

VARIATION IN TIME AND SPACE OF LEAF AREA INDEX IN A ZAMBESIAN
OPEN FOREST OF WETTER MIOMBO TYPE (LUBUMBASHI, ZAIRE)¹

Variation temporelle et spatiale de l'indice de surface foliaire d'une forêt claire
zambézienne de type miombo humide (Lubumbashi, Zaïre)

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RÉSUMÉ

Une forêt claire à Julbernardia paniculata et Brachystegia boehmii des environs de Lubumbashi a été étudiée pendant une année. Son indice de surface foliaire maximale est de 3,07 et le rapport entre valeur maximale et valeur minimal est de 3,72. Ces résultats sont discutés et comparés aux autres valeurs publiées pour les forêts tropicales.

ABSTRACT

An open forest dominated by Julbernardia paniculata and Brachystegia boehmii has been observed for twelve months. Maximum value of L.A.I. is 3.07, ratio between maximum and minimum is 3.72. These results are discussed as compared with other values available for tropical forests.

INTRODUCTION

Data available regarding leaf area index (L.A.I., i.e. the ratio of total leave surface - one side - of plants of a plot to the plot's surface) of tropical forests have been discussed recently by ALEXANDRE (1981) on the basis of a literature analysis. This author distinguishes four different approaches (optimal means, leaf biomass, allometric methods and results derived from litterfalls) and considers that the L.A.I. of tropical rain forests seems fairly constant and can be assigned a maximal annual value of 8.2, whilst structural heterogeneity and seasonality are important sources of variability.

¹ Note 61 of the "Contribution to the study of the open forest ecosystem (Miombo)"

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Lastly the analysis of ALEXANDRE (1981) pinpoints the variation of specific leaf surface according to their position in crown (KATO *et al.*, 1978) and the consequently importance of sampling. The lack of seasonal or monthly values of L.A.I. appears clearly, with the exception of two measurements conducted by GOLLEY and its team at Panama, respectively during dry and rainy season (GOLLEY *et al.*, 1975). Recently bimensual values of L.A.I. have been published for a Zambezian dry evergreen forest (MALAISSE, 1984).

The woodlands, which cover 2,864,650 km² or 9.1 % of Africa in the Zambezian region alone, according to the A.E.T.F.A.T. map (WHITE, 1981) are found in no less than 8 countries (Angola, Zambia, Mozambique, Tanzania, Zaire, Zimbabwe, Malawi and Burundi). In the Zambezian region four main types of woodlands may be recognized, namely :

	Area (km ²)	% age of the Zambezian region
Wetter Zambezian miombo open forest	1 239,975	33.35
Drier Zambezian miombo open forest	730,875	19.66
Colophospermum mopane woodland	354,900	9.54
Undifferentiated open forest and woodland	538,900	14.49
North Zambezian	(247,500)	(6.65)
South Zambezian	(136,575)	(2.89)

The wetter Zambezian miombo open forest ecosystem has been the subject of many studies, which have been reviewed recently (MALAISSE, 1978). Although data relating to leaf size, anatomy, sclerophyllly and light troughfall (MALAISSE *et al.*, 1982; VAN DER MEULEN & WERGER, 1984), to leaf biomass (MALAISSE *et al.*, 1972) and to litterfall (MALAISSE *et al.* 1975) are available, data on the leaf area index are lacking. This paper proposes to remedy this deficiency.

MILIEU

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 differences occur from year to year (716 to 1.758 mm). Half the daily precipitations are less than 5 mm, but these represent less than 10 per cent of the total 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 rainy 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 minima 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.

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.

Observations were made in the Miombo at the Kasapa, an open forest dominated by *Julbernardia paniculata* and *Brachystegia spiciformis*, 9 kms NE of Lubumbashi, and whose floristic composition (MALAISSE & MALAISSE-MOUSSET, 1970) as well as its transect (MALAISSE, 1976) have been described elsewhere.

METHODS

We have distinguished between the woody layers (tree and shrub layer) and the grass layer. The methods used differ according to the layer studied.

Woody layers

Several methods were used. They differ according to the composition of the open forest; namely monospecific type composed of diverse *Brachystegia*, notably *B. boehmii*, and mixed open forest where numerous tree species are observed.

Monospecific type : On a plot almost entirely dominated by *Brachystegia boehmii*, an average tree was chosen. It was felled and various characteristics were established, among which the total number of leaves. The total leaf area is deduced from density per hectare of trees in relation to the average specimen chosen.

Mixed type : A plot of 25 m x 25 m was chosen for study purposes. During the rainy season, the total number of leaves of each individual in the woody layers was established by a continual count of each of the branches. This work was undertaken

from ground level for shrubs and small trees, and by climbing into the canopy for trees. These values are used to establish the leaf area.

