei (W)	Ptelepsis myrtifolia (W)
	Strychnos decussata (Z)

Dispersal

Though an equal number of wind and animal dispersed canopy species occur in dry forest, when density data (from 1 ha sample) are added, those with physically thrown (active ballists) and wind dispersed seeds predominate by far (Fig 8.11). The high density of *Xylia torreana* and *Millettia mossambicensis* are responsible for active ballist dominance in this sample.

In the median tree layer the dominance by two active ballist species, *Craibia* and *Millettia*, over large areas is responsible for the low percentage of this dispersal type but with the highest density. This contrasts with the much lower variety of zoo-chorous species which occur in relatively small number.

TABLE 8.19

Analysis of Dry Forest 2 km northwest of Chitengo Camp on Rift floor (Sangarassa Forest)

(A) CANOPY & EMERGI	Total trees in 1 ha.	Rel. Freq.
Xylia torreana (X)	29	2
Pterocarpus antunessi	i (W) 28	28
Millettia mossambicer	nsis (X) 22	22
Newtonia hildebrand	tii (W) 14	14
Acacia welwitschii (W	/) 4	4
Millettia stuhlmannii	(X) 2	2
Hymenodictyon parv	ifolium (W) 1	1
Lecaniodiscus fraxini	folius (Z) 1	1
Ziziphus pubescens (2	2) 1	1
9 spp.	101	

Table 8.19 (continued)

13 spp.

Carlotte Control	Total trees	Rel. Freq.
	in 2500 m ²	%
Craibia zimmermannii (X)	80	51
Millettia mossambicensis (X)	32	20
Strychnos mitis (Z)	19	12
Hunteria zeylanica (Z)	11	7
Thilachium africanum (Z)	6	4
Cola greenwayi (Z)	2	7
Coffea racemosa (Z)	1	3
Cordia pilosissima (Z)	1	7
Diospyros senesis (Z)	1	1
Strychnos (spinosa) 'warty fr.' (Z)	1	1
Tarenna neurophylla (Z)	1	1
Xylia torreana (X)	1	1
Indet.	1	1

157

Alchornea laxiflora 73 Craibia zimmermannii 66 Thilachium africanum 44	22 20 13
Thilachium africanum 44	13
Phyllanthus kirkianus 28	8
Adhatoda bagshawei 24	7
Ancylanthus sessiliflorus 23	7
Pavetta catophylla 14	4
Millettia mossambicensis 10	3
Capparis erythrocarpos 6	3 2 2 2 2
Hunteria zeylanica 6	2
Canthium crassum 5	2
Vepris reflexa 5 Xeromphis obovata 5 Strychnos mitis 3 Xylia torreana 3	2
Xeromphis obovata 5	2
Strychnos mitis 3	-1
	1
Xylotheca tettensis 3	1
Combretum mossambicensis 2	1
Rubiaceae indet. 2	1
Tarenna neurophylla 2	1
Indet. 2	1

²⁷ spp. total (less than 1% omitted)



Table 8.19 (continued)

(D)	GROUNDLAYER < 50 cm	Occur. in 55 m ² Quad.	Rel. Freq. % (309)
	Craibia zimmermannii	28	9
	Acacia kraussiana	23	7
	Leptochloa uniflora g	22	7
	Justicia stachytarphetoides	21	7
	Justicia sp. (KLT 2591)	20	7
	llysanthes sp. ?	20	7
	Acacia welwitschii	13.	4
	Oplismenus burmanii g	13	4
	Barleria spinulosa	10	
	Dicliptera mossambicensis	10	3
	Psilotrichum scleranthum	10	3
	Alchornea laxiflora	9	3
	Lepturus radicans g		3
	Commelina sp.	9 8 8 7	3
	Hippocratea africana	8	3
	Strychnos mitis	7	2
	Abutilon lauraster	6	2
	Phyllanthus kirkianus	6	2
	Stylochiton sp.	5	2
	Cyperus mapanioides	5	3 3 3 3 3 3 2 2 2 2 2 2
	Justicia flava	5	2
	Hibiscus migeodii	. 5	2

45 spp. total (less than 2% omitted)

g = shade grasses

In the fieldlayer the reverse situation occurs where a large diversity of active ballists (mainly large woody *Acanthaceae*) are surpassed in density by relatively few zoochorous species (Fig 8.11).

When compared with other communities the importance of dispersal types in the canopy shows the same pattern as miombo. It shows a slight, though greater than its relationships with most other forest or thickets, resemblance to the *Acacia-Burkea* and mopane savannas. However, a closer relationship exists with the tropical rain forest zone on Gorongosa Mountain where anemochory is a feature of the canopy dominant *Newtonia buchananii*. Wind dispersal is also a feature of hygrophilous forest canopy trees such as *Khaya nyasica* and *Adina microcephala*.

The predominance of active ballists in all three woody strata of dry forest appears to be a unique feature in the transect. Where dry forest contains the euphorbiaceous *Androstachys johnsonii* as a single canopy dominant, explosive dehiscience remains the most important means of dispersal. However, subsequent zoochory, mainly by ground feeding doves, may be equally important, giving equal weight to the two methods.

129

Some of the lianes which reach the canopy in dry forest are also wind dispersed species, including *Combretum schumannii*, *Hippocratea africana*, *H. crenata* and *Strophanthus kombe*.

Environmental features

The most important features in the Rift Valley are the seasonal wet and dry extremes, the wet exaggerated by flooding or waterlogging to greater or lesser extent annually, and the dry exaggerated by widespread occurrence of veld fires.

As shown by Fig 4.11 the highest rains and most extensive floods recorded in the decade of readings from Chitengo Camp occurred in December 1969 (530 mm total), followed by three consecutive dry years with up to 163 mm less than mean annual rainfall. The year prior to the 1969/70 floods was the driest year recorded. Precipitation thus shows wide variation (> 60%) every year above and below the mean.

These extremes are aggravated by late summer droughts in January, February or March in six out of the ten years. These droughts are caused by the passage of hurricanes (tropical cyclones) in the Mocambique Channel (see Ch. 4). In 1972 two consecutive months were arid (Feb. and Mar.) resulting in widespread leaf discolouration and fall in certain deciduous trees, eg. *Sterculia* spp., *Lannea stuhlmannii*, *Commiphora schimperi*. With the recurrence of adequate rain, a new leaf flush and flowering, in some, was initiated. At this time the short grasslands on base saturated clays also become brown and dry out rapidly. The clear nights during these arid spells also result in valley fog development in summer.

As shown by Fig 4.13, the Urema Trough experiences a two month mild period in midwinter, followed by rapid heating up from the last week of July, becoming increasingly hot over the torrid dry season peak, prior to the rains.

In dry years veld fires begin early in the autumn and occur through until October, or as long as grass fuel is available. In wet years they occur from May or June onward. Fortunately the incidence of midwinter rain showers is often sufficient to douse the fires. Their resurgence is from honey and game hunters.

Few months in the decade of records received no rain. In the long term there are six wet months (4 perhumid) and six dry months (Fig 4.1).

The flood and ebb features of the Urema Trough are dealt with in Chapter 9. It is sufficient to emphasize that the moisture factor is the major environmental feature, particularly as extensive areas are saline clays.

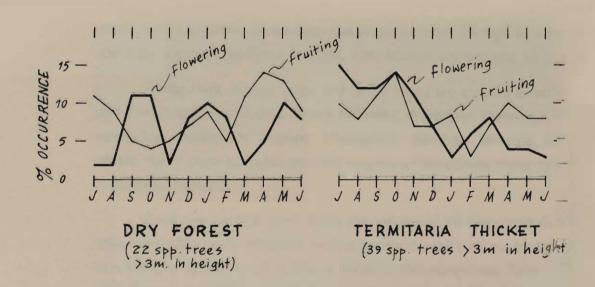


FIG 8.12 REPRODUCTIVE PHENOLOGY OF FOREST & THICKET COMMUNITIES ON THE RIFT FLOOR



Phenology

Leaf Phenophases

The march of the seasons as shown by leaf phenophases in the Rift Valley (Fig 8.9) although similar to that in the adjacent miombo has some marked differences (Fig 8.8). The Rift Valley savannas have more species in leaf in the torrid period and certain trees are more rapidly deciduous in the late summer. The small percent occurrence of bare trees in midsummer is due to the winterthorn *Acacia albida* which is active during the dry season. As I lived among the Rift savannas, a much more detailed record was kept of phenological events, which showed new leaf production in every month of the year.

