The Miombo ecosystem

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Introduction

Miombo is a type of woodland dominated by *Brachystegia-Julbernardia-Isoberlinia*. The common Bemba term miombo is also used for various component species (*Brachystegia*, in Malawi, Rhodesia, Tanzania and Zambia; *Julbernardia* and *Isoberlinia* in Zaire).

Woodland was defined at the Symposium of phytogeography at Yangambi (CCTA, 1956) and a Symposium was later held in Ndola (CCTA, 1959). Forest is a formation where the highest layer is formed of trees, the crowns of which are not necessarily interlocking but their density is sufficient to cause a herbaceous layer that is distinct from that of savannas. This definition permits the distinction between woodlands and tree and shrub savannas. This difference may be observed when the tree cover exceeds 60 per cent. Aubréville (1957) described the Shabian (a previous province of Katanga) woodland as a 'mixed formation with a sparse graminaceous layer, trees being 15 to 20 m high, that looks like a real forest. Few intermediates between the forest and the herbaceous layer. The trees have interlocking or nearly interlocking crowns, but the foliage is light, the branches being most often extended in umbrella fashion, so that the whole is light and airy, it is an open forest ("forêt claire"); the expression seems correct'.

Miombo has been considered as open deciduous microphyllous forest (Peterken, 1967), rain green forest (Lieth, 1974), tropophilous forest (Lebrun and Gilbert, 1954) and heterothermic forest (Streel, 1963). The miombo type woodlands are similar to the dondo, mikondo, tenda and tumbi of various authors.

An IBP Miombo Project (Malaisse, 1973) has been developed at the National University of Zaire. This has given rise to numerous publications which, with original results, are summarized here.

Climate

The macroclimate of the Lubumbashi region is characterized by a wet season (November to March), a dry season (May to September) and two transition months (October and April). The annual precipitation is *ca.* 1 270 mm, but large between year differences occur (716 to 1 551 mm). Very rarely a rainfall may exceed 100 mm (160 mm in 2 hours 40 min in 1923). Half the daily precipitations are less than 5 mm, but these represent less than 10 per cent of the total

TABLE 1. Climatic data measured at the Kaspa University Campus Station (Lubumbashi) from 1964–1970.

	J	F	M	A	M	J	J	A	S	O	N	D
$\overline{TM}$ (maximum: 32.8)	28.1	28.2	28.5	29.3	28.6	27.1	26.9	29.1	31.9	32.8	29.6	27.9
TM (maximum: 37.8)	36.4	31.0	31.7	33.0	34.2	30.5	35.0	35.0	37.8	36.6	35.5	32.5
$T\overline{m}$ (minimum: 4.2)	16.3	16.6	15.6	12.3	7.5	5.3	4.2	7.0	10.0	13.2	15.7	16.4
Tm (minimum: —1.5)	12.4	13.5	10.3	6.0	1.5	—1.0	—1.5	0.9	4.2	6.0	11.6	11.8
T (mean annual: 20.3)	22.2	22.4	22.1	20.8	18.1	16.2	15.6	18.1	21.0	23.1	22.7	22.0
P (annual total: 1 275.4)	299.1	247.4	174.9	36.5	3.7	9.2	0	0	4.1	36.1	186.2	278.2
R.H. (mean annual: 77.5)	89	90	89	82	76	76	73	63	58	53	82	87
Piche (mean annual: 3.5)	1.8	1.8	1.9	2.5	3.2	3.6	4.4	5.6	6.2	5.8	2.8	1.9
A (mean annual: 17.3)	11.8	11.9	12.8	16.9	21.1	21.7	22.2	22.2	21.9	19.6	13.8	11.9
R (mean annual: 460.5)	423	414	442	472	478	436	469	493	533	516	456	394
I (mean annual: 7.7)	4.9	4.8	5.9	8.3	10.0	9.7	10.3	9.9	9.8	8.9	6.1	4.2

Abbreviations

$\overline{TM}$:mean daily maximum temperatures (°C)
TM:absolute maximum temperature (°C)
$T\overline{m}$:mean daily minimum temperatures (°C)
Tm:absolute minimum temperature (°C)
T:mean monthly temperature (°C)
P:mean monthly rainfall (mm)
R.H.:relative humidity at 08.00 h (%)
Piche:Piche evaporimeter (mm/d)
A:mean daily temperature amplitude (°C)
R:mean radiation ($cal/cm^2/d$)
I:mean daily sunshine (h)

rainfall; daily rainfalls exceeding 50 mm represent 24 per cent of the total and occur on 4.3 days a year. On average there are 118 rain days.

The average temperature is *ca.* 20° C. It is lowest at the beginning of the dry season (mid-May to mid-July). The night minimum is most frequently *ca.* 06.00 h. Absolute minimums of 0° C are very rare but occur some years. October, or sometimes November, is the hottest month with a daily maximum of 31–33° C. The daily thermal range is small in the wet season and large in the dry season. The humidity of the air depends on the rainfall; it is minimal in October and maximal in February. The annual global radiation is 16.8×10^9 kcal/ha, of which 61 per cent is as direct radiation. Table 1 recapitulates the regional climate calculated from observations made at the meteorological station of the University campus of Lubumbashi.

The climate belongs to Koppen's Cw type with a dry season lasting an average of 186 days and an average rainfall of 1 270 mm.

Soils

The IBP sites are located on zonal soils of the Kaponda series (soil type A-2; Sys and Schmitz, 1959). These are deep, reddish-yellow lateritic soils, of fine clay texture, impermeable, but which drain well. The upper organic horizon is thin and does not exceed 2 cm; the A 1 horizon is also thin, less than 3 cm in general and exceptionally reaching 5 cm; the surface horizons overlie deeper redder horizons which are poorly differentiated. The average values of pH of 25 soil samples, over a year of observation and for each horizon level, are given in the following table (Luiswishi miombo site); the soils of the Kaponda series are characterized by a fairly pronounced acidity; on the other hand, it is likely that the higher values measured at the upper humiferous level are a direct consequence of bush fires. The C/N values were measured in January and September, the total carbon according to the modified method of Anne (1945) and the total nitrogen by the Kjeldahl method. The granulometric analyses made at various depths show a high predominance of fine elements (0–2 μ):

Depth (cm)	Grain size distribution (per cent)				
	Clay (0–2 μ)	Fine silt (2–20 μ)	Coarse silt (20–50 μ)	Fine sand (50–250 μ)	Coarse sand (350–2 380 μ)
5	36.5	13.9	24.3	14.3	10.9
10	36.4	14.1	26.0	13.1	10.4
20	36.7	15.1	24.9	12.4	9.7
50	40.3	16.7	21.6	11.3	9.4
100	41.8	14.6	26.1	10.5	6.9
200	35.1	12.3	34.4	11.4	6.5

Horizon	pH	C/N January 1969	C/N September 1969
L		20.6	17.5
F+H			
A 1 (—3 cm)	5.3	11.8	13.9
—10 to —20 cm	4.6	11.7	13.0

Structure and function

Distribution

According to the map of African vegetation published in 1959 by AETFAT (Association pour l'étude taxonomique de la flore d'Afrique tropicale) woodlands represent 12.1 per cent of Africa, i.e. *ca.* 3.765×10^6 km². According to Ernst (1971), this corresponds to the limits of resistance to heat and cold of the main trees (+48° C for the leaves and buds, —2° C for the stems of *Brachystegia spiciformis*). The area is subdivided into two blocks, a narrow strip situated north of the equator and a massive ensemble in the Zambezian domain. It is in the latter that the Zairian miombo is found occupying 11 per cent of the area of the Republic of Zaire.

Recent maps giving more detail of the distribution of woodlands are rare; examples include Angola (Grandvaux Barbosa, 1970), areas of Shaba (Sys and Schmitz, 1959; Streel, 1963; Malaisse, 1975) and the Selous Game Reserve in Tanzania (Rodgers, 1973).

The examination of new aerial photographs of Shaba allows a rapid detection of miombo, which is easily differentiated from the other main types of vegetation. However the dense thickets covering the termite hills occasionally modify its appearance.

The absence of a detailed map of Shaba vegetation is an important lack. Its construction from aerial photographs and, when they exist, controlled mosaics, does not present any important difficulties. Reconnaissances on the ground along carefully chosen itineraries are a necessary preliminary. It is desirable that such a map be drawn soon. It would not only give information on the distribution of the main types of vegetation but also allow a general evaluation of the vegetation biomass.