Several methods were proposed for the estimation of leaf area, namely photoplaniometry (VAN SEVEREN, 1969), planimetry by correlation which consists in establishing linear regression equations based on the product of the lamina's length x width and the comparison with standards (leaf image) (HELLER, 1971). We proceeded as follows. Leaves were collected at random at different heights of the crown foliage. In the case of compound leaves, on a sample of 1000 leaves, we firstly established the average number of leaflets. Then, for simple leaves and for leaflets, we established a diagram covering the frequency of the length relationship of the lamina from a sample of 500-1000 leaves, taking into account the variability of these dimensions. Figure 1 shows the stereogram thus obtained for *Parinari curatellifolia*.

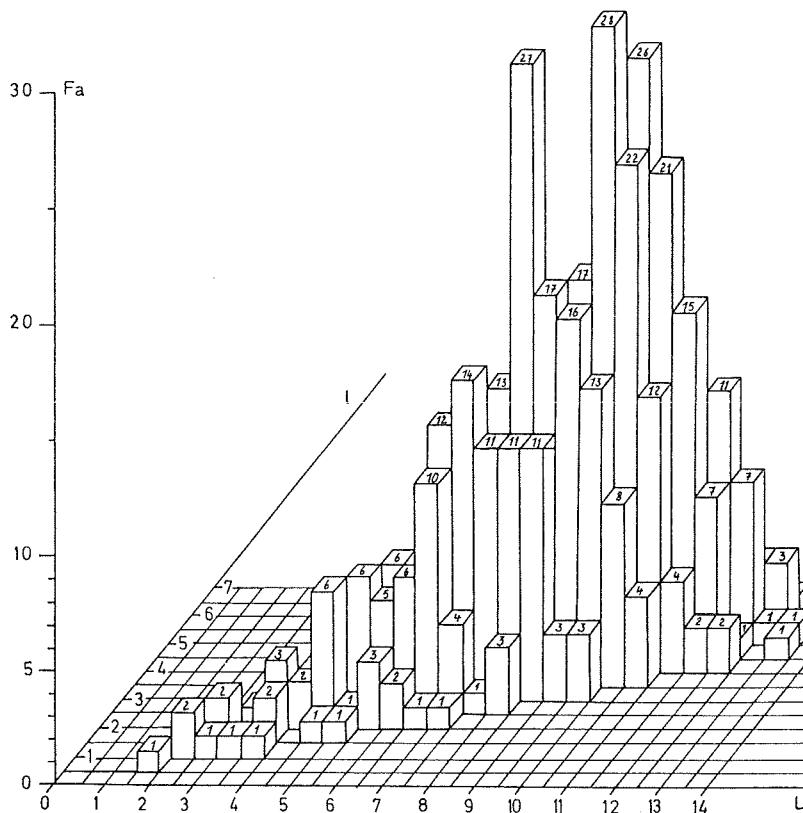


Fig. 1 : Stereogram obtained for 500 leaves of *Parinari curatellifolia* from the Kasapa miombo open forest.

The average area of each cell in the bivariata frequency table is calculated either by planimetry (in the case of irregularly shaped leaves) or by assimilation (with, in general, a correction factor) for simple geometric forms, mainly an ellipse. From this last value and the number of the cell we deduce the mean area of the lamina for each of the species considered. For vertical repartition, the leaf numbers per metre height was established for each individual. We did not take into account an eventual difference in leaf size according to position in the canopy.

For time variation, for each species, all the leaves on several test branches were counted on the 1st and 15th of each months. The values obtained on February 1st act as a reference. For species that lose all their leaves, this method presents no difficulties, as long as it is used from one defoliation period to the next. For evergreen species it is necessary to adjust the results. In the budding period, the mean leaf area was established each week.

Grass layer

20 plots of 1 m² were sample each week. They were sorted into biomass and necromass as well as into monocotyledons and dicotyledons. The leaf area of a fresh sample of material collected towards the middle of the months was mesured and afterwards dried, and this ratio matched with weekly dry matter weight for the two biomasses respectively.

RESULTS

A. Woody layers

Monospecific type

The quick method used allowed us to establish a preliminary estimation for the main rainy season (MALAISSE *et al.*, 1972), i.e. 2,129,000 leaves of *Brachystegia boehmii* per hectare, this forming 2,600 kgs dry of matter and a leaf area index of 3.47.

