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STRUCTURAL DIFFERENTIATION OF CONTIGUOUS SAVANNA WOODLAND TYPES IN ZAMBIA

Différenciation de la structure pour divers types de savanes boisées contiguës.

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RESUME

La structure de la végétation ligneuse de peuplements contigus appartenant à différents types de savanes boisées a été étudiée en Zambie à deux sites représentatifs respectivement d'un climat plus humide et d'un climat plus sec.

Les variables structurales telles que la hauteur de la tige, la circonférence et la surface terrière ont été calculées et comparées pour les diverses parcelles expérimentales. La diversité spécifique et les facteurs qui influencent la distribution de la végétation aux deux sites sont discutés. Bien que la structure de chaque parcelle expérimentale se différencie significativement de celle des autes parcelles, la surface terrière fut utilisée pour classifier la végétation en savanes boisées et forêts claires. L'article met en évidence le mérite de l'utilisation de variables structurales quantitatives en vue de la différenciation des types de savanes boisées et forêts en Zambie.

ABSTRACT

The structure of different contiguous savanna woodland stands was studied at two sites representing a wetter and drier climate in Zambia. Structural variables, such as, stem height, girth and basal area were calculated and compared among the vegetation samples. Species diversity and factors that influence vegetation distribution at the two sites are discussed. Although the structure of each vegetation sample differed significantly from that of other samples, basal area was used to classify the vegetation types into savanna woodland and forest types. The paper demonstrates the merit of using quantitative structural variables in differentiating Zambia savanna woodland and forest types.

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INTRODUCTION

The nomenclature of Zambia savanna woodlands is largely based on native terminology. There are, for example, five traditionally recognized savanna woodlands in Zambia : chipya, miombo, kalahari, mopane and munga (TRAPNELL, 1953; TRAPNELL & CLOTHIER, 1957; FANSHAWE, 1971; EDMONDS, 1976). The term miombo refers to one or more of the species of *Brachystegia*, *Julbernadia* or *Isoberlinia* (MALAISSE, 1978) while mopane refers to *Colophospermum mopane* and munga, to the species of *Acacia*. Kalahari woodland refers to the woody vegetation that covers the extensive wind-deposited sands in westerne Zambia that form part of the Kalahari desert soils of South-West Africa. Chipya is a chibemba term that describes a habitat in which dry-season fires are fierce. Chipya woodland is, therefore, a fire-tolerant pyrophilous vegetation.

FANSHAWE (1971) has discussed the derivation of savanna woodlands in Zambia. Apparently, on Kalahari sands of western Zambia, the partial destruction of dry forests leads to kalahari woodland invasion; but elsewhere this leads to invasion by miombo woodland. The complete destruction of forests, however, leads to regressive chipya woodlands (FANSHAWE, 1971; LAWTON, 1978). It is generally accepted that fire and man have played important roles in forest destruction in Zambia and, therefore, in the initiation of the regressive process from forest to chipya, miombo and kalahari savanna woodlands.

LAWTON (1978) developed a scheme, based on ecological species groups, for describing the dynamic relationships between forest and woodland vegetation types in north-eastern Zambia. However, this scheme cannot be rigidly applied because the responses of most Zambia savanna woodland species to environmental factors, in both time and space, are still poorly understood. For example, there is inadequate quantitative evidence about intrinsic and extrinsic factors that determine the structure and distribution of Zambia savanna woodland species.

A significat contribution to the understanding of structural and spatial differentiation of savanna woodlands and their determinants could be made through the study of contiguous savanna vegetation types which experience similar, although not necessarily the same, environmental conditions. The present study investigated contiguous savanna woodland types at two sites with the object of determining structural characteristics that distinguish these vegetation types and factors that contribute to the spatial differentiation of these woodlands. The nomenclanture of trees follows WHITE (1962).

STUDY SITES AND SAMPLING METHODS

The study was conducted at Nkolemfumu site which is located at latitude 10° 26' south and 31° 11' east in Kasama district of Northern Province and Chunga site at 15° 02' south and 25° 59' east in Mumbwa district of Central Province. At both sites, the rainy season lasts from November to April. Nkolemfumu site is within a 122-132 cm per annum rainfall belt while Chunga site is in the 91-102 cm rainfall belt. The Nkolemfumu site, therefore, represents a wetter climate while Chunga is a drier climate site.