Physiognomy, architecture and structure

General aspect

The tree layer is characterized by its light covering and slight density. The trunks are short and twisted; there are no buttresses except in the case of *Marquesia macroura*, so that well-formed logs are rare. The upper branches are twisted and spread out; the canopy often an umbrella shaped, especially in *Brachystegia* spp. The leaves are small; most often they are pinnate or bi-pinnate with short leaflet stalks. Only a few species of undergrowth have large leaves (*Uapaca* spp. and *Protea* spp.). The lamina is slightly flexible, with variable hairiness, and usually with an entire margin. The species tend to be heliophiles. The miombo flowers all year round. Cauliflory is rare but occurs on some *Ficus* spp., among others. Fruiting is abundant, but often occurs every two years for species or individuals. Dispersal is especially by animals.

Epiphytism is fairly wide-spread in the unburnt areas where carpets of heliophile orchids are found: *Bulbophyllum* spp., *Polystachya* spp. and *Calyptrochilum christianum*.

Crustose and foliose lichens are more abundant than fruticose ones which only occur in the upper part of the crowns, but all lichens and bryophytes are scarce. Epiphyte biomass distribution is illustrated in table 2 for a 16.7 m tall *Marquesia macroura.* Lianas are found but are not well developed because of the fires, some strangling species of *Ficus* are present. There are also a number of species of hemiparasitic Loranthaceae as well as the true parasites *Pilostyles aethiopica* on tree branches and *Thonningia sanguinea* on tree roots.

TABLE 2. Distribution of the biomass (g of dry matter) of epiphytes on a 16.7 m tall *Marquesia macroura.* Values per ha are forty times greater, *ca.* 15 kg.

Height on tree (m)	Mosses	Liver-worts	Lichens			Vascular plants
			foliose	crustose	fruticose	
0–1						
1–2	0.3					
2–3	1.3	0.6	0.3	6.5		2.6
3–4	2.1		8.5	15.2		
4–5	2.9	0.1	5.5	0.6		
5–6	6.1	0.4	4.4	5.7		
6–7	1.0		0.2	5.5		
7–8	1.2	0.1	0.5	2.1		
8–9	1.5	0.3	11.5	25.6	6.9	
9–10	5.3	0.6	13.0	9.5	3.5	5.1
10–11	1.3	0.1	4.3	54.8	0.2	
11–12	2.2		17.4	10.5	3.2	
12–13		0.1	6.9	20.2	8.9	
13–14			2.5	18.4	4.3	
14–15	0.3		2.2	35.1	0.9	
15–16			9.0	3.3	10.4	
16–17	0.1		16.8	31.3	4.4	
Total	25.6	2.3	103.0	244.3	42.7	7.7
Percentage	6.0	0.5	24.2	57.4	10.0	1.8

Clumps spared by fire develop rapidly into a dense structure, sometimes called *forêt claire muhuluteuse*, characterized by the exuberant understorey and lianas, the accumulation of litter and the poor development of the herb layer. The understorey is open, scattered with small trees and rare shrubs. The grass layer is more or less continuous and well developed. Sucker shoots are abundant and mix with the grasses which dominate in the gaps where the water-table is close to the soil surface after the last heavy rains. At the end of the wet season flower stalks exceed one meter in height.

Tall termitaria

Mounds built by *Macrotermes falciger* and reaching 8 m in height and 14–15 m basal diameter are characteristic; their density varies from 2.7 to 4.9/ha with an average cover of 6 per cent.

The termitophilous flora is formed of a mosaic of ecological groups amongst which xerophilous and eutrophic tendencies dominate. The xerophily is due to the high clay content of the termite mounds and their low rain-water penetration because of their conical form. The eutrophy is because their soil has a higher pH than the surrounding ground. The existence of limestone concretions at their centre has been noticed by many authors. Their detailed study is necessary, dealing with regional and local variations, and the presence and absence of termite activity (fossil termitaria do exist there).

Floristics and adaptations

A phytogeographical analysis of 235 characteristic species gives the following distribution (Schmitz, 1971);

6.6 per cent	endemic species in the neighbourhood of Lubumbashi
13.6 per cent	Shabano-Zambian species
30.0 per cent	Zambezian species
9.9 per cent	Zambezian and Oriental species
3.3 per cent	Zambezian and Austral-African or Sahel-Sudan species
6.6 per cent	Zambezian, Oriental and Somalo-Ethiopian, Austral-African, Sahel-Sudan or species of Madagascar
9.5 per cent	omni-Sudano-Zambezian species
2.5 per cent	Zambezian and Guinea species
2.9 per cent	Sudano-Zambezian and Guinea species
7.0 per cent	panafrican to cosmopolitan species
7.0 per cent	African species with varied distribution.

A preliminary phytogeographic analysis on 336 species whose presence has been observed on termite mounds, showed the clear preponderance of the Sudano-Zambezian type (Malaisse and Anastassiou-Socquet, 1977): 18.5 per cent of the plants belong to the Shabano-Zambian distribution type, 7.4 per cent to the Zambezian, 12.5 per cent to the Zambezian and Oriental, 12.2 per cent to the omni-Sudano-Zambezian, 11.3 per cent to other distribution types within the Sudano-Zambezian. 16.1 per cent of the plants are bridge species of the Sudano-Zambezian Guinea-Zairian type, whilst other bridge types (2.7 per cent), pluriregional (8.3 per cent), palaeotropical (6.2 per cent), pantropical (2.1 per cent), Afro-American (0.9 per cent) and cosmopolitan (1.8 per cent) elements play a minor role.

These analyses show a high proportion of Zambezian which spread little outside the limits of the Zambezian zone and few wide-ranging species (Schmitz, 1963).

The life-form spectra show a preponderance of phanerophytes:

	Phanerophytes	Chamaephytes	Hemicryptophytes	Geophytes	Therophytes
Gross spectrum (percentage)	41.3	16.6	7.2	27.2	7.7
Balanced spectrum (percentage)	47.1	6.3	19.1	26.2	1.6

Tropical regions with a clear-cut dry season have a typically tropophilous flora and a large number of tropophytes are deciduous (Schnell, 1970). During the dry season the relative humidity decreases to 10 per cent (daily average minimum, 32 per cent), whilst the soil hydration of the

upper 50 cm falls to 11 per cent. The existence of certain xeromorphic tendencies is not surprising. The leaves show:
— thick cuticles;
— reduced lamina surface, with rapid deciduousness; the lamina is sometimes lacking;
— lamina rolling;
— leathery laminas;
— development of supporting tissue;
— protection of the stomata by a thick indumentum, and sunken stomata;
— succulence (aquiferous parenchyma and viscous substances);
— sclerenchymatous sheath around vascular bundles.

Stems are frequently thorny, more woody or succulent. The roots are laterally or vertically extensive; xylopods are frequent.

These various morphological and anatomical adaptations especially characterize the flora of termite mounds. Prickles and fleshiness are the most spectacular.

Variation

The regional differences in the composition of the woodlands of Shaba were studied in detail by Schmitz (1963, 1971) who, using the Zurich-Montpellier phytosociological method, noted many associations. For this author, these should be grouped into three alliances.
— the Berlinio-Marquesion (Lebrun and Gilbert, 1954);
— the Mesobrachystegion (Schmitz, 1950);
— the Xerobrachystegion (Schmitz, 1950).

The first alliance comprises the deciduous and semi-evergreen miombos located mainly on the edge of the Guinea region. These are mainly tall woodlands, largely dominated by *Marquesia macroura* which has a short leafless period. The second alliance comprises the miombo on relatively fertile clay soils. The third alliance corresponds to miombo on drier, often shallow soils. These three alliances form an order which includes all the Zambezian woodlands, the *Julbernardio-Brachystegietalia spiciformis* (Duvigneaud, 1949). Above this order is the *Erythrophleetea africani circumguineensia* class (Schmitz, 1963), i.e. woodlands largely formed of Caesalpiniaceae, spread over the Guinea-Zairian region.

In Zambia, Fanshawe's (1969) analysis distinguished four types of woodlands, including miombo. Other divisions have been proposed by Trapnell (1937, 1943) for Zambia and Lees (1962) for the Copperbelt. Fanshawe (1969) quotes Savory (1963) who had established the soil preferences and rooting characteristics of the main species:

'*Julbernardia paniculata* is very adaptable and occurs on all sites;

'*Brachystegia spiciformis* prefers really deep soils and cannot stand waterlogging;

'*Brachystegia longifolia* prefers deep sandy soils, cannot penetrate murram but can live in a permanent (moving) water-table;

'*Brachystegia utilis* prefers deep loams and cannot penetrate hard murram;

'*Brachystegia floribunda* prefers heavy-textured soils and can penetrate murram;

'*Brachystegia boehmii* prefers clay loams and can penetrate murram;

'*Isoberlinia angolensis* is very adaptable and can live within a permanent (moving) water table'.