Species	Total number of leaves	Mean weight (g dry matter)	Biomass (g dry matter)	Average area of one leaf (cm ²)	Leaf area (m ²)
1. <i>Albizia adianthifolia</i>	3 909	1.304	5 097	218.19	85.29
2. <i>Anisophyllea boehmii</i>	31 183	0.130	4 054	15.42	48.08
3. <i>Baphia bequaertii</i>	8 794	0.272	2 392	30.34	26.69
4. <i>Brachystegia boehmii</i>	16 663	2.129	35 476	235.13	391.79
5. <i>Brachystegia spiciformis</i>	27 674	1.089	30 137	109.94	304.25
6. <i>Diplophyllum condyllocarpum</i>	1 995	0.217	433	19.54	3.90
7. <i>Ficus deltoidea</i>	6 545	0.239	1 564	14.70	9.62
8. <i>Jubaea chilensis</i>	26 287	0.207	53 547	243.66	640.50
9. <i>Monotes africanus</i>	34 261	0.103	3 529	23.97	82.12
10. <i>Monotes katangensis</i>	4 788	0.825	3 950	41.24	19.75
11. <i>Ochna schweinfurthiana</i>	4 071	0.311	1 266	17.86	7.27
12. <i>Parinari mobola</i>	29 535	0.394	11 637	29.48	87.07
13. <i>Pavetta schumaniana</i>	4 178	0.137	572	14.23	5.95
14. <i>Pericopsis angolensis</i>	751	0.855	642	132.14	9.92
15. <i>Pterocarpus angolensis</i>	884	2.242	1 982	178.09	15.74
16. <i>Schwarztzia madagascariensis</i>	3 184	0.948	3 018	89.87	28.62
17. <i>Syzygium macrocarpum</i>	7 623	0.580	4 421	34.07	25.97
18. <i>Tapinanthus erianthus</i>	1 725	0.120	207	6.04	1.04
19. <i>Uapaca kirkiana</i>	575	1.143	657	127.89	7.35
20. <i>Uapaca nitida</i>	3 714	0.601	2 232	44.83	16.65
21. <i>Uapaca pilosa</i>	812	0.999	811	183.19	14.88
Total for the experimental plot (1/16 ha)	219 151		167 625	1 832.45	
Values per hectare		3 506 416	2 682 003		
				29 319.04	

Table I : Numbers of leaves, leaf area and leaf biomass of the Kasapa miombo (February, 1977).