The land at both sites is flat with a slope of less than one degree. Nkolemfumu site is within the Bangweulu-Chambeshi land region of MANSFIELD *et al.* (1976) which has highly leached sandy soils with a low cation-exchange capacity of 117-409 kg per ha. The soil pH is 4.0-5.5 with an organic carbon content in the top 10 cm of the profile ranging from 0.23-5.72 % (MANSFIELD *et al.*, 1976).

The Chunga site, on the edge of the Kafue flood-plain in the Kafue National Park, has two distinct soil types. Part of the site has a sandy soil belonging to the kalahari contact soils of TRAPNELL & CLOTHIER (1957) with a pH of 5.3-6.5. These soils are pale-coloured and leached with a low productivity. Part of Chunga site is covered with clay alluvium. This clay soil is part of the flood-plain soils that are highly siliceous which accounts for the great shrinkage, swelling and deep cracking in the dry season of this soil. The clay is base rich with pH 6.2-9.0 and a pronounced horizon of calcareous concretions, sometimes with magnesium, calcium and sodium salts in the subsoil (TRAPNELL & CLOTHIER, 1959). The soil is hard when dry and extremely plastic when wet with a low permeability. Apparently the organic and nitrogen content of this clay alluvium is very similar to that of the adjacent sandy soils (TRAPNELL & CLOTHIER, 1957).

According to the vegetation types of FANSHAWE (1971), Nkolemfumu site is covered with miombo and chipya savanna woodlands. The chipya woodland has relatively dense and tall (up to 1.5 high) bunch grasses which typify chipya habitats. The adjacent miombo woodland has sparse and short (under 0.5 m high) grasses and herbs. The miombo woodland at Nkolemfumu is characterized by the presence of *Brachystegia spiciformis*. The sandy protion of the Chunga site is covered with miombo

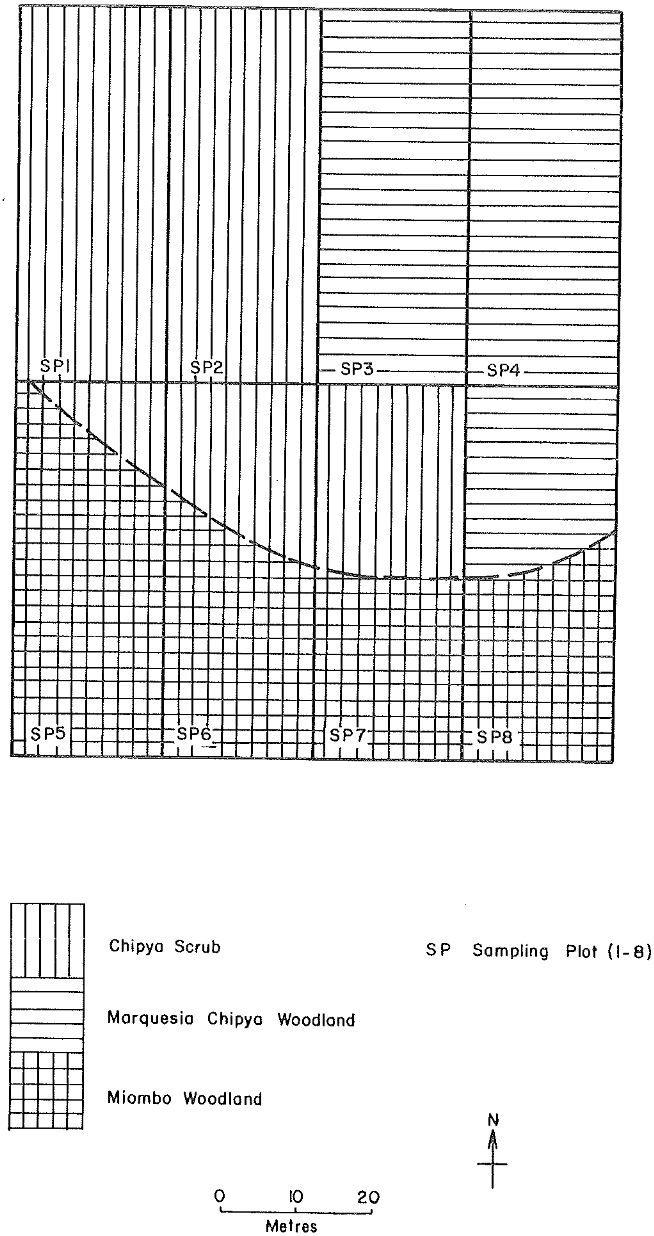

Fig. 1 : Distribution of vegetation types at Nkolemfumu sample plots.