Reproductive Phenology

Again the Rift savanna trees show a parallel with the miombo, their main flowering peak occurring in October with a second lesser peak in late summer and autum (Fig 8.9). A much larger number of Rift savanna trees, however, flower throughout the year and three fruiting peaks are evident, in July October, and over the autumnal equinox. Both savanna types show low flower and fruiting occurrence over the summer solstice.

Bimodal peaks in nutrient levels over the equinox periods is intimated by the spring flowering peak and the fruiting peak in autumn.

Termitaria thicket tree components genrally show a similar pattern to the Rift savannas but have the highest flowering peaks in July and October, coincident with, or following the winter solstice and spring equinox. A third, smaller flowering peak occurs in March (Fig 8.12).

Contrasting with all these patterns is that of dry forest on the Rift floor which exhibits boldly defined trimodal flowering peaks over the equinoxes and the summer solstice (Fig 8.12), parallel to the flowering of the mountain summit grassland components. The flowering peaks are followed three to four months later by three fruiting peaks, in July, January, and April (Fig 8.12).

Succession

Savanna and thicket components are actively invading floodplain grasslands on all fronts, depending on the soil type exposed by inadequate flooding or waterlogging.

Base saturated clays are invaded by *Hyphaene benguellensis* and *Colophospermum mopane* but these never occur together in the Urema Trough. Where floodplain gilgai microrelief is invaded by mopane and *Acacia borleae*, the seeds appear to survive best on the microridges where they form a clumped pattern. Mature mopane woodlands clearly show the original microrelief patterning although the irregularities are in many sites flattened out by erosion.

Fever tree *Acacia xanthophloea* is the most vigorous invader of hydromorphic clays, and *Acacia albida* invades on sandy alluvium. In some areas an aggressive invasion of floodplain grassland by suffrutices with large basal root plates is preceding the above tree succession. *Duosperma quadrangulare* and *Cienfugosia hildebrandtii* are the most common suffrutex invaders, with *Maerua brunnescens* to a lesser extent.

Sandy clays, duplex sands and sandy loams are invaded directly by savanna and thicket species including *Acacia sieberana*, *Piliostigma thonningii*, *Dalbergia melanoxylon*, *Combretum fragrans*, *Crossopterix febrifuga*, *Borassus aethiopum* and others. All of these suffrutex and tree invaders of floodplains characteristically occur in pure species stands.

Once tree saplings grow above the canopy of the grass stratum they are conspicuous perch sites in otherwise treeless grasslands, and their use by frugivores results in a saltatory succession of thicket as the second invading phase. Termite hills in grassland cause a similar direct invasion of woody thicket species to occur as they are also used as perch sites by frugivores.

Where dongas have cut into the floodplain clays *Ziziphus mucronata* and *Anti-desma venosum* (both zoochorous species) are the most common invaders along these seasonal watercourses.

Various thicket types are extending in some areas by coalescence of clumps, whilst in other areas they are in a homeostatic state neither expanding or contracting. Active extension of thicket clumps occurs chiefly on the sandier soils, whilst a more static situation exists where the thicket clumps occur on termite hills or around tree-bases in saline clay areas. In saline clay areas, tree-base thickets appear to be confined by the higher water input from stemflow runoff of rain from the 'mother-tree' around which they were initiated. The importance of this phenomenon in dry areas has been measured by Glover et. al. (1962) in East Africa.

The preferential use of termitaria and tree-base thickets results in a trampled out perimeter which protects the clumps from fire. In many termite hill sites however, a natural firebreak is afforded by the change from tall to medium height grasslands to



PLATE 20 SWAMP FOREST & FYNBOS ON THE CHERINGOMA COAST



(A) External aspect of tall (25 m) swamp forest down the centre of a dambo viewed from the fringing miombo-forest mosaic. Predominant upper canopy trees are Adina microcephala and Barringtonia racemosa.



(C) Oblique air view of pure stands of *Philippii simii* fynbos scrub-thicket patches on white podsolized sands, surrounding a forest patch formed by coalescence of termitaria thickets. 'Blackwater' catchment areas.



(B) Internal view of the same swamp forest shown in (A) with the tree trunks festioned by the climbing fern Stenochlaena tenuifolia. The primitive epiphytic quillwort Psilotum nudum hangs from rot-holes and clefts in tree trunks.



(D) Internal view of 3 to 4 m high fynbos scrub-thicket showing senile stage of collapsed stems in foreground providing an opening for a new even-aged colonization of fynbos. Fire rejuvenates this community in the same way (heath cyclical succession).



short, or lawn-like grasses on the saline micropediment around the base of the termitaria.

As shown in Section 6.3 however, termite hills undergo a process of landscape reversal to form pans in areas of high browsing ungulate density.

Only on the microscale on the Rift floor are new grasslands being formed. These sites are on the aggraded floors of the donga incisions of the plains. Everywhere else (excluding slack areas) the young stages of savanna trees and shrubs are encountered in floodplain grasslands. Within a decade many of the areas designated as grasslands by this study will have been converted to the duplex savanna structure with growth of the saplings above the grass canopy. If the active erosion process continues unabated on the Rift floor, within two or three decades savanna will have taken over large sectors of the floodplains. The southern margin of the Urema Plains is where fast invasive sequences are taking place.

8.6 CHERINGOMA PLATEAU AND COAST

As the miombo of the coastal cuesta is generally similar to that of the Midlands, the diversity of plant communities in this area will be described solely by means of profile and photographic examples.

8.7 PLANT COMMUNITY RELATIONSHIPS

A preliminary analysis of the relationships of grass and woody communities in the montane to mangrove transect was made using Sorenson's Coefficient of Similarity (vide Curtis 1959: 83). The formula used is 2W/a+b, where a is the total number of species in one community and b the total of another, and w is the number of species common to both. The resulting index of similarity is expressed as a percent.

The major relationships are presented in diagrammatic form (Fig 8.13) which show several interesting patterns.

GRASSLAND COMMUNITIES

The closest affinity (52%) is shown between the miombo grass stratum and those of the Rift Valley savannas. Montane grasslands and the coastal high watertable dambo grasslands show a relatively high affinity of 25%. Shade grass communities are most similar between the mountain rain forest and coast moist evergreen forests.

Suprisingly, the grass communities of heavy floodplain alluvia show relatively low affinities when comparing those of the Urema Trough with the Zambeze Delta (Fig 8.13). This may be explained by the mosaic dominance of a few species over large areas.

WOODY COMMUNITIES

Gorongosa Mountain

The three communities show little affinity with each other despite their being closely juxtaposed.

Midlands

Likewise, relatively little relationship is exhibited by the communities contained in the Midland miombo. The highest (< 20%) is between miombo and the termitaria inclusions.

Rift Valley

The conspicuous feature of the Rift Valley communities is the large number of closed canopy systems which are related to one another clinally; from mopane to dry forest and riverine thicket (Fig 8.13). For example, mopane and dry forest related directly have few species in common, but they are strongly related via a series of three thicket types. The mixed savannas have a relatively low affinity with any of the closed communities,

131



PLATE 21 CHERINGOMA LITTORAL COMMUNITIES



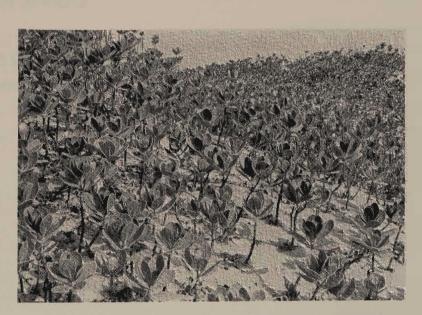
(A) Dune scrub-thicket near the Chiniziua River mouth. Main components are *Trachylobium verrucosum*, *Macphersonia hildebrandtii*, *Mimusops caffra* and *Hyphaene natalensis*.