In the sense of Schlenker, miombo forms a regional association, including a large number of local variations which are closely connected with edaphical conditions. Lawton (1972) distinguishes several ecological groups in an intensive study of Zambian miombo. He first recognizes two groups: the fire-hardy chipya ecological group; and the fire-sensitive dry evergreen forest ecological group or muhulu (mateshi in Zambia). In addition there are the *Brachystegia-Julbernardia* woodland canopy group, the *Uapaca* group and the ubiquitous group of species with ecological wide range. These groups are not discrete but, as his principal components analysis shows, form a vegetation continuum. The groups are related to soil differences, especially of depth and moisture availability in the dry season, and to the severity or fire which causes some of them to be dynamically related.

In general, the flora on termite mounds is different from that of the surrounding miombo. Moreover, the termite mound flora varies within the Zambezian region. Wild (1952) found 72 termitophilous species, including 10 Capparidaceae in Rhodesia. Only 17 of these species were found on the Shabian termite mounds; only one near the Rio Queve in Cela, Angola (Diniz and Aguiar, 1972); and none spread to the edge of the Chambesi plain in northern Zambia (Lawton, 1972). The number of termite mound species is large: 208 woody species in Zambia (Fanshawe, 1969), 212, including grasses, in Shaba (Schmitz, 1963).

Many authors have emphasized the differences of this flora from the surrounding vegetation. Thus Mullenders (1954) points out that, in the Kaniama region (lower Shaba) the vegetation of the (almost all uninhabited) termite mounds is extremely poor and varies according to the association in which they occur. Fanshawe (1969) distinguishes five habitats (miombo, Kalahari, mopane, munga and riparian) where termite mounds are found and each contains particular species. Another reason for this variation is the presence or absence of termite activity. Only active mounds would have a characteristic vegetation. There are several stages from an active termitarium to a non-active, eroded ones which are often called fossilized. A succession and a zonation occur from typical termite mound vegetation to the ordinary miombo or savanna. This change towards miombo is more rapid at the base of the termite mound and thus it is possible to observe differences on the same termitarium.

Fire

Natural fires have been seen in Shaba at the beginning of the wet season, but these are very rare. The rain that normally follows lightning generally extinguishes these natural fires. Fire is almost always started by man. Generally it takes place once a year during the dry season. Early burning (before the end of June) is less intense and less destructive to woody plants than late burning when the grass is drier and there is more tree litter on the ground and when regrowth may have commenced. Some areas may remain unburnt for one or several years; young trees and climbers grow in these.

Burning experiments carried out at Ndola (Trapnell, 1959; Lawton, 1972) and Lubumbashi (Delvaux, 1958; Symoens and Bingen-Gathy, 1959) show the following species groups:

— fire-tolerant species: *Parinari curatellifolia*, *Erythrophleum africanum*, *Pterocarpus angolensis*, *Anisophyllea boehmii*, *Diplorhynchus condylocarpon*, *Combretum* spp., *Ochna schweinfurthiana*, *Ochthocosmus lemaireanus*, *Strychnos innocua*, *S. cocculoides*, *S. spinosa*, *Maprounea africana*, *Hymenocardia acida*, *Syzygium guineense* subsp. *macrocarpum* and *Uapaca nitida*;
— semi-tolerant species: *Baphia bequaertii*, *Pseudolachnostylis maprouneifolia*, *Strychnos pungens*, *Isoberlinia angolensis*, *Uapaca kirkiana*, *Bridelia cathartica*, *Hexalobus monopetalus*, *Xylopia odoratissima*, *Uapaca pilosa*;
— fire-tender species: the woodland canopy dominant species of *Brachystegia* and *Julbernardia*, *Chrysophyllum bangweolense*, *Garcinia huillensis*, *Bridelia duvigneaudii*. Trapnell (1959) also listed intolerant species but these, mainly forest climbers and evergreen trees such as *Entandrophragma delevoyi*, *Artabotrys monteiroae*, *Uvaria angolensis*, etc., occur in Shaba in the dry evergreen forest.

Architecture

The density of the strata varies considerably and it is difficult to give average heights. On the main IBP research site, Malaisse distinguished three layers:

— a dominant tree layer, 14–18 (–21) m tall, with a density of *ca.* 65 trees/ha;
— a secondary tree layer, 8–12 (–14) m tall, with a density of *ca.* 80 trees/ha;
— a shrub layer, <8 m tall with 375–500 stems/ha.

The secondary tree layer may be locally absent. Late fires and cutting cause shrubs to branch at or near the base: thus one plant of *Diplorhynchus condylocarpon*, subsp. *mossambicensis* may have *ca.* 20 stems at 1.3 m and the understorey remains open in spite of the large number of stems.

This is why the basal area measured at 1.3 m above ground level is an excellent way to evaluate the density of miombo. It varies from 12 to 25 m²/ha. The dominant tree layer represents *ca.* 35 per cent of the total basal area. When the basal area is less than 10 m²/ha, the composition of the grass layer is different and the vegetation is wooded savanna. Frequency by diameter classes were (IBP site, on 0.5 ha plots):

Diameter classes (cm)	Trees/ha
0–<5	358
5–<10	264
10–<20	174
20–<30	54
30–<40	18
40–<50	14
50–<60	4
100–<110	2

Regular burning hastens the death of weak and small trees. The following results indicate the amount of dead standing trees:

Diameter classes (cm)	Dead trees/ha	Basal area (m²/ha)
0–<5	18	0.02
5–<10	16	0.05
10–<20	16	0.2
20–<30	4	0.2

Miombo has several local types and a relative floristic richness; at least 480 species with an average of 138/ha (table 3).

TABLE 3. Floristic diversity of a miombo woodland.

Family	Number of species	Stems≥10 cm DBH (percentage)
Tree and shrub layers		
Apocynaceae	1	22
Caesalpiniaceae	4	15
Combretaceae	1	6
Dipterocarpaceae	3	13
Euphorbiaceae	5	12
Papilionaceae	4	11
Rosaceae	1	2
Rubiaceae	4	3
17 other families	20	15
	43	
Grass layer		
Acanthaceae	4	
Commelinaceae	5	
Compositae	11	
Cyperaceae	4	
Gramineae	14	
Iridaceae	4	
Lamiaceae	5	
Papilionaceae	14	
Rubiaceae	12	
26 other families	39	
	112	

At the research station, numerous branched *Diplorhynchus* spp. swell the numbers of Apocynaceae; elsewhere Caesalpiniaceae often represent 40 per cent or more of the tree population.

There remain several gaps in knowledge. The list of miombo species is richer than the reported statistics due to incomplete identifications. A key based on leaves and seedlings would be most valuable, even for the genera such as *Brachystegia*. Studies of variation in density and basal area should be undertaken to aid understanding miombo dynamics, change towards a dense dry forest or wooded savanna and regeneration.

Function

Phenology

Miombo shows well-defined seasonal variations correlated with rainfall and temperature. Phenologically there

TABLE 4. Miombo diaspores, weights and areas.

Species	Number of diaspores observed	Fresh weight of disseminating units (g)			Maximum surface of diaspore's projection (cm²)			Ratio x:y (g/cm²)
		minimum	mean (x)	maximum	minimum	mean (y)	maximum	
Afrormosia angolensis	16	0.65	1.23	1.99	10.7	19.31	31.2	0,0637
Albizia antunesiana	30	0.36	1.23	2.05	17.4	48.43	80.7	0,0254
Brachystegia spiciformis	100	0.34	0.70	0.97	1.6	2.74	3.4	0,2544
Combretum zeyheri	25	1.04	1.71	2.85	13.1	25.14	36.0	0,0682
Dalbergia boehmii	75	0.05	0.10	0.23	3.9	5.87	13.7	0,0174
Dioscorea bulbifera	100	—	0.007	—	1.4	2.01	2.5	0,0035
Monotes africanus	25	0.31	0.58	0.93	4.0	7.81	12.5	0,0747
Ochna schweinfurthiana	150	0.07	0.299	0.57	0.14	0.49	0.79	0,6102
Parinari curatellifolia	77	6.12	13.94	24.34	3.2	6.45	10.0	2,1612
Pseudolachnostylis maprouneifolia	66	1.95	3.12	4.28	1.8	2.28	2.9	1,3672
Pterocarpus angolensis	16	2.60	3.97	6.34	56.0	82.93	118.0	0,0478
Strophanthus welwitschii	100	—	0.0158	—	3.46	10.75	15.76	0,0015
Strychnos innocua	10	42.45	72.41	119.75	16.5	24.49	36.6	2,9567
Uapaca kirkiana	25	3.86	8.10	15.84	2.9	4.92	7.7	1,6444
Vitex mombassae	80	1.51	3.34	5.75	0.84	2.16	3.28	1,5461

are five seasons: cold dry season (May–July), hot dry season (August–September), early wet season (October–November), main wet season (December–February) and late wet season (March–April) (Malaisse, 1974).