woodland with a herbaceous layer similar to that found in Nkolemfumu miombo woodland. Adjacent to the Chunga miombo woodland, is the munga woodland on clay alluvium. However, in spite of its name, the munga woodland had no *Acacia* species. The munga woodland portion of the site had been burnt at the time of sampling and the fire had left stems charred up to several metres high, perhaps indicating the intensity of munga woodland fires. FANSHAWE (1971) has described munga woody species as notoriously fire tolerant.

Sixteen woodland enumeration samples were obtained at Nkolemfumu and Chunga : eight samples at each site. Each sample plot was 20 X 50 m. At Chunga the eight samples were made up of two sets of four contiguous samples separated by a 5-m wide track. One set of the samples came from miombo woodland while the other set came from munga woodland.

At Nkolemfumu the vegetation boundary between chipya and miombo woodlands was irregular and sample plot boundaries did not coincide with the vegetation boundary (Fig. 1). Some vegetation samples, therefore, contained an admixture of chipya and miombo woodland components. Vegetation samples, therefore, were conveniently classified as (with sample plots in Fig. 1 in parentheses) : chipya scrub (1-2), *Marquesia* chipya (3-4), miombo (5) and chipya/miombo composite (6-8).

In each sample plot, all stems greater than 9 cm girth at knee height (about 0.3 m above ground) were identified, enumerated and girth at breast height (bh = 1.3 m above ground) measured and recorded. Branches of trees at or below knee height were enumerated separately. Stems were also classified into height classes : under 2 m, 2-5 m, 5-10 m and over 10 m. Samples were obtained in September 1983 at Chunga and in August 1984 at Nkolemfumu.

RESULTS

The stem height structure of samples is given in Tab. I. A pair-wise chi-square comparison of samples revealed no significant differences in stem height structures between the following sample pairs : (i) miombo at Chunga and Nkolemfumu (ii) chipya-miombo composite and munga, (iii) chipya - miombo composite and *Marquesia* chipya at P = 0.05. All the other sample pairs revealed significantly different stem height structures : $X^2 \geqslant 8.17$; $P \leqslant 0.05$.