(B) Coastal erosion with dead mangroves and estuarine muds within high tide reach of waves. Retrograding beaches typical of major part of Mocambique Coast.



(C) Parallel barrier bar (swashbank) dunes & slacks in the southern sector of the Zambeze Delta. Rises fixed by thicket and the linear depressions are viei grasses. Mangroves to the left.



(D) The dune forming strand plant *Scaevola thunbergii* on hummock fore-dunes built up by accretion of wind-blown sand around its sympodial growth.



(E) Internal view of mangrove forest at low tide. Adventitious roots of Rhizophora mucronata centre and pale trunks and pencil pneumatophores of Avicennia marina on the right.



Cheringoma Plateau and Coast

Only riverine and swamp forests show a high number of species in common (51%), and the remainder only a median to low affinity despite their close juxtaposition in the field. This feature appears to be characteristic of communities on leached acid soils.

SUMMARY OF COMMUNITY RELATIONSHIPS BETWEEN EACH PHYSIOGRAPHIC UNIT

The miombo of the Midlands and coast plateau have the highest number of species in common (67%) yet this is a low figure for an ecosystem which is essentially homogenous in its species array over extensive areas. A high affinity is probably not attained because of the many forest margin and median layer species which invade miombo on the white duplex sands. If the miombo on the red lotosols alone are compared with the Midlands the number of species in common is very much higher.

The mixed Rift savannas have an index of 48% with the Midland miombo, and 38% with the coast miombo due to the species common to sand savannas wherever they occur in the transect.

The next highest number of species in common are shared by termitaria thickets of each unit excluding the mountain.

Overall, therefore, the closest relationships are shown by the Rift Valley communities due primarily to the widespread occurrence of the same zoochorous species in all perch, water-based and bare soil sites.

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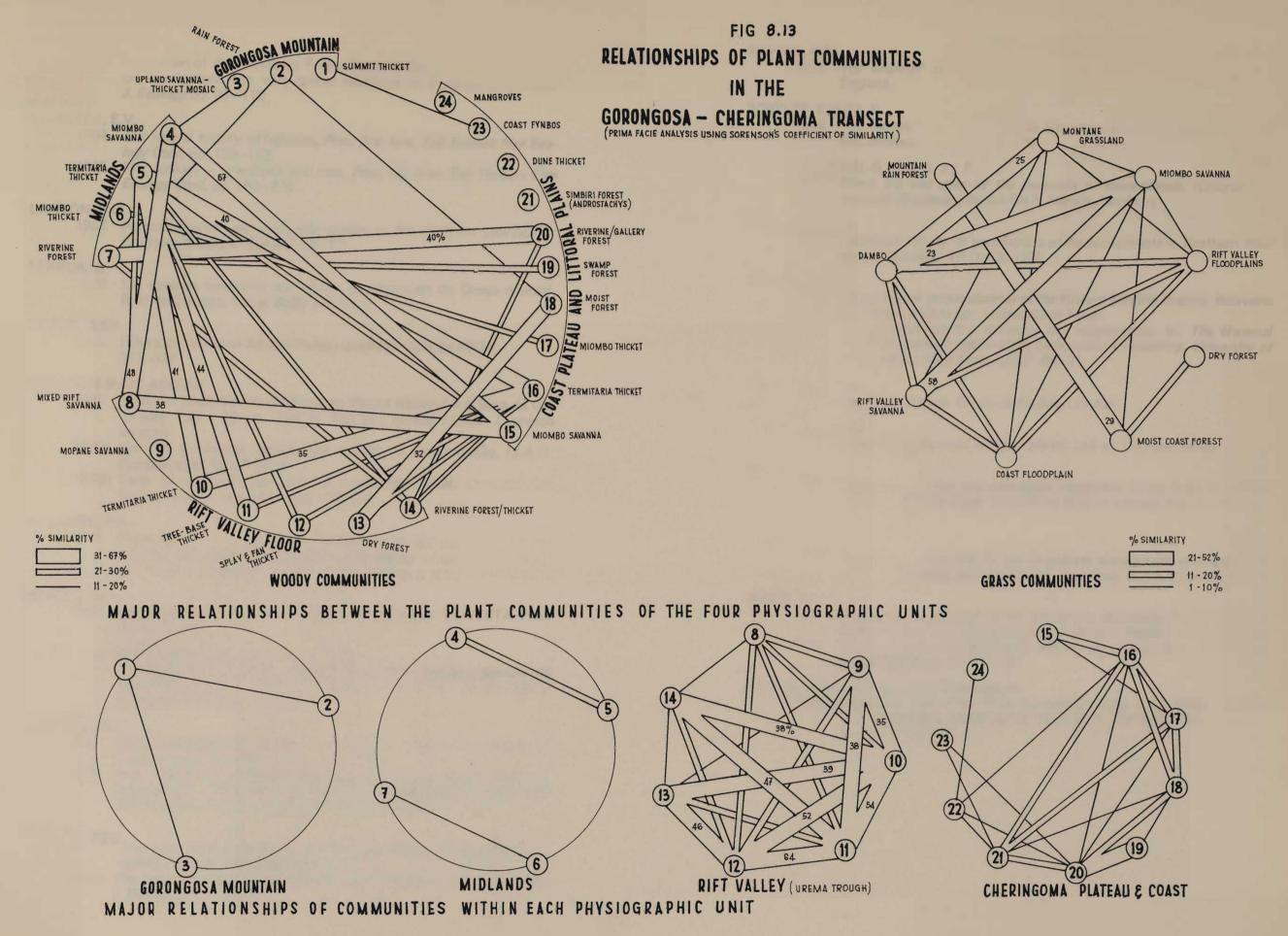
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132