The Zairian miombo flowers all year round but the different layers have their own rhythms of flowering. The tree and shrub layers show a flowering maximum during the dry hot season although some shrubs flower as soon as the rains end. The grass layer has two maxima: the largest, especially of hemicryptophytes, in the main wet season and the second, especially of geophytes and geofrutex, in September.

Fruiting shows a seasonal rhythm with a maximum during the hot dry season. The quantity of fruit produced annually varies enormously: from 1968 to 1971, only 160 kg/ha (dry matter) compared with 2 t/ha in 1972; 1970–1971 was a wet year and 1971–1972 a very sunny dry year. Individual trees tend to fruit abundantly in alternate years; in the intermediate years they fruit partially or not at all. For the dominant trees, the maximum recorded values are in the range of 25–30 kg (dry matter) per tree of which, for certain Caesalpiniaceae, 84 per cent accounts for the valves of the pods and the rest for the seeds. Tables 4 and 5 summarize fruit and seed dimensions and production.

TABLE 5. Total production of fruit or seeds for miombo species.

Species	Number of fruit or seeds per tree	Height (m)	Crown projection (m²)	Girth at 1.3 m (cm)	Total production of fruit or seeds (g)		Individual seed dry weight (g)	Maximum dispersal (m)
					fresh weight	dry weight		
Albizia adianthifolia	10 620	11	86.9	101.4	444	397	0.037	103
Brachystegia spiciformis (valve of pod)	4 036	14	56.1	96.3	—	22 446	5.561	13
Brachystegia spiciformis (seed)	7 921	13	78.2	112.4	4 647	4 196	0.530	20
Chrysophyllum bangweolense	1 250	7.2	27.1	68.3	54 071	—	—	6
Combretum zeyheri	293	5.8	20.7	37.8	502	291	0.993	42
Hymenocardia acida	7 101	8.4	4.2	66.4	538	239	0.034	28
Ochna schweinfurthiana	17 057	6.1	12.5	41.8	5 100	3 151	0.185	6
Pseudolachnostylis maprouneifolia	2 877	6.8	47.8	91.2	8 976	3 087	1.073	9
Pterocarpus chrysothrix	2 530	13	173.0	164.5	8 475	5 027	1.987	20
Strophanthus welwitschii (seed)	2 338	4.4	2.3	6.8	37	33	0.014	>250
(follicle)	7	4.4	2.3	6.8	—	72	10.27	2
Strychnos innocua	177	5.8	39.2	48.0	12 817	9 733	54.989	6
	462	8.3	51.6	78.9	—	—	—	7
Swartzia madagascariensis	298	8.2	27.1	59.4	3 327	1 273	4.272	7
Uapaca kirkiana	3 998	8.7	49.6	74.7	5 168	2 067	0.517	8
Vitex doniana	1 326	7.2	28.3	70.1	10 389	3 173	2.393	5
Vitex mombassae	1 978	4.6	30.7	67.3	5 616	2 532	1.33	5

TABLE 6. Relative frequency (in percentage) of fruit dissemination types for some Zairian forests.

Vegetation type	Equatorial dense forest	Semi-deciduous forest	Transition forest	Mountain forest	Forest on waterlogged soil	Miombo
Area	Befale-Equator	Befale-Equator	Kivu	Kivu	Tshuapa-Equator	Southern Shaba
Source	Nanson and Gennart, 1960 (reported by Evrard, 1968)		Liben, 1962		Evrard, 1968	Malaisse (unpublished)
Autochory	37.9	33.5	14	8	12.0	30.4
Zoochory	54.7	54.5	57	49	59.4	38.5
Anemochory	7.0	11.5	24	37	22.2	31.1
Hydrochory	0.4	0.4	5	6	6.4	0

An analysis of the dissemination of 135 miombo specesi shows a slight emphasis on zoochory; this contrasts with other types of forests in Zaire (table 6).

Hydration has not been studied in the Zairian miombo but Ernst and Walker (1973) found a slight seasonal variation in Rhodesia. The young leaves of the main species in October give values between 230 and 280 per cent (of dry matter) whilst the older leaves remain within narrower limits of 100 to 130 per cent from December to leaf-fall in July. Osmotic pressure shows a marked seasonality. In young tree leaves it is less than 10 atmospheres, but increases rapidly to reach a first maximum (17–18 atmospheres) at the end of October; in the middle of the main wet season it decreases to 12–16 atmospheres and then rises progressively until the onset of the dry season; these high values remain until leaf-fall.

More information on the phenology of fruiting is required especially of the main woody species, particularly as so many fruits are edible. Hydration of the different organs of the characteristic species in each layer should be followed throughout the year.

Regeneration dynamics

Lawton (1972) provides information on regeneration. When an area is cleared for cultivation it is replaced by *Diplorhynchus condylocarpon, Hymenocardia acida, Pericopsis angolensis, Pterocarpus angolensis, Syzygium guineensis* subsp. *macrocarpum* and *Vitex doniana.* The two last species form patches of canopy at a height of 4 m which partially suppresses the tall grasses and bracken. *Uapaca* species (mainly *U. benguelensis, U. kirkiana, U. nitida* and *U. sansibarica*) established themselves under these conditions. When their canopy is 4–12 m tall, the herb stratum is reduced to sparse short grass mostly covered with leaf litter. Under these conditions fires creep along the ground and the *Brachystegia-Julbernardia* spp. as well as *Marquesia macroura* may regenerate. They overtop and shade out the *Uapaca* although some *Uapaca* trees survive, while the first group of colonizing species forms a coppice; only if the canopy is opened again will they regrow.

Vegetation biomass and primary production

The completion of observations on the biomass and productivity of woody strata should be one of the primary objectives of miombo research. An indication of the average growth of three trees in the neighbourhood of Lubumbashi is given by Schmitz (1971) (table 7).

TABLE 7. Mean growth of three miombo trees in the neighbourhood of Lubumbashi.

Age (years)	Girth (cm) *Julbernardia paniculata*	*Brachystegia spiciformis* var. *latifoliolata*	*Parinari curatellifolia* subsp. *mobola*
5	10	18	12
10	19	32	25
15	28	44	37
20	34	55	48
25	42	65	60
30	49	74	71
35	56	83	82
40	63	91	94
45	69	99	106
50	76	106	118
60	89	119	142
70	103	130	166
80	117	140	192
90	130	148	218
100	144		
110	157		
120	171		
130	185		
140	198		
150	212		
160	226		

The analysis of grass and shrub productivity is complete. Annual production and biomass of the grass layer in the miombo have been studied by Freson (1973) who showed a highly positive correlation (r=0.72) between rainfall and organic matter production. The above-ground biomass increases rapidly from September to a maximum in January.

The dead biomass appears in December and increases rapidly from January to April (table 8). The losses due to herbivores also begin in December and are highest in March.

TABLE 8. Productivity (dry matter, g/m^2) of the grass layer of miombo (modified from Freson, 1973).

Month	Biomass	Monthly change in biomass	Dead biomass including litter fall	Consumption loss	Net production
1969					
September	0	—	0	0	0
October	25.1	25.1	0	0	25.1
November	69.9	44.8	0	0	44.7
December	129.0	59.1	12.4	0.6	72.1
1970					
January	221.8	92.8	17.1	1.2	111.2
February	180.4	—41.5	57.2	3.6	19.3
March	151.6	—28.7	48.4	5.4	25.1
April	141.8	— 9.8	20.3	4.6	15.1
May	135.5	— 6.4	14.4	3.0	11.0
June	133.7	— 1.7	5.9	1.1	5.3
July		Burnt on 2 July			

The annual primary production of the above-ground part of the grass layer of the miombo is 3.3 t/ha/a, which corresponds to 15.4×10^6 kcal/ha/a. The losses by fire were estimated at 71 per cent of the total organic matter present when the fire started.

For the shrub layer, observations were made on *Baphia bequaertii*, a species with a relatively straight trunk and rarely branching below 1.5 m height (table 9).

TABLE 9. Dry weight biomass of leaves and wood of *Baphia bequaertii* by height classes.

Height (m)	DBH (cm)	Leaves (g)	Wood (g)
2–3	3.0	252	1 091
3–4	6.2	1 249	8 051
4–5	9.4	2 865	26 747
5–6	12.2	3 212	54 255
6–7	15.7	4 841	70 236
7–8	18.3	5 552	96 701

The dry weight (g) biomass of two *Baphia bequaertii* shrubs was as follows:

Height of shrub (m)	5.5	5.7
Root depth (cm)		
0–50	6 872	13 142
50–100	5 281	1 529
>100	55	35
Total	12 208	14 706

This is only 15 per cent of the above-ground biomass.

Four years observations on a 1/8 ha plot with an initial basal area for all woody plants of 13.335 m^2/ha showed an average growth of 0.388 m^2/ha/a. This growth was spread irregularly between the various size categories; girths between 30 and 40 cm showed the maximum growth. The annual dead biomass was 0.037 m^2/ha and newly fallen trunks represented 0.018 m^2/ha.