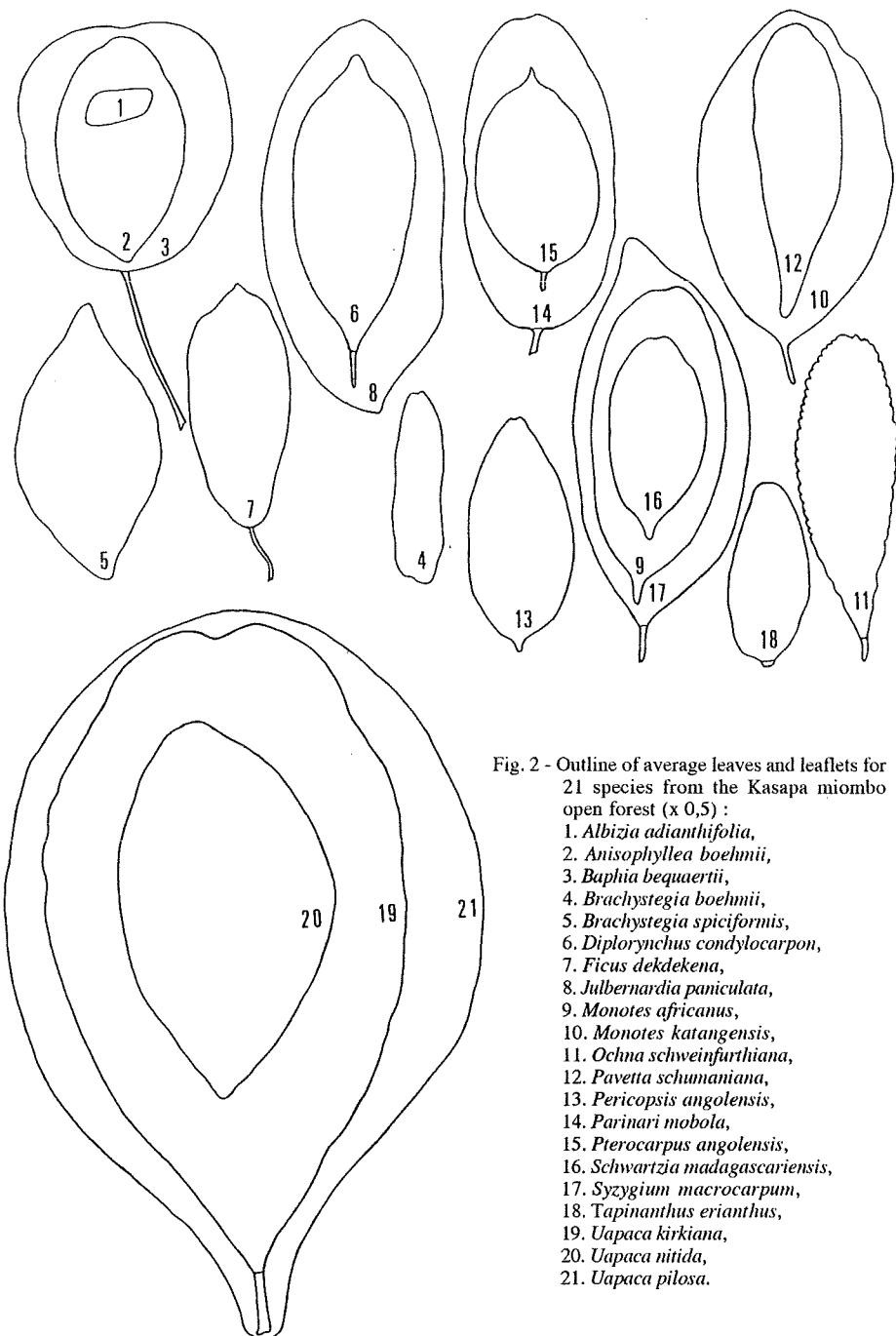


Fig. 2 - Outline of average leaves and leaflets for 21 species from the Kasapa miombo open forest (x 0,5) :

- 1. *Albizia adianthifolia*,
- 2. *Anisophyllea boehmii*,
- 3. *Baphia bequaertii*,
- 4. *Brachystegia boehmii*,
- 5. *Brachystegia spiciformis*,
- 6. *Diplorynchus condylocarpon*,
- 7. *Ficus dekkdena*,
- 8. *Julbernardia paniculata*,
- 9. *Monotes africanus*,
- 10. *Monotes katangensis*,
- 11. *Ochna schweinfurthiana*,
- 12. *Pavetta schumaniana*,
- 13. *Pericopsis angolensis*,
- 14. *Parinari mobola*,
- 15. *Pterocarpus angolensis*,
- 16. *Schwartzia madagascariensis*,
- 17. *Syzygium macrocarpum*,
- 18. *Tapinanthus erianthus*,
- 19. *Uapaca kirkiana*,
- 20. *Uapaca nitida*,
- 21. *Uapaca pilosa*.

Mixed type

The experimental plot contained 21 species. Table I presents the leaf number, biomass and leaf area in February in the Kasapa miombo open forest. The outline of leaf and leaflet corresponding to the mean area of each of the 21 species is drawn in Figures 2. Figures 3 and 4 sum up the results obtained for total leaf area for the woody layers. They show that in vertical distribution, the tree layer is not easily distinguished from that of shrubs. This is due to the existence on the Kasapa site of tall and medium trees in the tree layer, and of the growth of several stems out of the shrub and into the tree layer.

The diversity of the shrubs of 1 to 5 metres height is however clear. Figure 4 which shows the variation of leaf area in the woody layer in time shows that the Zambezian open forest of Miombo type, in spite of the great seasonal development of the leaf canopy is never completely bare, at least when fire is absent. For the woody layers, the minimal leaf area is between 1st and 15th September (Fig. 5). By interpolation this would be on the 12th September, the day on which the area of new leaves would exceed that of the old. On the other hand, leaf area remains very stable from 1st November to 15th February, i.e. for the greater part of the rainy season.

Foliation, or more generally the renewal of vegetation activity is a phenomenon which depends largely on fire occurring or not. It is possible to indicate groups of species having early, average, late, and very late foliation. In the case of fire, the date of fire passage (early or late) and its intensity will influence renewal of activity, whose time span will be disturbed. Most often a shortening of the renewal period may be observed after late fire.

We were able to establish, when fire is absent, the following classification as the average season of foliation for the main species in the Miombo :

- Early foliation : *Brachystegia spiciformis*, *Albizia adianthifolia*, *Baphia bequaertii*, *Ochthocosmus glaber*, *Strychnos inocua*, *Ekebergia benguelensis*, *Diplorynchus condylocarpon*.

- Average foliation : *Brachystegia boehmii*, *Pericopsis angolensis*, *Monotes katangensis*, *Schwartzia madagascariensis*, *Uapaca kirkiana*, *Dalbergia boehmii*, *Strychnos cocculoides*, *Hymenocardia acida*, *Annona senegalensis*, *Pseudolachnostylis maprouneifolia*, *Syzygium guineense* subsp. *macrocarpum*, *Vitex mombassae*, *Julbernardia paniculata*, *Erythrophleum africanum*.