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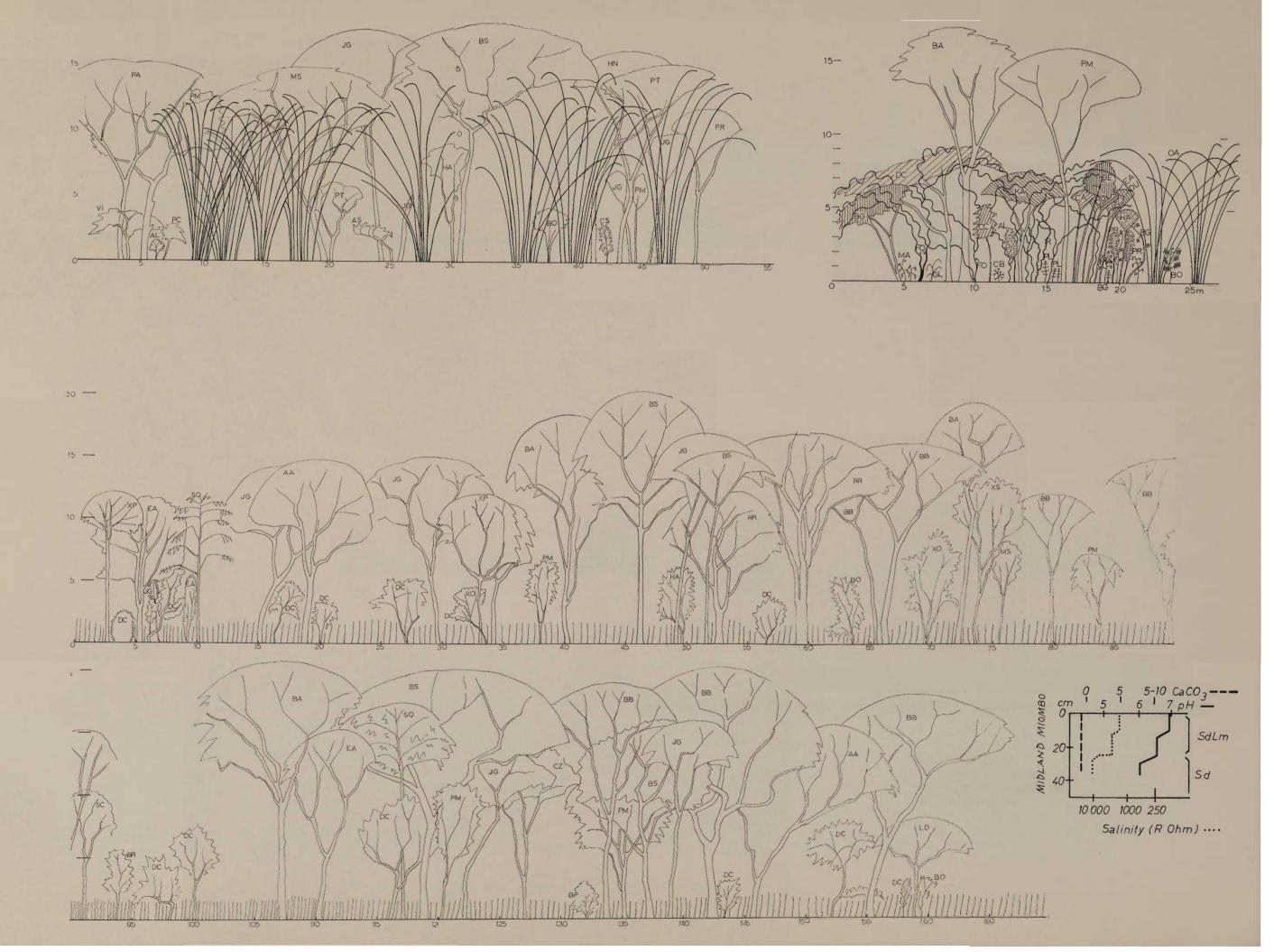
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MIOMBO WITH BAMBOO

(belt 10m wide)

- AL Allophylus alnifolia
- Annona senegalensis
- Byrsocarpus orientalis
- BS Brachystegia spiciformis
- CS Commiphora serrata
- JG Julbernardia globiflora
- HA Hymenocardia acida
- HN Hyteropyxis natalensis
- MS Millettia stuhlmannii
- OA Oxytenanthera absyssinica
- PA Pterocarpus angolensis
- PC Psychotria capensis
- PM Psuedolachnostylis maprouneifolia
- PR Pterocarpus rotundifolia
- PT Piliostigma thonningii
- VI Vangueria infausta

FIG 8.14 PROFILES OF MIDLAND PLANT COMMUNITIES

MIOMBO SAVANNA WOODLAND (belt 10m wide)

- AA Amblygonocarpus andongensis
- BA Burkea africana
- BB Brachystegia boehmii
- BO Byrsocarpus orientalis
- BP Bauhinia petersiana
- BR Brackenridgea arenaria
- BS Brachystegia spiciformis
- DC Diplorhychus condylocarpon
- CZ Combretum zeyheri
- Erythrophleum africanum
- Julbernardia globiflora
- Hymenocardia acida
- LD Lannea discolor
- MS Millettia stuhlmannii
- Pseudolachnostylis maprouneafolia
- Ricinodendron rautanenii
- Sclerocarya caffra
- Sterculia quinqueloba
- XO Xeromphis obovata
- XP Xylopia parviflora
- Xeroderris stuhlmannii

MIOMBO THICKET

(belt 2m wide)

- AL Allophylus alnifolia
- BA Burkea africana
- BE Bersama abyssinica
- BG Bauhinia galpinii
- BO Byrsocarpus orientalis
- CA Cassia abbreviata
- Carissa bispinosa
- Canthium crassum
- DC Diplorhynchus condylocarpon
- DU Diospyros usambarensis
- EN Euclea natalensis
- FO Friesodielsia obovata
- GL Grewia lepidopetala
- HA Harrisonia abyssinica
- JG Julbernardia globiflora
- KA Kigelia africana
- MA Markhamia acuminata
- QA Oxytenanthera abyssinica
- OO Ozoroa obovata
- Polysphaeria lanceolata
- Pteleopsis myrtifolia
- Pavetta revoluta
- Rhoicissus sp.

(belt 2m wide)

BG

CA

CB

FO

AL Allophylus alnifolia BA /Burkea africana

Bersama abyssinica

Bauhinia galpinii

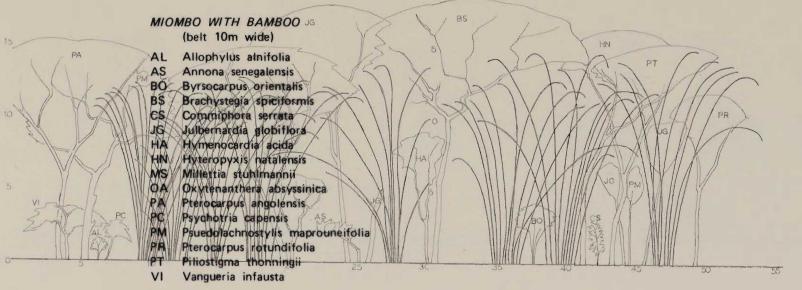
BO Byrsocarpus orientalis

Cassia abbreviata

Carissa bispinosa

CC Canthium crassum
DC Diplorhynchus condylocarpon
DU Diospycos usambarensis
EN Euclea natalensis