These results emphasize the necessity of continuing research on productivity to obtain more precision especially on above-ground biomass, monthly growth in girth of the main species and root productivity of the different layers.

Secondary production

Studies dealing with the secondary production have recently started and the only results available are for numbers and biomass of certain taxa (table 10). The two most important herbivore taxa are the Acridians and the caterpillars. The Acridians show the highest numbers during the main wet season.

Caterpillars are among the largest forest herbivores. Miombo caterpillars seem mostly to eat one species (*Ekebergia benguelensis* for *Rhenea mediata*), or one family (Caesalpiniaceae for *Elaphrodes lactea*, Passifloraceae for *Acraea natalica*, Myrtaceae for *Charaxes druceanus*, Annonaceae for *Xanthopan morgani*, Moraceae for *Pseudoclanis postica*, Lamiaceae for *Precis octavia*, etc.). Less common are caterpillars eating only one genus (*Ficus* for *Myrina silenicus*). On the other hand, several caterpillars seem to feed on plants belonging to two or three unrelated families; they might have a phytochemical relationship. Thus *Hippotion celerio* and *H. eson* feed on Vitaceae, Balsaminaceae and Araceae. Table 11 presents information on the diet of characteristic caterpillars.

Elaphrodes lactea (Lepidoptera, Notodontidae) feeds on Caesalpiniaceae and because of their predominance in the tree stratum is capable of spectacular destruction and total defoliation over large areas. The rapid multiplication of this insect was reported in the Lubumbashi region in 1934 and in 1969–1970 when observations were made. The main predators are birds, notably the black-headed oriolo, Hemiptera, spiders, chameleons and lizards. Parasites have been observed at various stages: Chalcidians on eggs, Ichneumonids and Tachinids on caterpillars. In 1970 82.3 per cent of the eggs hatched; half of the young caterpillars became adult and 74 per cent of these made cocoons, but only 51 per cent became chrysalids; only 8.3 per cent of the eggs gave rise to butterflies. With a sex-ratio (♂/♀) of 11.5, there is effective population control by parasites and predators in the second year of its multiplication.

Rearing experiments showed that, at their peak density, their monthly leaf consumption was 733 m^2/ha (a dry weight of 98 kg/ha) and the dry weight of their faeces was 90 kg/ha. This represents an enormous transfer of green leaf material to the soil; its effect on tree growth is unknown but new leaves appear in May or June.

Other species have also high densities (table 12). All the *Pericopsis angolensis* trees were defoliated in March 1971 when the *Uapaca* spp. were attacked by a *Parasa* sp.

TABLE 10. Comparison of the monthly average number and live weight biomass (g/1 000 m²) of the main animal groups in the herb layer for the dry and wet seasons in burnt and unburnt miombo during 1973–1974.

	Unburnt				Burnt 5 July 1973					
	Dry season		Wet season		Dry season				Wet season	
					before fire		after fire			
	Number	Biomass	Number	Biomass	Number	Biomass	Number	Biomass	Number	Biomass
Araneidea	236	28	308	108	147	35	39	10	257	84
Acridoidea	227	582	118	253	296	884	26	43	124	240
Tettigonioidea	33	32	29	41	41	37	0	0	29	32
Grylloidea	55	36	164	166	65	41	19	18	190	240
Blattodea	96	24	203	79	137	32	89	14	123	63
Mantodea	25	39	57	50	28	36	5	3	29	31
Heteroptera	131	51	208	135	201	67	10	6	86	56
Homoptera	82	12	58	17	92	20	16	1	71	22
Coleoptera	22	12	87	90	32	18	2	—	74	79
Caterpillars	5	6	50	75	20	11	1	1	34	60

TABLE 11. Diet of some miombo caterpillars.

Caterpillar family and species / Plant species:	*Thunbergia lathyroides*	*Syzygium guineense*	*Stephania abyssinica*	*Pterocarpus angolensis*	*Ochna schweinfurthiana*	*Marquesia macroura*	*Markhamia obtusifolia*	*Julbernardia paniculata*	*Flacourtia indica*	*Ficus persicifolia*	*Fagaria chalybea*	*Erythrophleum africanum*	*Erythrina tomentosa*	*Ekebergia benguelensis*	*Dalbergia boehmii*	*Ceropegia meyeri-johannis* var. *verdickii*	*Canthium crassum*	*Bridelia ferruginea*	*Brachystegia spiciformis* var. *latifoliolata*	*Brachystegia microphylla*	*Brachystegia longifolia*	*Brachystegia boehmii*	*Baphia bequaertii*	*Annona senegalensis*	*Amorphophallus abyssinicus*	*Allophyllus africanus*	*Albizia antunesiana*	*Adenia gummifera*
ACRAEIDAE																												
Acraea natalica																												×
ARCTIIDAE																												
Aganaïs baumanniana										×																		
ATTACIDAE																												
Bunaea caffraria														×														
Cirina forda												×															×	
Tagoropsis hanningtoni																										×		
DANAIDAE																												
Danaida chrysippus																×												
EUPTEROTIDAE																												
Camerunia flava																	×											
LASIOCAMPIDAE																												
Batalebeda strandi				×											×													
Epitrabela argyrostigma								×																				
Pachymeta robusta																			×									
LIMACODIDAE																												
Parasa viridissima								×											×			×						
NOCTUIDAE																												
Diva casta			×																									
Naurilia arcuata						×																						
Oraesia excavata			×																									
Rhanidophora cinctigutta	×																											
NOTODONTIDAE																												
Antheua tricolor																							×					
Cerurina marshalli									×																			
Desmocraera interpellatrix rileyi		×																	×	×	×	×					×	
Elaphrodes lactea				×				×																				
NYCTEMERIDAE																												
Hibrildes ansorgei																		×										
NYMPHALIDAE																												
Charaxes bohemanni																							×					
PAPILIONIDAE																												
Papilio demodocus											×																	
SPHINGIDAE																												
Coelonia fulvinotata							×																					
Hippotion osiris																									×			
Libyoclanis punctum					×																							
Platysphinx stigmatica piabilis				×									×		×								×					
Xanthopan morgani																								×				

Studies on population dynamics of the main species of Lepidoptera should be undertaken as soon as possible. Certain Hemiptera and plant-eating Coleoptera also show rapid multiplication and their study is desirable.

TABLE 12. Main Lepidoptera of the Kaspa miombo (+++ >2 500 caterpillars/100 m^2; ++ >250; + >25).

Season	1968–1969	1969–1970	1970–1971	1971–1972	1972–1973	1973–1974
Attacidae						
Cyrtogone sp.	+	—	—	+	—	—
Lasiocampidae						
Pachymeta robusta	—	—	—	—	—	+
Limacodidae						
Parasa cf. *urda*	—	+	++	—	—	—
Lymantriidae						
Dasychira goodi	—	—	—	+	+	—
Notodontidae						
Elaphrodes lactea	+++	+++	—	—	—	—
Thaumetopoeidae						
Paradrallia rhodesi	+	+	++	+	—	—
Tortricidae						
unidentified species	—	—	+	—	—	—

Rodents have not been studied in the Zairian miombo. For a Zambian miombo on hydromorphic soils Sidorowicz (1974) found miombo to be poorer in small mammals than *Loudetia* savannas, alluvial savannas with *Acacia*, or thickets on halomorphic soils. He noted in the miombo the presence, in decreasing importance, of *Praomys natalensis*, *Tatera leucogaster*, *Saccostomus campestris* and *Beamys major*, and considered that carnivorous mammals, birds and reptiles and parasites controlled the density of rodents; they were well adapted to fire. Dowsett (1966) in the Ngoma area of the Kafue National Park, in Zambia, has studied, during the wet season, the game population structure and biomass in the miombo; the study area was a self-contained ecological unit, comprising 31 km^2 of woodlands. The following table gives for each species the density and biomass per km^2 of suitable habitat:

	Density per km^2	Average weight (kg)	Biomass (kg/km^2)
Wildebeest (*Connochaetes taurinus*)	1.62	195	315.6
Waterbuck (*Kobus defassa*)	1.47	147	216.4
Hartebeest (*Alcelaphus lichtensteini*)	1.47	140	206.4
Reedbuck (*Redunca arundinum*)	2.31	52	120.3
Sable (*Hippotragus niger*)	0.66	180	119.6
Zebra (*Equus burchelli*)	0.42	250	104.6
Elephant (*Loxodonta africana*)	0.02	4 980	99.7
Kudu (*Tragelaphus strepsiceros*)	0.58	140	81.4