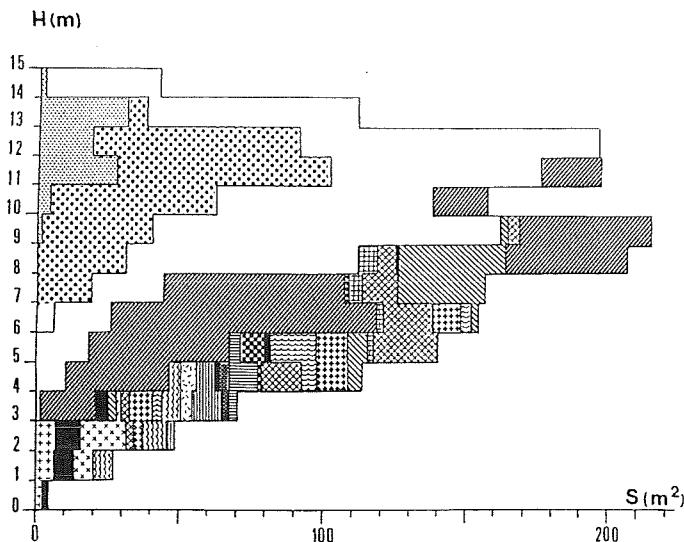


Fig. 3 : Vertical repartition of woody layers' of leaf area in the Kasapa miombo open forest (February 1977).

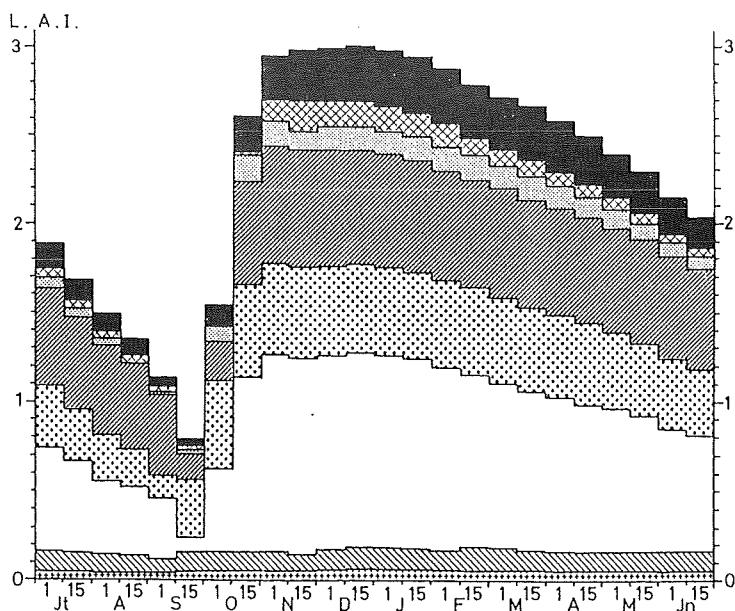


Fig. 4 : Fornightly woody layers' leaf area index in the Kasapa miombo open forest (climatic year : 1976-1977).

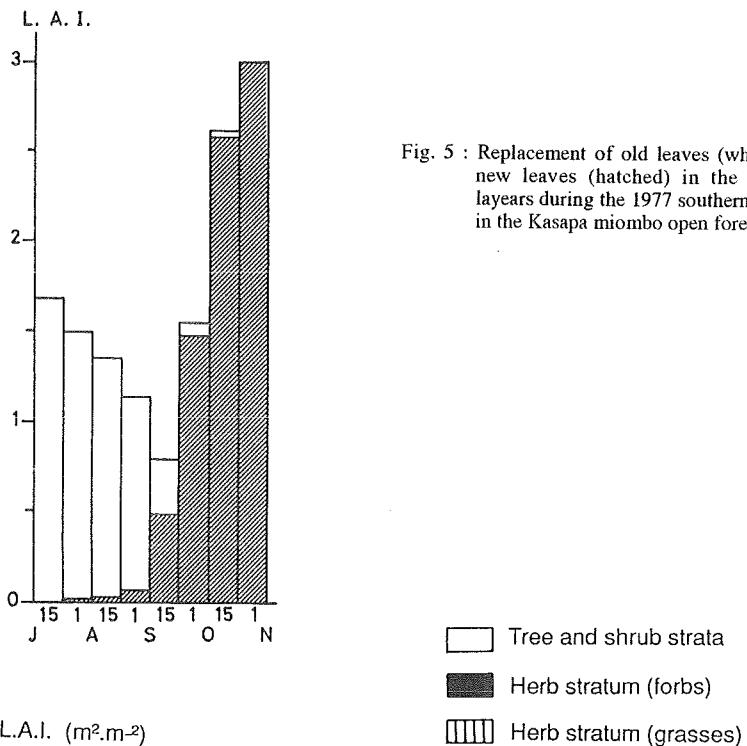


Fig. 5 : Replacement of old leaves (white) by new leaves (hatched) in the woody layears during the 1977 southern spring in the Kasapa miombo open forest.