Friesodielsia obovata Grewia lepidopetala



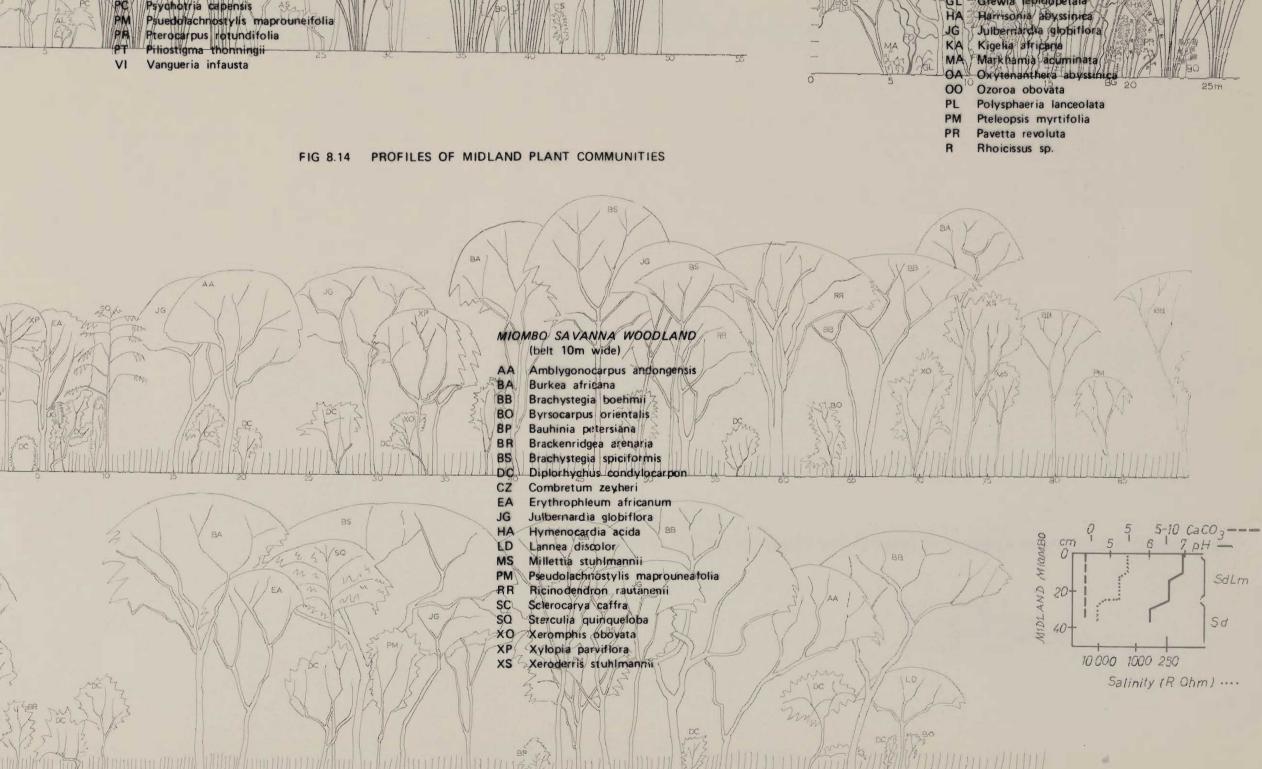




FIG 8.15 PROFILE OF THREE-STAGE INVASION OF FLOODPLAINS BY FEVER TREE WOODLAND

AA Acacia albida
AX Acacia xanthophloea
HB Hyphaene benguellensis
MP Mimosa pigra







WINTERTHORN WOODLAND ON FLOODPLAIN MARGINS

AA Acacia albida

HB Hyphaene benguellensis

FIG. 8.16 PROFILES OF MARGINAL WINTERTHORN WOODLAND AND A SAND-CLAY SAVANNA MOSAIC ON THE RIFT FLOOR

SAND-CLAY ALLUVIOCATENA SA VANNA SEQUENCE

AN Acacia migrescens

BA Burkea africana

C Combretum fragrans

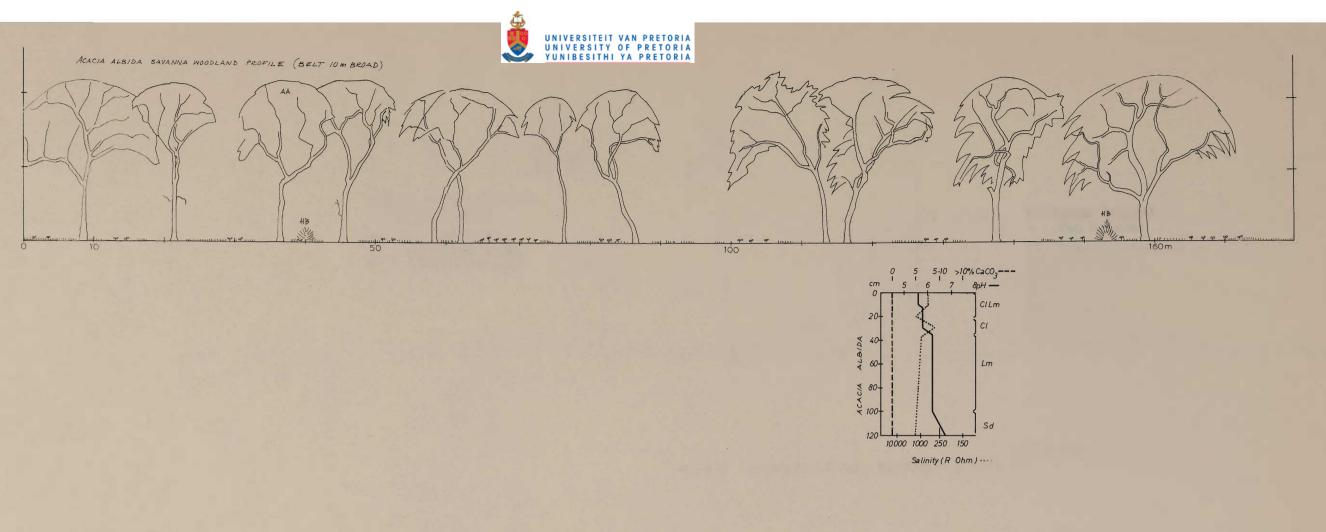
CF: Crossopterix febrifuga

CK Cleistochlamys kirkii

DIJ Diospyros usambarensis LC Londocarpus capassa

TS Terminalia seriosa

XS Xeroderris stuhlmannii



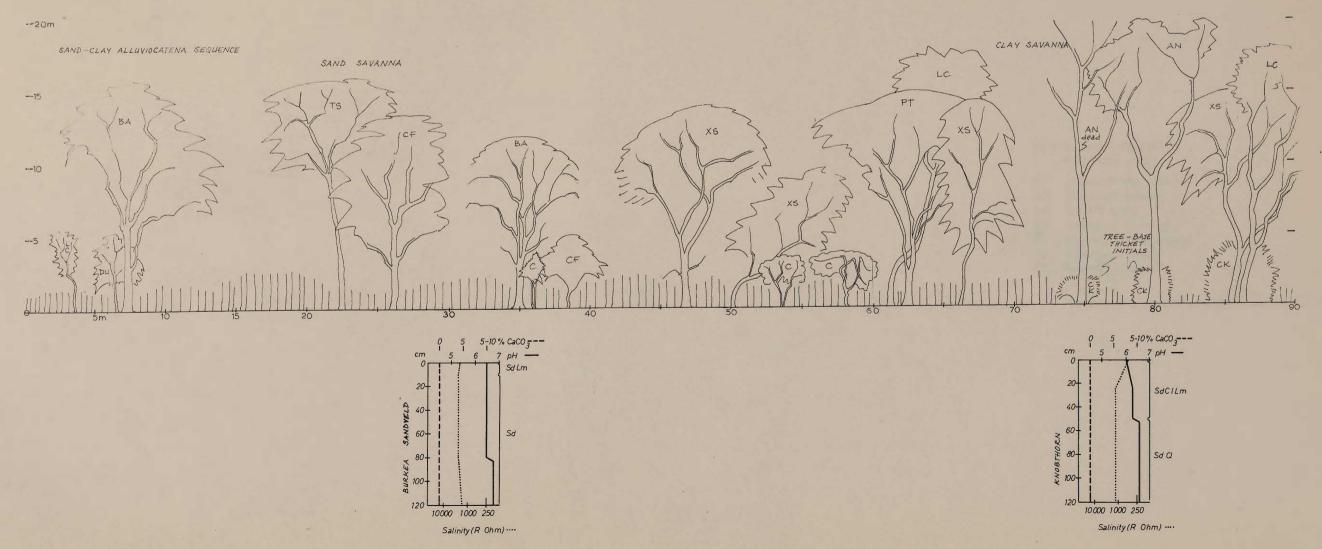
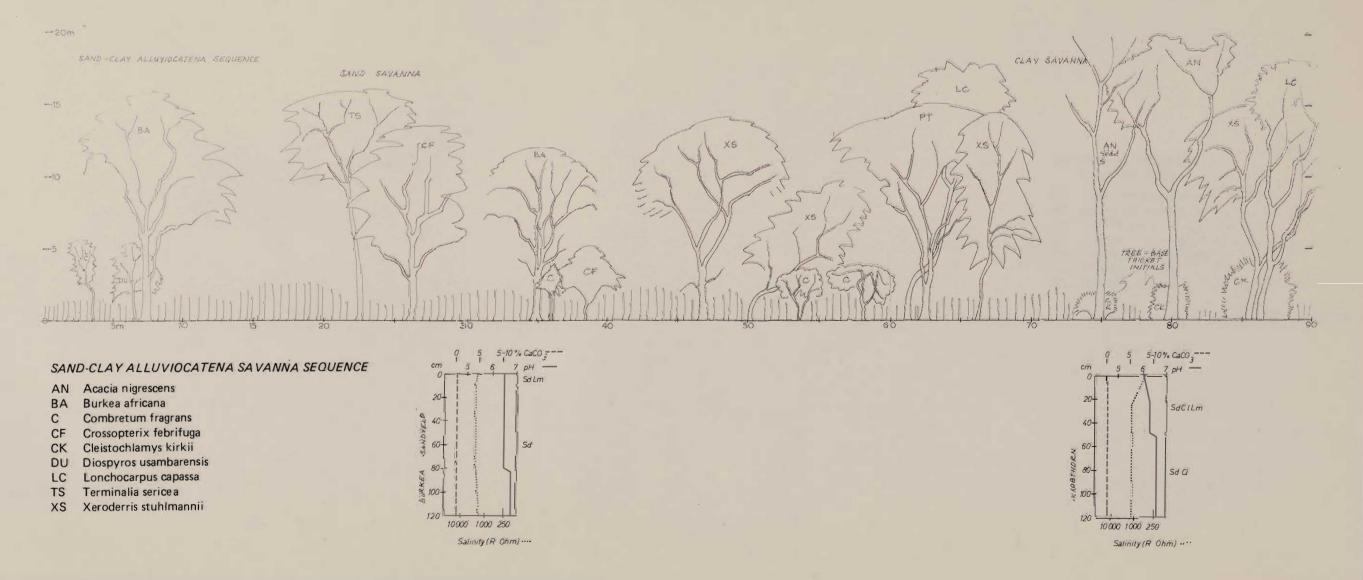