	Density par km^2	Average weight (kg)	Biomass (kg/km$_2$)
Roan (*Hippotragus equinus*)	0.23	140	32.3
Warthog (*Phacochoerus aethiopicus*)	0.39	68	26.5
Eland (*Taurotragus oryx*)	0.04	362	14.5
Lion (*Panthera leo*)	0.08	154	12.3
Common duiker (*Sylvicapra grimmia*)	0.01	14	11.0
Bushbuck (*Tragelaphus scriptus*)	0.31	32	9.8
Spotted hyaena (*Crocuta crocuta*)	0.15	59	8.8
Sharpe's grysbok (*Raphicerus sharpei*)	0.85	7	6.2
Impala (*Aepyceros melampus*)	0.08	59	4.7
Cheetah (*Acinonyx jubatus*)	0.08	27	2.2
Baboon (*Papio ursinus*)	0.23	14	3.1
Vervet monkey (*Cercopithecus aethiops*)	0.50	3	1.6
ckal Ja(*Canis adustus*)	0.23	5	1.2

Tertiary production

Studies of the carnivores are still scanty, but a preliminary study of spiders has been completed. The spiders living in the tree and shrub and grass strata can be divided into six behaviour patterns which correspond to their ecological niches:

- sedentary spiders that build large vertical webs on the periphery of the tree crowns;
- spiders that are commensal to the first;
- sedentary spiders that build horizontal webs, mainly at branch level;
- sedentary spiders that spin small vertical webs in trunk irregularities;
- hunting spiders that move quickly;
- mimic hunting spiders with long immobile waits.

Nephila pilipes pilipes is very abundant and has a relatively permanent web with long sticky threads. Its life-cycle has been studied: copulation occurs in April and eggs are laid inside cocoons stuck to the leaves and branchlets at the beginning of the dry season; after activity inside the cocoon, the young spiders leave them from mid-August to mid-October for a community life; in October-November each establishes an individual web and they have several instars before becoming adults. The diet of the young spiders is 59 per cent Hymenoptera, 22 per cent Coleoptera and 11 per cent Diptera. Adults eat Acridians, Heteroptera, adult Lepidoptera and bees. During May the dry weight of food captured daily by the population is 7.9 g/ha compared with 0.97 g/ha in mid-December. Amongst predators are rodents for eggs, the lizard *Mabuya* spp. and spiders for the young, and chameleons and *Ammophila* (Sphecidae) for the adults. 87 per cent of the eggs hatch and most losses are due to parasites, especially Chalcidians. Thus the numbers per hectare vary from 188 000 young spiders in October, 36 320 in November, 24 160 in December, 8 320 in March, 1 610 in May and 790 in June just before burning.

The variation in numbers and biomass of spiders in the herb stratum has been followed over a year, on burnt and unburnt sites (table 10). They are two maxima (April with 335 and November with 347 individuals/100 m²) and a minimum in September (unburnt 80/100 m² and burnt 34/100 m²). The maximum fresh weight biomass occurs in November (16.9 g/ha) and the minimum just after burning (0.4 g/ha). The relative importance of the different families at the end of the wet season has been estimated (table 13).

These results indicate future research on carnivorous groups or those with a mixed diet; ants and Heteroptera are most in need of study.

TABLE 13. Relative frequency (percentage) of spiders in the grass layer of the miombo.

(March 1973)	
Lycosidae	18.5
Salticidae	10.5
Oxyopidae	10.1
Drassidae	9.4
Clubionidae	9.1
Thomisidae	9.1
Pisauridae	7.0
Ctenidae	5.6
Araneidae	5.6
Sparassidae	4.5
Theridiidae	3.1
Asamiidae	2.8
Other families which represent less than 2 per cent	4.7

Water balance and biogeochemical cycles

Water balance

Rainfall interception and stemflow in the tree and shrub strata on a 625 m² plot (with 52 woody plants; equivalent to 832/ha and a basal area, at 1.3 m above-ground level, of 19.6 m²/ha) are shown in table 14. The proportion intercepted appears to be related to the duration and intensity of the rainfall rather than the leaf canopy. The dense herb layer will, no doubt, considerably reduce the amount of water reaching the ground surface.

Alexandre (1973) tried to establish a global water balance. Of the *ca.* 1 200 mm/a rainfall, scarcely 50 mm/a flow away. This mainly occurs during the second half of the wet

TABLE 14. Water balance in the Kaspa miombo during 1973 and 1974 on a 625 m² plot.

Period	Rainfall (mm)	Penetration						Interception	
		Throughfall		Stemflow		Total			
		mm	Percentage	mm	Percentage	mm	Percentage	mm	Percentage
1973									
January[1]	239.0	201.6	84.4	3.3	1.4	204.9	85.8	34.1	14.2
February[1]	228.5	198.3	86.8	5.0	2.2	203.3	89.0	25.2	11.0
March	95.8	82.0	85.6	1.5	1.5	83.5	87.1	12.3	12.9
April	118.3	88.0	74.4	2.2	1.9	90.2	76.3	28.1	23.7
May-August	0.0	—	—	—	—	—	—	—	—
September	21.5	18.9	88.0	0.3	1.4	19.2	89.4	2.3	10.6
October	10.1	7.2	72.4	0.0	0.2	7.2	72.6	2.9	27.4
November	119.6	95.3	79.7	2.0	1.7	97.3	81.4	22.3	18.6
December	272.4	198.8	73.0	1.8	0.7	200.6	73.7	71.8	26.3
Total	1 105.2	890.1	80.5	16.1	1.5	906.2	82.0	199.0	18.0
1974									
January	363.6	294.6	81.0	3.8	1.0	298.4	82.0	65.2	18.0
February	217.7	185.4	85.2	2.9	1.3	188.3	86.5	29.4	13.5
March	370.5	284.6	76.8	5.8	1.6	290.4	78.4	80.1	21.6
April	52.7	40.7	77.2	0.3	0.6	41.0	77.8	11.7	22.2
May	90.9	75.5	83.0	0.5	0.6	76.0	83.6	14.9	16.4
June	0.0	—	—	—	—	—	—	—	—
July	0.0	—	—	—	—	—	—	—	—
August*	(3.4)								
September	0.0	—	—	—	—	—	—	—	—
October	2.4	1.9	78.2	0.0	0.0	1.9	78.2	0.5	21.8
November	63.4	48.6	76.6	1.2	1.9	49.8	78.5	13.6	21.5
December	301.9	217.1	71.9	6.0	2.0	223.1	73.9	78.8	26.1
Total	1 463.1	1 148.4	78.5	20.5	1.4	1 168.9	79.9	294.2	20.1

* Throughfall not measured; rainfall exceptional (observed only twice in 53 years) and not taken into consideration.
1. Observations on 400 m².

season, when the water-table is near the ground surface in the dembo savannas that periodically flood. The infiltration water in the first half of the wet season restores the soil to field capacity; this represents an average of 220 mm for the soil above the capillary fringe. A similar volume feeds the water-table. With the growth of vegetation, the interception increases to 35 per cent (19 per cent by the tree and shrub layers). Infiltration of stemflow is *ca.* 18 mm, and direct evaporation 200 mm. During the dry season, the actual evapotranspiration (ETR) is equal to 360 mm, and 680 mm during the wet season except in October and November when plant growth is high. Over the whole year evapotranspiration is 1 050 mm, of which 200 mm evaporate directly and 850 mm transpire. Transpiration was 3 mm/a during the wet season and 1.5 mm during the dry season. Rivers flow at a rate equivalent to 160 mm/a which represents a run-off coefficient of only 13 per cent.

Litter fall and decomposition

92 per cent of the miombo species are deciduous and the annual leaf-fall of the tree and shrub layers is 2.5–3.4 t/ha of dry matter, with an average of 2.9 t/ha. This represents 68 per cent of the total litter (table 15).

TABLE 15. Variations in litter fall (dry matter in g/m^2) in the Kaspa miombo (1968–1973).

Year	Leaves	Flowers and fruits	Wood	Total
1968	261.0	9.9	96.7	367.6
1969	338.5	26.8	78.7	444.2
1970	295.0	19.5	84.9	399.4
1971	307.5	11.4	86.1	405.0
1972	255.5	201.0	90.6	546.8
1973	271.1	37.3	85.6	394.0
Average	288.1	51.0	87.1	426.2

In 1973, a study of the litter fall gave the following percentages:

leaves	68.1	scales and buds	0.45
fruits	6.7	wood (diameter <1.5 cm)	17.3
flowers	2.2	wood (diameter >1.5 cm)	2.7
lichens	0.03	bark	1.5
fungi	0.04	dead animals	0.4
mosses	0.01	excrements	0.7

The contribution made by large branches is being studied. Flowers and scales contribute little, but a large number of species have heavy fruits. The litter on the ground is highest during the early wet season (4.4 t/ha) and minimal during the cold dry season just after burning (1.6 t/ha) and before the leaves dried by the fire begin to fall; the average is 3.3 t/ha/a.