Fig. 2 shows the stem gbh distribution patterns of the different

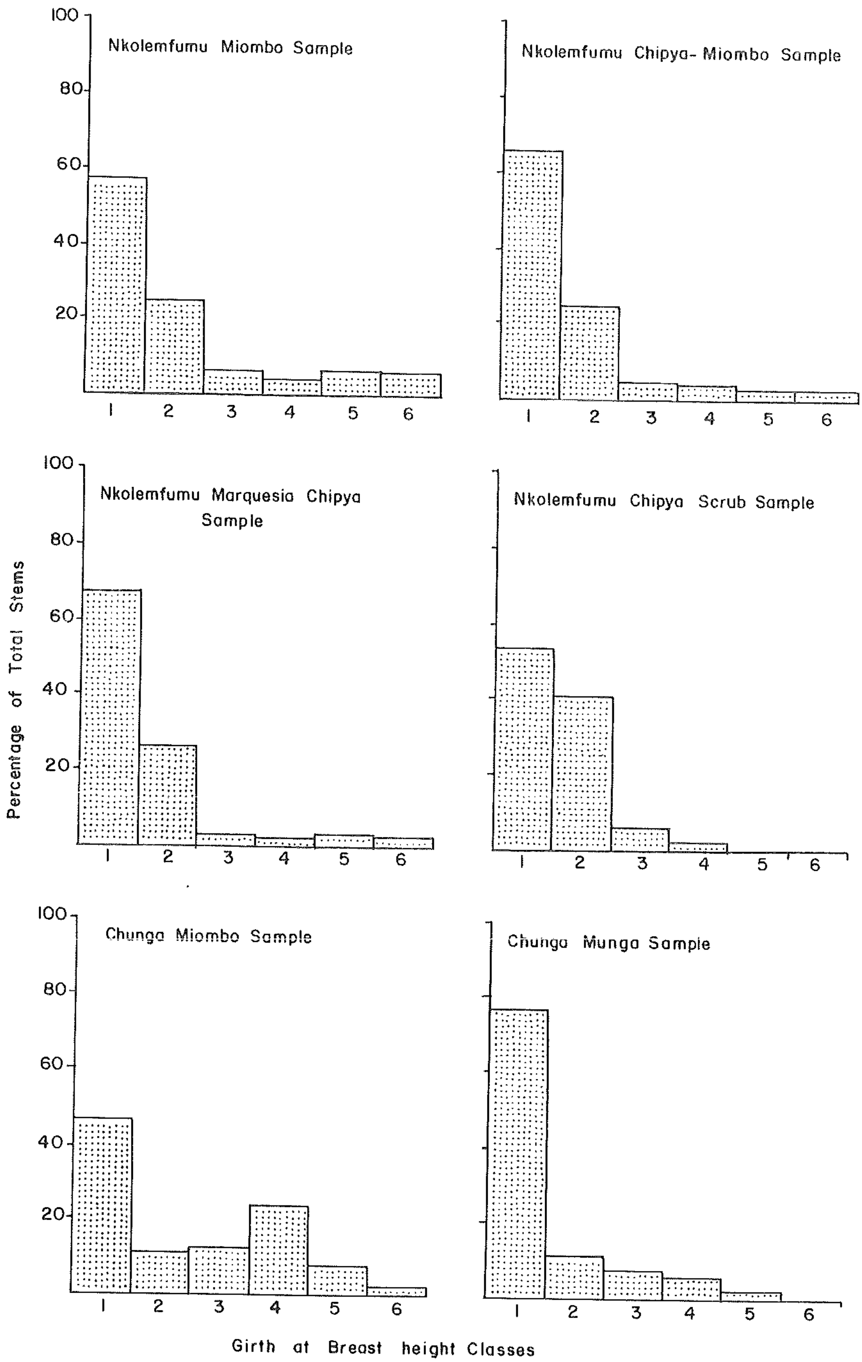

Fig. 2 : Distribution of stems by girth at breast height classes in vegetation samples. Girth classes are as follows : under 31 cm (1) 31-60 cm (2) 61-90 cm (3), 91-120 cm (4), 121-150 cm (5) and over 150 cm (6).

samples. Except for the miombo woodland sample at Chunga, all samples exhibited a reversed "J" distribution pattern in which the frequency of stems decreased with each successive higher gbh class. The Chunga miombo sample had two peak gbh classes : the under 31 cm gbh class and the 91-120 cm gbh class (Fig. 2). The pair-wise chi-square comparison between samples showed that all pairs of samples were significantly different in their stem gbh frequency distributions, except between chipya-miombo composite and *Marquesia* Chipya samples and the former and the miombo sample at Nkolemfumu (Tab. II).

Stem density was lowest at Chunga where this was estimated at 328 and 678 per ha in miombo and munga woodlands. At Nkolemfumu, estimated stem density of 725 per ha in chipya scrub was the lowest but ranged from 1,240 - 1,343 per ha in the other vegetation types.

The distribution of basal area at bh is given in Tab. III. The estimated basal area of 7.8 m^2 per ha in chipya scrub and munga samples was the lowest. The basal area in the miombo sample at Nkolemfumu was almost three times that observed in the miombo sample at Chunga. The *Marquesia* Chipya and the chipya-miombo composite samples at Nkolemfumu had basal area of 17.8 - 20.2 m^2 per ha which are intermediate between those observed in the miombo samples at Chunga and Nkolemfumu. Samples also differed in the relative distribution of basal area among stem gbh classes (Tab. III). Three classes of samples can be distinguished. Firstly, there are samples with a pronounced concentration of basal area in the largest gbh class, examplified by the miombo samples. Secondly, there are those samples with a lower concentration of basal area dominance by the largest gbh class as observed in the chipya-miombo composite, *Marquesia* chipya and munga samples. Thirdly, the chipya scrub sample in which there is a reduced basal area dominance among gbh classes but the concentration is in the medium stems (31 - 90 cm gbh class).