FIG. 8.16 PROFILES OF MARGINAL WINTERTHORN WOODLAND AND A SAND-CLAY SAVANNA MOSAIC ON THE RIFT FLOOR

10000 1000 250 150 Salinity (R Ohm)





BORASSUS PALM SAVANNA (belt 10m wide)

BO Borassus aethiopum

LC Lonchocarpus capassa

PT Piliostigma thonningii

TREE-BASE THICKET

(beit 5m wide)

CE Capparis erythrocarpos

CK Cleistochlamys kirkii

CM Combretum mossambicensis

SC Scierocarya caffra

SP Spirostachys africana

ZM Ziziphus mucronata

FIG 8.17 PROFILES OF PALM SAVANNAS & THICKETS ON THE RIFT FLOOR

HYPHAENE BENGUELLENSIS SAVANNA (belt 10m wide)

AS Acacia sieberana

HB Hyphaene benguellensis

TERMITARIA THICKET (beit 10m wide)

CK Cleistochlamys kirkii

DS Diospyros senensis

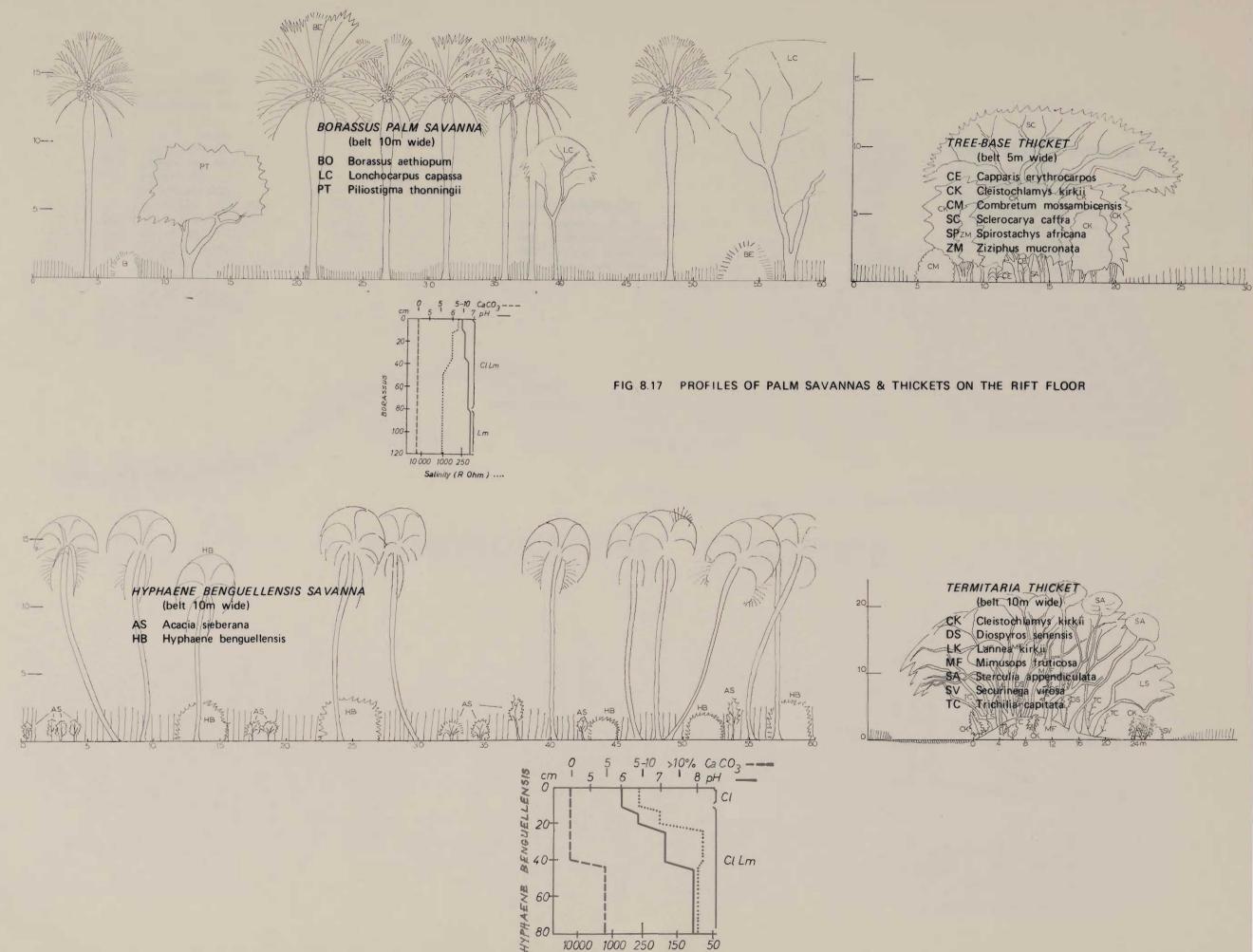
LK Lannea kirkii

MF Mimusops fruticosa

SA Sterculia appendiculata

5v Securinega virosa

TC Trichillia capitata



Salinity (ROhm) ----



DRY FOREST

- AD Adansonia digitata
- CC Canthium crassum
- CK Cleistochlamys kirkii
- CM Canthium martinii
- DS Diospyros senensis
- DG Drypetes gerrardii
- DQ Diospyros quiloensis
- HC Heinsia crinita HZ Hunteria zeylanica
- LF Lecaniodiscus fraxinifolia
- MM Millettia mossambicensis
- NH Newtonia hildebrandtii
- PA Pterocarpus antunesii
- PK Phyllanthus kirkianus
- SM Strychnos mitis
- SP Salvadora persica
- TA Thilachium africanum
- TC Trichilia capitata
- VZ Vepris zambesiaca
- XT Xylia torreana