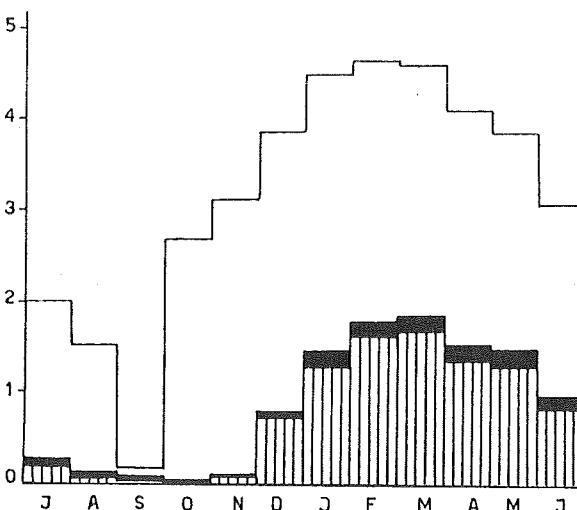


Fig. 6 : Relative importance of monocotyledon and dycotyledon leaf areas throughout the year in the Kasapa miombo.

- Late foliation : *Pterocarpus angolensis*, *Monotes africanus*, *Combretum mollis*.
- Very late foliation : *Pavetta shumaniana*.

B. Grass layer

Data relating to the grass layer are presented in Figure 6 which shows the relative and absolute importance of monocotyledons and dicotyledons throughout the year when fire is absent.

On the other hand the grass layer, as much throughout the year as during the rainy season, shows important variations in blade area.

DISCUSSION

Several comments arise from the analysis of the data presented here. Our results can easily be integrated into the few values available about tropical forests' L.A.I. (Table II). It should be remembered that most of the studies dealing with forests take only the tree layer into account, while research conducted in savannas are frequently devoted to the grass layer. Tree and shrub layers values for miombo are comprised between those of South Asian monsoon tropical forests (KIRA *et al.*, 1976) and Australian *Eucalyptus* forests (CARBON *et al.*, 1979).

Regarding seasonality, ALEXANDRE (1981) assumes that for tropical rain forests, at the time of maximum defoliation, the L.A.I. could diminish at half the maximum value, if Golley team's results (GOLLEY *et al.*, 1975) may be generalized. The 2.11 ratio observed at Panama agrees very well with the 1.91 observed for a Zambezian dry evergreen forest. When seasonality is stronger, as in the miombo open forest for instance, this ratio will increase. For the Kasapa miombo it was of 3.72 in absence of fire. However L.A.I. measurements in a subtropical dry forest of Porto Rico show no more than c. 50-percent reduction in foliage area between wet an dry periods over the 30-months observation period (MURPHY & LUGO, 1986).

At Kasapa miombo, severe late fires strongly reduce the importance of leaves' canopy or even induce complete defoliation of both the tree and shrub layers. Effect of fire has not been the subject of a particular study. Variability of impact both on

Plant community (species dominant)	Location (Country)	L.A.I. (m ² . m ⁻²)	References
Tropical rain forest (<i>Cavanillesia plantanifolia</i>)	Santa Fe (Panama)	22.4	Golley <i>et al.</i> , 1975
Tropical rain forest	Khao-Chong (Thailand)	12.3	Kira <i>et al.</i> , 1964
Tropical rain forest	Pasoh (Malaysia)	8.0	Kato <i>et al.</i> , 1978
		7.46	Kira, 1978
Subtropical wet forest	El Verde (Porto Rico)	7.34	Weaver <i>et al.</i> , 1986
Seasonal evergreen forest (<i>Dipterocarpaceae</i>)	South-western Cambodia (Cambodia)	7.34	Hozumi <i>et al.</i> , 1969
Monsoon tropical forest (<i>Shorea robusta</i>)	Mirzapur (India)	6.8	Misra <i>et al.</i> , 1967
Tropical rain forest	Manaus (Brazil)	6.6	Nonato da Conceicao,
		6.6	1977
Tropical rain forest (<i>Dacryodes excelsa</i>)	El Verde (Porto Rico)	6.6	Jordan, 1969
		6.4	Odum <i>et al.</i> , 1970
Tropical rain forest (<i>Artocarpus hirsuta</i> and <i>Palaquium ellipticum</i>)	Agumbe (India)	6.08	Rai, 1979
Tropical rain forest	Lower Rio Negro (Brazil)	6.0	Williams <i>et al.</i> , 1972
Mountain rain forest (<i>Cyrilla racemiflora</i> and <i>Chaetocarpus globosus</i>)	Mull Ridge (Jamaica)	5.7	Tanner, 1980
Mountain rain forest (<i>Lyonia octandra</i> and <i>Chaetocarpus globosus</i>)	Mor Ridge	5.5	Tanner, 1980
Montane rain forest (<i>Dacrycarpus cinctus</i> and <i>Podocarpus archboldii</i>)	Marafunga (New Guinea)	5.5	Edwards & Grubb, 1977