The number of species per sample plot was lowest at Chunga, where a mean of 9.6 species was recorded. But the mean number of 10.0 species per sample plot in the munga samples was slightly higher than that of 9.3 in the miombo samples. The total number of species recorded in miombo and munga woodlands at Chunga was 17 and 18, respectively.

At Nkolemfumu, the number of species per sample plot ranged from 12 - 26. The chipya scrub samples with 12 - 14 species per sample plot

Site	Sample plots	Woodland type	Sample stems	Percent distribution of stems by height classes			
				Under 2 m	2–5 m	5–10 m	Over 10 m
Chunga	1 – 4	Miombo	120	23.3	31.7	18.3	26.7
	5 – 8	Munga	266	29.0	49.2	15.0	6.8
Nkolemfumu	1 – 2	Chipya scrub	146	12.3	67.1	17.8	2.7
	3 – 4	Marquesia					
		Chipya	262	18.3	57.3	18.7	5.7
	5	Miombo	123	17.9	46.3	19.5	16.3
	6 – 8	Chipya–Miombo					
		Composite	408	20.3	56.1	15.7	7.8

Tab. I : Stem height distribution in contiguous woodland samples at Nkolemfumu and Chunga.

Site	Sample type	NKOLEMFUMU				CHUNGA	
		Miombo	Chipya-Miombo composite	Marquesia chipya	Chipya scrub	Miombo	Munga
Nkolemfumu	Miombo	–	6.62	11.18*	19.15*	25.23*	19.09*
	Chypia-Miombo composite		–	2.57	18.90*	74.70*	20.31*
	Marquesia chipya			–	15.39*	73.86*	22.18*
	Chipya scrub				–	59.39*	49.64*
Chunga	Miombo					–	45.86*
	Munga						–

Tab. II : Chi-square test between gbh structures of savanna woodlands at Chunga and Nkolemfumu study sites. Asterisked Chi-square values were significantly different form expectation at $P < 0.05$.

Site	Sample	Basal area (m^2) density		Percent basal area distribution by stem gbh classes		
		Per 0.10 ha plot	Per 1.00 ha (estimate)	Under 31 cm	31–90 cm	Over 90 cm
Nkolemfumu	Miombo	3.197	31.97	4.0	18.0	78.0
	Chipya-Miombo composite	2.024	20.24	9.2	27.0	63.8
	Marquesia chipya	1.781	17.81	12.3	31.5	56.2
	Chipya scrub	0.778	7.78	16.1	59.3	24.6
Chunga	Miombo	1.137	11.37	1.3	21.1	77.6
	Munga	0.780	7.80	10.6	42.0	47.4

Tab. III : Distribution of basal area at breast height in different vegetation samples at Nkolemfumu and Chunga.

was floristically the poorest and the chipya-miombo composite samples with 21 - 24 species per sample plot, the richest. Although the number of 26 species in one *Marquesia* chipya sample plot was the largest recorded but in another *Marquesia* chipya plot there were only 20 species. The miombo sample plot at Nkolemfumu had 22 species.

The majority of species (70-100 %) in all sample plots were represented by 10 or less stems per sample plot (Tab. IV). The highest concentration of stems in a single species was observed in chipya-miombo, *Marquesia* chipya, chipya scrub and munga sample plots. Miombo samples showed no such specific stem population concentration (Tab. IV).

Combretum sp. and *Grewia bicolor* were common understorey species in the Chunga woodlands. In addition, *Pseudolachnostylis maprouneifolia* and *Albizia antunesiana* in the munga and *Diplorhynchus condylocarpon* and *Burkea africana* in the miombo woodlands were also common. *D. condylocarpon, Maprounea africana, Ochna* sp., *Pterocarpus angolensis, Syzygium guineense* ssp. *macrocarpum* and *Viridivia suberosa* were abundant undersorey species in at least three vegetation samples at Nkolemfumu. *Uapaca kirkiana* and *Garcinia huillensis* were abundant in chipya-miombo composite sample plots, *Pericopsis angolensis* in miombo and *Marquesia* chipya sample plots and *Hymenocardia acida* in chipya scrub and *Marquesia* chipya sample plots.