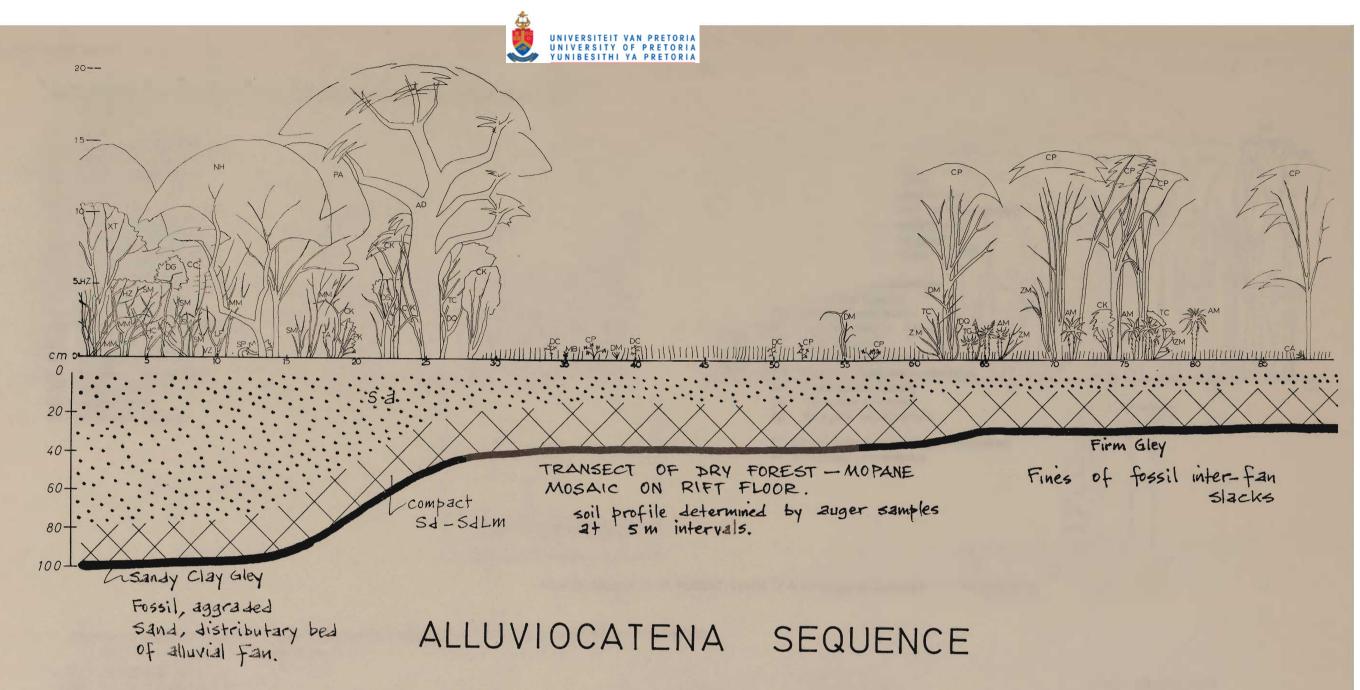
DAMBO GRASSLAND

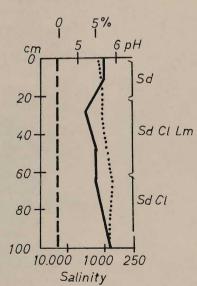
- CP Colophospermum mopane
- DC Dichrostachys cinerea
- DM Dalbergia melanoxylon
- MB Maerua brunnescens

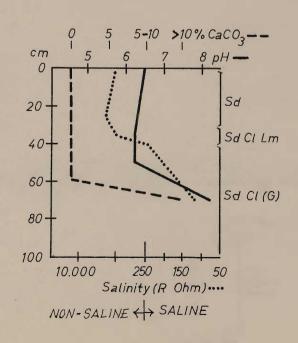
MOPANE SAVANNA WOODLAND

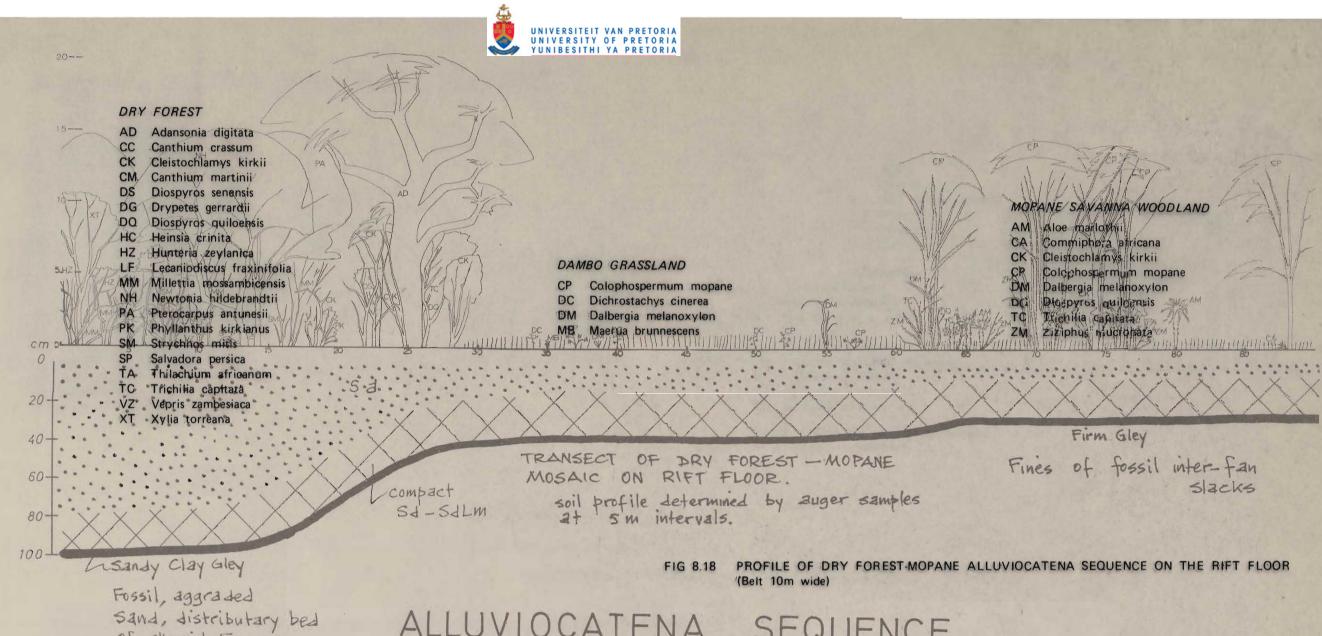
- AM Aloe marlothii
- CA Commiphora africana
- CK Cleistochlamys kirkii
- CP Colophospermum mopane
- DM Dalbergia melanoxylon
- DO Diospyros quiloensis
- TC Trichilia capitata ZM Ziziphus mucronata

FIG 8.18 PROFILE OF DRY FOREST-MOPANE ALLUVICCATENA SEQUENCE ON THE RIFT FLOOR (Belt 10m wide)

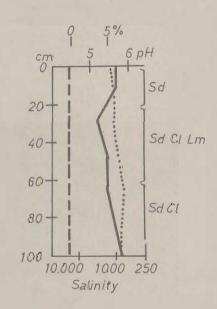




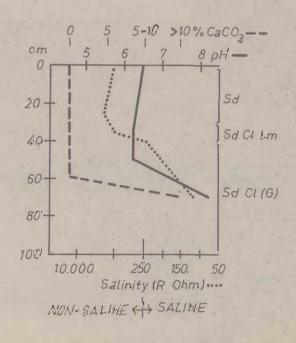




ALLUVIOCATENA SEQUENCE



of alluvial fan.





BRACHYSTEGIA SAVANNA CANOPY RELICS IN SUBMATURE MOIST EVERGREEN FOREST

(belt 5m wide)

BS Brachystegia spiciformis

CG Cassipourea gummiflua

CL Cleistanthus schlechterii

CZ Craibia zimmermannii

DG Drypetes gerrardii

ES Erythrophleum suaveolens

GT Grewia transzambeziaca

HZ Hirtella zanzibarica

MB Memecylon sansibaricum

MD Manilkara discolor

MS Millettia stuhlmannii

PB Pachystela brevipes

PL Pteleopsie myrtifolia

PM Psuedobersama mossambicensis

PS Paropsia schliebeniana

SG Syzygium guineense

SZ Suregada zanzibariensis

UK Uapaca kirkiana

UN Uapaca nitida

VP Vincentella passargei

MOIST EVERGREEN FOREST ON DUPLEX SANDS

(belt 5m wide)

AG Anthocleista grandiflora

BM Balanites maughamii

CE Chlorophora excelsa

CG Cassipourea gummiflua

CS Craterispermum schweinfurthii

DA Diospyros abyssinica? (nkomanghamba)

ES Erythrophleum suaveolens

F Ficus sp. (large oval leaves)

HZ Hirtella zanguebarensis

I Indet.