Litter decomposition is performed by three principal agents: micro-organisms, termites and fire. Soil micro-organisms show a relative homogeneous spatial distribution and a well-defined seasonal periodicity. However, the rate of decomposition of the leaves of different species varies greatly; those which are slowly decomposed protect the soil from the first showers at the beginning of the wet season and slow down erosion; they seem to occur more frequently in the miombo than in tree savannas.

Termites (table 16) are very active except during the hot dry season, when the fires are most destructive. The activity of the latter takes over that of insects.

Three diet patterns can be distinguished among termites: humivorous, lignivorous and mixed. The humivorous genera (*Cubitermes*, *Anoplotermes*, *Crenitermes* and *Basidentermes*) excrete organic compounds that are more resistant to degradation by physico-chemical agents and bacteria. The lignivorous termites (*Microcerotermes*, *Amitermes* and the Macrotermitinae in general) eat dead intact plant material; their superficial attacks are particularly spectacular and their densities may exceed 15 000/m^2.

The coefficient of decomposition k (see chapter 13) varies between 1.32 and 1.11 according to whether or not fire has occurred. The cumulative effect of termites and fire doubles the speed of litter decomposition.

Biogeochemical cycles

Biogeochemical cycles have not been studied but preliminary chemical analyses suggest:

— the leaves of the main species show little difference in macro-elements composition (in per cent of dry weight): N=1.5–2.9; K=0.6–1.2; Ca=0.16–0.90; P=0.07–0.15; Mn=0.05–0.32; Fe=0.013–0.027; Na, Cu and Zn = traces;

— one-year-old branchlets and roots have fairly similar amounts (N=1.3–1.6) which are higher than those of the trunks and large branches (N=0.4–0.6).

Ernst (1975) has studied the variation of the mineral content of tree leaves in a Rhodesian miombo located at Warren Hill (17° 50′ S, 30° 57′ E), during the main wet season. Mean results for the dominant trees (*Brachystegia* spp. and *Julbernardia* spp.) were 3.89 of ash (per cent of dry weight) and 524 (Ca), 150 (Mg), 78 (K), 19 (Na), 10 (Mn), 52 (P) and 28 (Cl) μg/g of dry weight Three dominant trees were surveyed from the time of flushing to that of shedding. With the exception of iron, manganese and sodium, they seemed to be able to similarly accumulate mineral elements, but young leaves were richer in nitrogen, phosphorus and potassium than mature ones, whilst the concentrations of aluminium, calcium, iron, manganese and sodium increased until abscission.

Freson (1974) has shown that the mineral output by rivers was *ca.* 124 kg/ha/a.

The study of biogeochemical cycles should be undertaken as soon as possible; a separate and detailed study should be made of the nitrogen cycle, because of its agricultural importance.

TABLE 16. Abundance and biomass of the main groups of soil fauna in the Zairian miombo (Goffinet, 1973a and b, 1975).

	Density (individuals/m²)	Biomass (dry weight, mg/m²)
Protozoa (testaceous Rhizopoda)	1.44×10^6	—
Acarida	81 514	30.92
Collembola	14 531	14.70
Protura	213	—
Diplura	206	—
Thysanura	1	—
Pauropoda	1 882	—
Symphylans	90	—
Homoptera (larvae)	1 985	—
Oligochaetae (worms)	10	225.69
Molluscs	rare	negligible
Isopoda	rare	—
Pseudo-scorpions	5.21	—
Araneidae	11.83	47.55
Chilopoda	4.71	10.04
Diplopoda	4.17	71.24
Isoptera { hypogeous termites	469.92	lignivorous 60
Isoptera { epigeous termites		humivorous 250
— lignivorous (*Macrotermes*)*	± 200	950
— humivorous (*Cubitermes*)	860	490
Embioptera	0.54	0.39
Dictyoptera	5.17	29.41
Dermaptera	0.46	—
Orthoptera	2.17	22.66
Formicidae	390.92	31.23
Homoptera (adults)	9.17	45.17
Thysanoptera	38.46	0.09
Psocoptera	10.25	0.07
Holometabolic larvae	69.17	263.97
Coleoptera (adults)	21.29	71.37
Carabidae		7.47
Tenebrionidae		1.02
Lagriidae		5.12
Elateridae		0.14
Curculionidae		0.09
Scolytidae		0.38
Staphylinidae		2.33
Scarabaeidae		49.23
Other families		5.59

* Approximative value on the basis of 2 million individuals per nest of *Macrotermes falciger*.

Man-made modifications

The regressive succession

The miombo is generally not considered as a climatic climax, but is a fire climax. The climatic climax is the very rare and disappearing dense dry forest called muhulu. Its detailed study is therefore urgent. Wood cutting and fire have changed it into miombo woodland; and this fire climax still covers 85 per cent of Upper Shaba but it is being replaced by savannas.

The dense dry forest is a closed vegetation type with several strata; most of the trees in the upper layers lose their leaves for a very short period; the understorey is evergreen or deciduous and the grass cover is discontinuous. The savanna consists of grasses reaching 1.1 m in height, with scattered shrubs.

The characteristics of the three stages of such a regressive series (dense dry forest—open woodland—savanna), often called the muhulu—miombo—savanna regression, are shown in table 17.

Savanna formation increases the mean annual temperature, its mean daily amplitude, and decreases the relative humidity. Such changes, on a large scale, may modify the regional climate and the water balance. Moreover, the savanna protects the soil less than the forest and woodland. For a territory mainly covered by woodland, the minerals exported are *ca.* 125 kg/ha/a; they could increase as a result of the progressive extension of anthropic savannas.

The comparative study of the three stages in the regressive series would provide very useful information for the management of dry tropical regions. The role of litter, the evolution of the soils, the water balance and the biogeochemical cycles, should be the primary themes. In spite of their small area, the remaining muhulu require immediate study and protection.

E. umbellata, *E. camaldulensis*, *E. citriodora*, etc.) have been used in experimental plantations and although the best species may not yet be clear, the beneficial results of *Eucalyptus* on a carbonized surface is confirmed. The plantations always yield >300 m³/ha at 25 years and sometimes

TABLE 17. Ecological characteristics of dry dense forest, woodland and savanna in Upper Shaba (modified from Freson *et al.*, 1974).

	Dry dense forest	Woodland	Savanna
CLIMATE			
Mean annual temperature (°C)*	19.2	20.6	22.1
Mean daily amplitude (°C)*	10.4	16.5	20.8
Solar radiation at 1.3 m (per cent of external)	2.3	26.8	100.0
Throughfall (per cent of rainfall)	57.7	78.8	100.0
Mean annual relative humidity (per cent)	81.7	71.8	64.0
SOIL			
Depth of A_1 (cm)	5–10	2–3	0–1
pH (A_1)	4.2	5.3	5.9
Mean annual humidity (per cent) at:			
10 cm	27.6	16.7	18.7
25 cm	24.4	17.9	17.2
50 cm	21.8	18.0	18.6
100 cm	21.3	19.2	19.4
VEGETATION			
Height (m)	18–22	14–17	1.1–5
Species diversity**	105	480	330
Number of woody plants/ha	8 500	500–900	30–70
Basal area at 1.3 m (m²/ha)	35–45	15–25	0.5
Total dry weight biomass (t/ha)	320	150	10

* soil, screened temperature.
** number of phanerogams in whole flora.

Forestry

The soils of woodlands are relatively poor and are unsuited for permanent agriculture, and require considerable vegetation cover to protect them from erosion and degradation; they should remain under forest land-use. Foresters have therefore tried to adapt techniques in order to manage such immense areas.

The natural forest may be enriched by the introduction of indigenous or introduced species (Schmitz, 1959). The experiments on indigenous species generally failed and only two exotic species (*Cupressus lusitanica* and *Callitris* sp.) gave acceptable results and these required protection against fire for several years.

Coppice growth may be stimulated by mechanically clearing at ground level and burning the material as small heaps in order not to kill the stumps. This encourages the production of dense regeneration except on the small burning sites. Early burning is carried out until the coppice regrowth is high enough to shade out the grasses. Later thinning improves the production of the best stems. After 20 years girth increase decreases. Further experiments on this method are necessary.

Several species of *Eucalyptus* (*E. saligna*, *E. maculata*,

exceed 500 m³/ha (Schmitz, 1969). The natural coppice, which needs the same care as the stands enriched with *Eucalyptus*, only produces a quarter of this. At twelve years of age, one hectare of seedlings can produce 6 tons of charcoal.

Pinus kesiya shows rapid growth, a relatively dense cover in young formations and reaches adult height in 4–5 years. It has a fairly straight trunk, but often shows a curve at the base. *P. insularis* has equal growth, straighter trunks and no basal curve, but its cover is less dense. Together with the very fire sensitive *Cupressus lusitanica*, these are the three conifers that are best adapted to local conditions.