The common canopy (over 10 m tall) species at Nkolemfumu were *B. spiciformis, Parinari curatellifolia, Combretum collinum* and *Marquesia macroura.* In the chipya scrub there were scarcely any stems over 10 m tall : the four canopy stems recorded in chipya scrub plots belonged to *P. curatellifolia, Burkea africana, D. condylocarpon* and *P. maprouneifolia*. In the Chunga miombo sample plots the abundant canopy species were *B. spiciformis* and *Julbernardia paniculata,* while *Pericopsis angolensis* was the common canopy species in the munga sample plots.

DISCUSSION

According to LAWTON (1978) the vegetation in north-eastern Zambia is primarily determined by the history of burning at any particular site, rather than by climate or edaphic factors.
However, rainfall and soil type may affect vegetation type and biomass. For exemple, the differences in basal area between miombo woodlands at

Site	Sample plot (0.1 ha)	Total species	Distribution of species by stems/species 1	2–10	11–20	21–30	31–50
Chunga	Miombo sample						
	1	8	50.0%	50.0%	0.0%	0.0%	0.0%
	2	8	37.5%	50.0%	12.5%	0.0%	0.0%
	3	11	27.3%	72.7%	0.0%	0.0%	0.0%
	4	10	50.0%	40.0%	10.0%	0.0%	0.0%
	Munga sample						
	5	7	28.6%	57.1%	0.0%	0.0%	14.3%
	6	9	33.3%	44.5%	11.1%	0.0%	11.1%
	7	13	46.2%	46.2%	7.6%	0.0%	0.0%
	8	11	27.3%	45.5%	18.2%	9.0%	0.0%
Nkolem-fumu	Chipya scrub sample						
	1	14	50.0%	42.9%	7.1%	0.0%	0.0%
	2	12	16.7%	66.7%	8.3%	0.0%	8.3%
	Marquesia chipya sample						
	3	20	25.0%	65.0%	5.0%	0.0%	5.0%
	4	26	30.8%	57.7%	7.7%	0.0%	3.8%
	Miombo sample						
	5	22	27.3%	50.0%	22.7%	0.0%	0.0%
	Chipya-Miombo composite sample						
	6	24	37.5%	54.3%	4.1%	0.0%	4.1%
	7	21	28.6%	57.1%	9.5%	0.0%	4.8%
	8	21	19.0%	52.4%	19.0%	4.8%	4.8%

Tab. IV : Species abundance at Nkolemfumu and Chunga sample plots. Species have been classified by number of stems per species.

Chunga and Nkolemfumu may be related to differential rainfall at the two sites because both sites have similar dystrophic soils.

The influence of soil type was clearly evident at Chunga where an abrupt vegetation boundary between miombo and munga woodlands coincides with the soil boundary. The munga woodland flourishes on the clay soil while miombo woodland grows on the sandy soil. Since both these soils are dystrophic (TRAPNELL & CLOTHIER, 1957), it is apparent that soil permeability and moisture stress determine the vegetation type at Chunga site. FANSHAWE (1971) considers that munga woodland is either biotically or edaphically controlled. Both impermeability of the soil and flooding tend to favour munga woodland in flat topography in the drier region of Zambia. However, even the distribution of certain miombo species is edaphically controlled. Studies by SAVORY (1963) showed that *B. spiciformis* prefers really deep soils ans is waterlogging intolerant. Thus the absence of *B. spiciformis* and perhaps *J. paniculata* on the clay soil at Chunga is directely related to the impermeability and waterlogging of the clay soil. Thus althouth most munga woodland species are fire tolerant (FANWHAWE, 1971) the fierce munga fires probably play a secondary role in the spatial distribution of munga and miombo woodlands at Chunga.

At Nkolemfumu there was no obvious soil difference between the traditionally recognized chipya and miombo woodlands, although the irregular vegetation boundary was also abrupt (Fig. 1), as was the case at Chunga site. However, in order to appreciate the determinants of vegetation distribution at Nkolemfumu, it is important to consider the autecology of some key species. LAWTON (1978) classified *D. condylocarpon, H. acida, M. africana* and *S. guineense* ssp. *macrocarpum* as typical chipya fire tolerant small trees. But he also included in the chipya species group *Burkea africana, Combretum collinum ; Erythrophleum africanum, Pericopsis angolensis* and *Pterocarpus angolensis* which occur in chipya habitats as coppice and/or large scattered trees. However, although *Parinari curatellifolia* exhibits similar growth forms in chipya habitats, LAWTON (1978) considered the coppice form of *P. curatellifolia* to belong to the chipya vegetation while its canopy form to belong to the dry evergreen forest where it occurs in association with *M. macroura* and *B. spiciformis*. The latter is also a member of the miombo woodland.