M Memecylon sansibaricum

MD Manilkara discolor

MS Millettia stuhlmannii

N 'ndambanhati' - indet.

OC Olea capensis

PB Pachystela brevipes

PM Pseudobersama mossambicensis

RF Rothmannia fischeri

SG Syzygium guineense

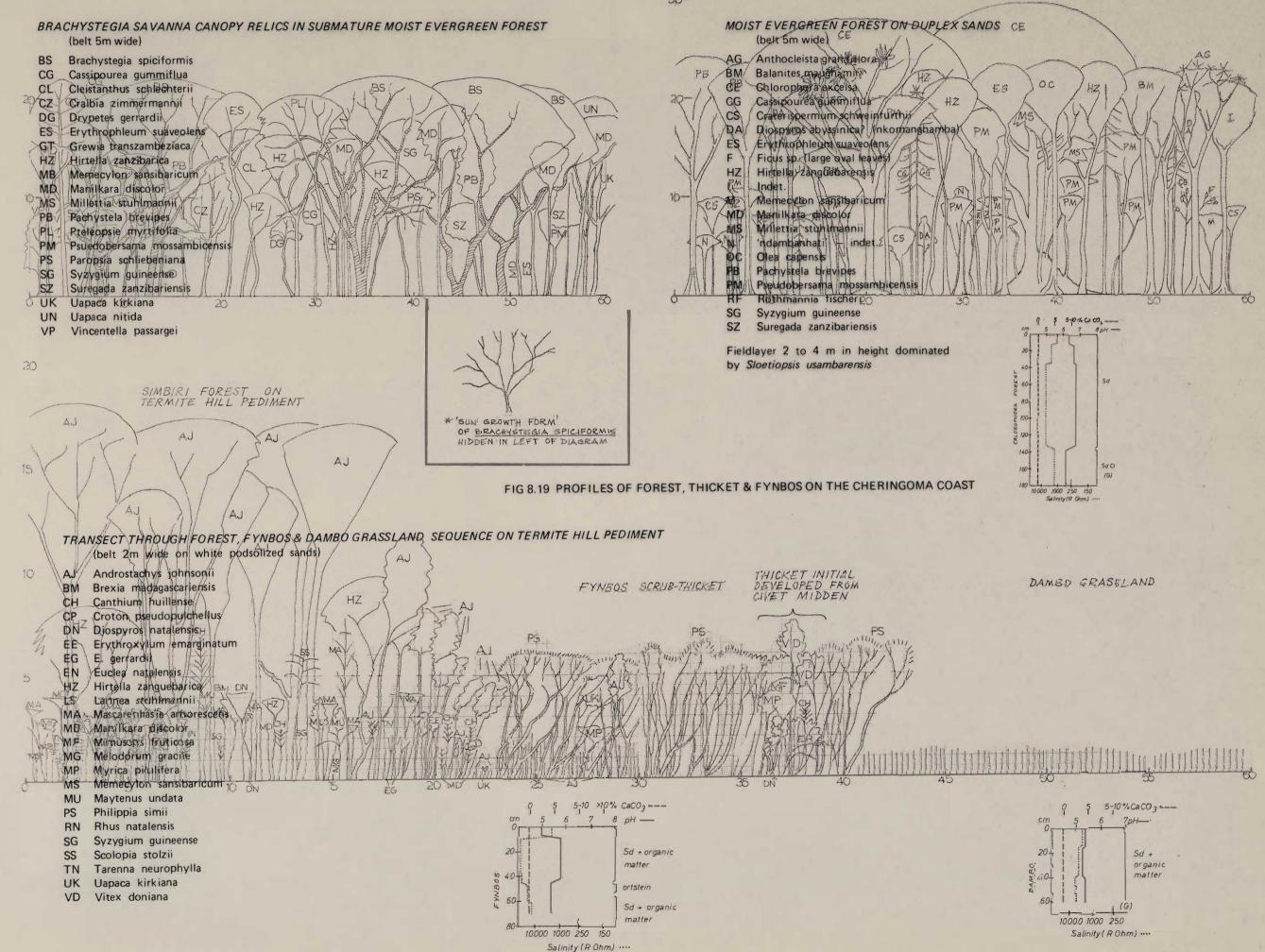
SZ Suregada zanzibariensis

Fieldlayer 2 to 4 m in height dominated by Sloetiopsis usambarensis

FIG 8.19 PROFILES OF FOREST, THICKET & FYNBOS ON THE CHERINGOMA COAST

TRANSECT THROUGH FOREST, FYNBOS & DAMBO GRASSLAND SEQUENCE ON TERMITE HILL PEDIMENT (belt 2m wide on white podsolized sands)

- AJ Androstachys johnsonii
- BM Brexia madagascariensis
- CH Canthium huillense
- CP Croton pseudopulchellus
- DN Diospyros natalensis
- EE Erythroxylum emarginatum
- EG E. gerrardii
- EN Euclea natalensis
- HZ Hirtella zanguebarica
- L'S Lannea stuhlmannii
- MA Mascarenhasia arborescens
- MD Mlanilkara discolor
- MF Mimusops fruticosa
- MG Melodorum graciile
- MP Myrica pilulifera
 MS Memecylon sansibaricum
- MU May/tenus undata
- PS Philippia simii
- RN Rhus natalensis
- SG Syzygium guineense
- SS Scolopia stolzii
 TN Taremna neurophylla
- UK Uapaca kirkiana
- VD Vitex doniana





SWAMP FOREST - DAMBO MARGIN SEQUENCE (belt 5m wide)

AG Anthocleista grandiflora

AM Adina microcephala

BM Bridelia micrantha

BR Barringtonia racemosa

CF Clappertonia ficifolia

CG Cassipourea gummiflua

CS Craterispermum schweinfurthii

EG Erythroxylum gerrardii

FT Ficus trichopoda

HA Homalium abdessammadii

HM Harungana madagascariensis

KN Khaya nyasica

MA Mascarenhasia arborescens

PB Pachystela brevipes

PF Parkia filicoidea

SA Scleria angusta

SG Syzygium guineense

FIG 8.20 PROFILES OF SWAMP FOREST, TERMITARIA THICKET & LITTORAL COMMUNITIES

PROFILE OF ESTUARINE MANGROVE & DUNE SCRUB-THICKET SEQUENCE (beft 2m wide)

AM Avicennia marina

BG Bruguieria gymnorhiza

CT Ceriops tagal

DN Diospyros natalensis

EG Eugenia capensis

EL Enterospermum littorale

FI Flacourtia indica

GS Guettarda speciosa

MC Mimusops caffra

MU Maytenus undata

OD Olax dissitiflora

RH Rhus natalensis
RM Rhizophora mucronata

SI Sideroxylon inerme

TC Trachylobium verrucosum

DAMBO THICKET ISLANDS ON TERMITE HILLS

(belt 10m wide)

- AC Afzelia cyanzensis
- AV Antidesma venosum
- CL Cleistanthus schlechterii
 CS Craterispermum schweinfurthii
- ES Erythrophleum sugveolens
- GT Grewia transzambeziaca
- HC Hiensia crinita
- HZ Hirteija zanzibarica
- MD Manilkara discolor
- MP Maprounea africana
- MF Mimusops fruticosa
- MS Millettia stuhlmannii
- OA Oxytenanthera abyssinica
- PB Pachystela brevipes
- PC Parinari curate/lifolia PL Polysphaeria lanceolata
- SG Syzygium guineense
- TE Tabernaemontaria elegans
- UK Uapaca kirkiana
- UN U. nitida