The role of fire and protection against it are controversial topics. Experiments made by Delvaux (1958) and observations of Symoens and Bingen-Gathy (1959) suggest that the productivity of protected plots is higher than that of early burnt plots. But an accidental fire in protected areas causes considerable loss and the yield is then less than that of early burnt area. Moreover, early burning is better than protection for the rapid selection of the best elements of the stand. It is always possible to change from early burning to protection; the reverse is not possible. The high tolerance of certain pines and eucalypts to fire could be improved by early burning; the obsession of fire would thus be eliminated and an acceptable rate of wood production would be obtained.

Charcoal, which has been produced from miombo for a long time has given rise to industry and commerce. The needs of the mining towns of Shaba grow and thousands of uncontrolled people are deforestating the region. All charcoal for domestic use is provided by traditional exploitation using the forest stack method. The stack capacity is normally 20 m^3 but may reach 60 m^3. In spite of its low yield (a maximum of 17.5 per cent of the wood weight is carbonized), it meets the consumer's demand which is much more for easy use than quality.

Unfortunately, traditional scattered cutting and defective regrowth on huge areas is disastrous. After cutting, the forest is scattered with clearing where grass and a few worthless trees grow. Thus the derived savannas spread progressively and these at best, under present conditions, could evolve only into wooded savannas.

Pastoralism

The best fodder species are the grasses *Setaria thermitaria* and *Brachiaria brizantha*, and several leguminous species of *Indigofera*, *Crotalaria*, *Eriosema* and *Vigna*. These species are rarely abundant and the low palatability would dictate a carrying capacity of one head of cattle per fifteen hectares at least.

During the dry season the cellulose content of the grass increases whilst the protein content decreases. Hence, the need for early burning and supplementary feeding by silage. For a Zambian miombo, Rees (1974) suggests cutting down the trees and shrubs at ± 1.2 m height (the chitimene system). The stumps produce numerous shoots during the dry season and their young leaves, containing four times the protein of the grass layer, are browsed by cattle. Grazing will change the flora and experiments are needed for the introduction and extension of cattle-raising.

Glossina morsitans, the vector of trypanosomiasis is not found in the grass savannas of the high Shabian plateaux which are the zones of cattle-breeding. The present prohibition of hunting, in as much as it is respected, should allow large mammals to re-establish and trypanosomiasis to spread, although most workers now conclude that the control of large wild mammals has no effect on tsetse in savanna areas.

Any livestock scheme necessitates dips twice a month to protect against ticks which carry anaplasmosis, piroplasmosis, etc. Hence cattle should not wander for more than 10 km from a central point.

Miombo contains several plants that are poisonous to cattle and poisoning is fairly frequent at the beginning of the wet season. A list of these plants is required, and botanical and toxicological research is urgent. *Buphane disticha* and *Gnidia kraussiana* are the two main species responsible for lethal poisoning. Poisoning was also observed after the cattle have eaten *Gloriosa superba*, *Peucedanum wildemanianum* and *Urginea altissima*, and various *Moraea* spp. The elimination of underground organs of toxic plants is the only way of avoiding fatal accidents; the uprooting of bulbs and rhizomes is a lengthy task, but possible over small areas (the case of a society that destroyed 20 000 bulbs in Shaba has been recorded). Such an operation remains problematical for large areas.

Traditional use

Miombo also provides food, medicinal, ichthyotoxic plants and fibres; meat and livestock products. The miombo of the

TABLE 18. Food value of some Zairian miombo products (after Heymans *et al.*, 1970; Thoen *et al.*, 1974).

	Water (%)	Dry matter (%)	Percentage of the dry weight					
			Ash	Lipids	Nitrogen	Protein	Fibre	Calcium
Cantharellaceae								
Cantharellus spp.	89.2	10.8	12.0	6.6	3.0	19.0	4.9	—
Amanitaceae								
Termictomyces spp.	87.8	12.1	8.8	4.1	6.3	39.1	7.0	—
Boletaceae								
Boletus granulatus	85.5	14.5	4.5	4.7	3.1	19.5	9.6	—
Tricholomataceae								
Schizophyllum commune	35.0	65.0	3.0	0.5	2.7	17.0	4.0	—
Russulaceae								
Lactarius spp.	89.3	10.7	7.0	6.7	3.6	22.7	7.2	—
Acrididae								
Homoxyrrhepes punctipennis	74.6	25.4	4.5	4.9	11.3	70.6	—	0.13
Notodontidae								
Elaphrodes lactea (dried caterpillars)	14.6	85.4	3.4	29.6	9.6	60.1	—	0.06
Termitidae								
Macrotermes sp. (soldiers)	66.0	34.0	6.8	5.3	9.8	61.3	—	0.17
Stenogyridae								
Achatina sp.	80.5	19.5	6.6	4.1	8.7	54.4	—	1.44

Lubumbashi region produces more than fifty edible plant species: berries of *Strychnos* and *Chrysophyllum bangweolense*; drupes of *Vitex*, *Parinari* and *Uapaca*; false fruit of *Ficus*, berry-like and fleshy fruit of *Syzygium* and *Aframomum*; flowers and seeds of *Sphenostylis*, aggregated fruit of *Annona*, tubers of *Dioscorea* spp. and certain orchids, bulbs of *Cyanastrum johnstonii*, young shoots of *Adenia gummifera* and *Pteridium aquilinum*. In addition there are more than twenty mushrooms. Besides wild meat, caterpillars, grasshoppers and termites are the insects that are most often eaten. Their food value (table 18) and their importance (Lambrecht and Bernier, 1953) have been defined.

Medicinal plants in Shaba have been listed and described by Schmitz (1967).

The miombo also produces ichthyotoxic plants (although some are not used as such in Shaba): *Pterocarpus angolensis*, *Strychnos innocua*, *Syzygium guineense*, *Ziziphus mucronata* subsp. *rhodesica* and *Balanites aegyptiaca*, the use of which has been noticed in Zambia and in Cameroon. *Diospyros mweroensis*, *Neorautanenia pseudopachyrhiza*, *Gnidia kraussiana* and *Euphorbia* cf. *ingens* are used in the Zairian miombo. *Diospyros mweroensis* (katula) is the wild plant that is most used, with the cultivated *Tephrosia vogelii* (buba), second.

The inventory and study of the food value of animal and plant products should be continued. A list of medicinal and ichthyotoxic plants should be made giving the vernacular and scientific names as well as determining the active chemicals. This would be a valuable guide for selecting species on which a thorough phytochemical study should be undertaken.

Research needs and priorities

Woodlands cover 12 per cent of Africa and represent one of the most important of its plant formations. Miombo is the major woodland type. This ecosystem has been the subject of multidisciplinary study in Zaire but several gaps remain and it is necessary to continue research.

The first area of study should be its structure and function, the degree of modification it can tolerate, and its ability to reach equilibrium. It is necessary to determine the productivity of the main plant species, including the roots; the composition and role of the various groups of animals, notably the ants, grasshoppers, birds and termites. The incidence of various types of fire should be further specified as should the biogeochemical cycles which will indicate ways of improving the ecosystem.

A second area of study is towards a more rational land use. It is therefore necessary to map the different types of vegetation in Upper Shaba and to determine more precisely the factors which control its various facies, and especially the relationships between soil and vegetation. Research is necessary on the two possible fundamental options: forestry and grazing. Forest development implies controlled felling and a better knowledge of natural regeneration and planting of indigenous and exotic species, including fruit trees like mango and guava. Grazing implies the increase of cattle health, improving the food during the dry season, reducing the frequency of dip treatments and delimiting areas cleared of toxic plants.

The last area of study should be the history of vegetation and human activities in Upper Shaba. The long controversy as to whether dry forest is the climatic climax of Upper Shaba or an edaphic climax with a limited distribution, might be solved if areas of woodlands on various soils and at different stages of evolution could be protected and observed over fifteen years. An ecological study of the few remaining dry forest patches should be undertaken immediately. It should include the micro-climate, water balance, leaf-fall, accumulation and decomposition of litter, and soil characteristics. The flora inventory of Schmitz (1963) should be extended by phenological data. These dry forests should be protected as natural reserves.

The survey and evaluation of natural foods should include phenological and ecological observations which would allow an estimation of the maximum human carrying capacity in undisturbed miombo. This would tie in with research by the anthropologists of the National Museums of Zaire. In the same way an inventory of the medicinal and ichthyotoxic plants should be completed, giving their vernacular and scientific names, and their active chemicals when these have been elucidated. This work would be a valuable guide for selecting more detailed phytochemical studies. These two inventories should be completed rapidly, as the traditional knowledge is quickly being lost because of changing customs and migrations.

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