Table II - Leaf area index (L.A.I.) of tropical forests

Plant community (species dominant)	Location (country)	L.A.I. (m ² · m ⁻²)	References
Mixed tropical rain forest	San Carlos (Venezuela)	5.2	Jordan & Uhl, 1978
Tall Amazon Caatinga forest (<i>Micrandra sprucei</i>)	San Carlos (Venezuela)	5.08	Klinge & Herrera, 1983
Dry evergreen forest (<i>Entandrophragma delevoyi</i>)	Luiswishi (Zaire)	5.0	Malaisse, 1984
Tropical rain forest	French Guyana	5.0	Bonhomme <i>et al.</i> , 1973
Flooded forest	Lower Rio Negro	4.9	Williams <i>et al.</i> , 1972
Subtropical dry forest (<i>Gymnanthes lucida</i> and <i>Exostema caribaeum</i>)	Guanica (Porto Rico)	4.2	Murphy & Lugo, 1986
Monsoon tropical forest (<i>Lagerstroemia calyculata</i> and <i>Dipterocarpus obtusifolius</i>)	Ping Kong (Thailand)	3.9	Kira <i>et al.</i> , 1967
Lowland rain forest	(Ivory Coast)	3.7	Müller & Nielsen, 1965
Miombo open forest (<i>Julbernardia paniculata</i> and <i>Brachystegia boehmii</i>)	Kasapa (Shaba, Zaire)	3.47	Malaisse <i>et al.</i> , 1972
Eucalyptus forest (<i>E. marginata</i> and <i>E. calophylla</i>)	Western Australia (Australia)	3.07	Present study
		2.4	Carbon <i>et al.</i> , 1979
Subtropical dry forest	Guanica (Porto Rico)	2.02	Weaver <i>et al.</i> , 1986
Lower mountain rain forest (<i>Tabebuia rigida</i> and <i>Eugenia borinquensis</i>)	Luquillo (Porto Rico)	1.99	Weaver <i>et al.</i> , 1986
Guinean preforested savannah	Olokemeji (Nigeria)	1.46	Hopkins, 1968
Eucalyptus forest (<i>E. diversicolor</i>)	Western Australia (Australia)	1.3	Carbon <i>et al.</i> , 1979

Table II - (Continued)

structure and biomass of time of burning has frequently been commented upon elsewhere (TRAPNELL *et al.*, 1976; GELDENHUYSEN, 1977; LAWTON, 1978; RUTHERFORD, 1981; TROLLOPE, 1982) and will not be reviewed here.

The absence of climbers in the study plot and their scarcity in miombo in general should be compared with their importance in tropical rain forests : 36 % of the leaf biomass at Ipissa in Gabon (HLADIK, 1974), over one third of the rain forest in Thailand (OGAWA *et al.*, 1965), 16.8 % of the L.A.I. in a Zambezian dry evergreen forest (MALAISSE, 1974).

This second approach of L.A.I. in miombo of wetter type also avoids the various aspects of herbivory. Few informations are available about the impact of folivores in Zambezian open forests and woodlands, with the exception of caterpillars spectacular defoliations (MALAISSE, 1978) whose main dietary sources are, as far as miombo is concerned, Caesalpiniaceae (MALAISSE, 1983). ALEXANDRE (1981) reports that an adequate mean value for foliar losses by herbivorous animals is 7.8 % in tropical forests, but he considers that herbivory on leaf area is negligible !

REFERENCES

- ALEXANDRE, D.Y., 1981. L'indice foliaire des forêts tropicales.- Analyse bibliographique. *Acta Oecol., Oecol. Gener.*, 2(4), 299-312.
- BONHOMME, R., VARLET-GRANCHER, C. & OLDEMAN, R.A.A., 1973. Mesures préliminaires des rayonnements solaires au-dessus et à l'intérieur de la forêt guyanaise. I.N.R.A., document interne (cité par ALEXANDRE, 1981).
- CARBON, R., BARTLE, G. & MURRAY, A., 1979. Leaf area index of some Eucalypt forests in South-west Australia. *Aust. For. Res.*, 9, 323-326.
- EDWARDS, P.J. & GRUBB, P.J., 1977. Studies of mineral cycling in a montane rain forest in New Guinea. I. The distribution of organic matter in the vegetation and soil. *J. Ecol.*, 65(3), 943-969.
- GELDENHUYSEN, C.J., 1977. The effect of different regimes of annual burning on two woodland communities in Kavango. *S. Afr. For. J.*, 103, 32-42.
- GOLLEY, F., MCGINNIS, J., CLEMENTS, R., CHILD, G. & DUEVER, M., 1975. *Mineral cycling in a tropical moist forest ecosystem*. Athens, Univ. Georgia Press, 248 p.
- HELLER, H., 1971. Estimation of photosynthetically active leaf area in forests. In Ellenberg H. (ed.) : Integrated experimental ecology, Springer verlag, Berlin, Ecological studies, 2: 29-31.