Species	Total stems	Under 31 cm	31-60 cm	61-90 cm	Over 90 cm
		Girth at breast height classes			
		Miombo sample			
B. spiciformis	18	27.8%	38.8%	16.7%	16.7%
M. macroura	13	38.5%	15.4%	15.4%	30.7%
P. curatellifolia	7	0.0%	0.0%	0.0%	100.0%
		Chipya-Miombo composite sample			
B. spiciformis	27	37.0%	29.6%	18.6%	14.8%
M. macroura	26	26.9%	30.8%	0.0%	42.3%
P. curatellifolia	2	0.0%	0.0%	0.0%	100.0%
		Marquesia chipya sample			
B. spiciformis	0	-	-	-	-
M. macroura	9	11.1%	33.3%	11.1%	44.5%
P. curatellifolia	6	0.0%	0.0%	0.0%	100.0%
		Chipya scrub sample			
B. spiciformis	0	-	-	-	-
M. macroura	0	-	-	-	-
P. curatellifolia	1	-	-	-	100.0%

Tab. V : Stem girth at breast height (gbh) structure of three canopy species at Nkolemfumu.

The burning experiments in miombo woodland at Ndola in the Copperbelt Province of Zambia showed that *P. curatellifolia* survives late dry season fires and is, therefore, considered to be a fire tolerant species (TRAPNELL, 1959). In contrast, *B. spiciformis* is fire intolerant and cannot withstand late dry season or fierce fire (TRAPNELL,1959). Little is known about the responses of *M. macroura* to burning, although it has generally been considered to be fire intolerant (TRAPNELL, 1959 ; LAWTON, 1978).

The stem gbh structure of the common canopy species at Nkolemfumu is given in Tab. V. Except for an old large *P. curatellifolia* stem (192 cm gbh) in the chipya scrub sample plots, this species, *B. spiciformis* and *M. macroura* were absent in chipya scrub. *B. spiciformis* was also absent in *Marquesia* chipya sample plots. Thus although *M. macroura* is said to be fire intolerant, this species was surviving in a chipya habitat at Nkolemfumu and was represented by all stem size classes. Within its range of distribution, *B. spiciformis* was also represented by all stem size classes at Nkolemfumu. Only *B. curatellifolia* was not regenerating at Nkolemfumu because it was only represented by large stems and yet this species is known to be fire tolerant and survives as coppice in chipya habitats (TRAPNELL, 1959; LAWTON, 1978).

There is no doubt that fire is a significant determinant in controlling vegetation distribution at Nkolemfumu, but it might not be the only determinant. It is suggested that the soil may also play an important role although direct evidence of this was not available. But the absence of regeneration in *P. curatellifolia* and the absence of *M. macroura* in chipya scrub cannot be adequately explained by the fire factor alone.

MALAISSE (1984) has used basal area to classify vegetation types as follows : savanna grassland (under 1 m^2/ha), tree savanna (1-5 m^2/ha), savanna woodland (5-15 m^2/ha), open forest (15-25 m^2/ha) and closed forest (30-40 m^2/ha). On this basis, the chipya scrub at Nkolemfumu and the miombo and munga woodlands at Chunga represent different savanna types, while the *Marquesia* chipya with a basal area nearly 18 m^2 per ha falls into the open forest with tall grass vegetation type. Only the *Brachystegia - Parinari - Marquesia* or miombo vegetation at Nkolemfumu with a basal area of about 31 m^2 per ha can be regarded as a closed forest type. This vegetation type has also been referred to as a dry evergreen forest by LAWTON (1978). Woody species diversity was also higher in the forest vegetation types than in the savanna woodland types (Tab. IV). Other structural attributes also showed that each of the vegetation types studies differed significantly from the others. This demonstrates the merit of using structural variables, such as, stem height, gbh and basal area in differentiating Zambia savanna woodland types.

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