- HLADIK, A., 1974. Importance des lianes dans la production foliaire de la forêt équatoriale du Nord-Est du Gabon. *C. R. Acad. Sc. Paris*, Série D, 278: 2527-2530.
- HOPKINS, B., 1968. Vegetation of the Olokemeji forest reserve, Nigeria. Part V. The vegetation of the savanna site with special reference to its seasonal changes. *J. Ecol.*, 56(1), 97-115.
- HOZUMI, K., YODA, K., KOKAWA, S. & KIRA, T., 1969. Production ecology of tropical rain forests in south-western Cambodia. I. Plant biomass. *Nature & Life in South east Asia*, 6, 1-51.
- JORDAN, C.F., 1969. Derivation of leaf area index from quality of light on the forest floor. *Ecol.*, 50, 663-666.
- JORDAN, C.F., & UHL, C., 1978. Biomass of a 'tierra firme' forest of the Amazon basin. *Oecol. Plant.*, 13, 387-400.
- KATO, R., TADAKI, Y & OGAWA, H., 1978. Plant biomass and growth increment studies in Pasoh forest. *Malay. Nat. J.*, 30(2), 211-224.
- KIRA, T. 1978. Community architecture and organic matter dynamics in tropical lowland rain forests of Southeast Asia with special reference to Pasoh Forest, West Malaysia. In P.B. Tomlinson & M.H. Zimmermann (eds) : Tropical trees as living systems, Cambridge Univ. Press, London, 561-590.
- KIRA, T., OGAWA, H., YODA, K. & OGINO, K., 1964. Primary production by a tropical rain forest of southern Thailand. *Bot. Mag. Tokyo*, 77, 428-429.
- KIRA, T., OGAWA, H., YODA, K. & OGINO, K., 1967. Comparative ecological studies on three main types of forest vegetation in Thailand. IV. Dry matter production, with special reference to the Khao Chong rain forest. *Nature & Life in South-East Asia*, 5, 149-174.
- KLINGE, H. & HERRERA, R., 1983. Phytomass structure of natural plant communities on spodosols in Southern Venezuela : the tall Amazon Caatinga forest. *Vegetatio*, 53, 65-68.
- LAWTON, R.M., 1978. A study of the dynamic ecology of Zambian vegetation. *J. Ecol.*, 66(1), 175-198.
- MALAISSE, F., 1976. Quelques méthodes d'étude de la structure en forêt. Exemple d'application au miombo zairois, écosystème forestier tropical. In La pratique de l'Ecologie - Méthodes écologiques d'étude du paysage et de la nature. Adm. gén. Coop. Dév. (A.G.C.D.), Bruxelles, 104-118.
- MALAISSE, F., 1978. The miombo ecosystem In Tropical forest ecosystems, a state-of-knowledge report prepared by UNESCO/UNEP/FAO, Unesco, Paris, *Natural resources research*, XIV, 589-606.
- MALAISSE, F., 1983. Trophic structure in Miombo Zambezian tropical woodland. *Ann. Fac. Sc. Lubumbashi*, 3, 119-162.
- MALAISSE, F., 1984. Structure d'une forêt dense sèche zambézienne des environs de Lubumbashi (Zaïre). *Bull. Soc. roy. Bot. Belgique*, 117(2), 428-458.

- MALAISSE, F., ALEXANDRE, J., FRESON, R., GOFFINET, G. & MALAISSE-MOUSSET, M., 1972. The miombo ecosystem : a preliminary study *In P et F Golley (eds) : Tropical ecology, with an emphasis on organic production*, Athens (Georgia, U.S.A.), 363-405.
- MALAISSE, F., FRESON, R., GOFFINET, G. & MALAISSE-MOUSSET, M., 1975. Litterfall and litter breakdown in miombo. *In F. Golley and E. Medina (eds) : Tropical Ecological Systems. Trend in terrestrial and aquatic research*. Springer Verlag, New York-Heidelberg-Berlin, *Ecological Studies*, 11, 131-152.
- MALAISSE, F., KITEMBO, M. & COLONVAL-ELENKOV, E., 1982. Sur l'existence d'un type d'anatomie foliaire particulier et dominant chez les essences des forêts claires zambéziennes. *Bull. Soc. roy. Bot. Belg.*, 115(2), 357-371.
- MALAISSE, F. & MALAISSE-MOUSSET, M., 1970. Contribution à l'étude de l'écosystème forêt claire (Miombo) : Phénologie de la défoliation. *Bull. Soc. roy. Bot. Belgique*, 103, 115-124.
- MISRA, R., SINGH, J. & SINGH, K., 1967. Preliminary observations on the productivity of dry matter by Sal (*Shorea robusta*). *Trop. Ecol.*, 8, 94-104.
- MÜLLER, D. & NIELSEN, J., 1965. Production brute, pertes par respiration et production nette dans la forêt ombrophile tropicale. *Det Forstlige Forsvarens i Danmark*, 29(2), 69-160.
- MURPHY, P.G. & LUGO, A.E., 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. *Biotropica*, 18(2), 89-96.
- NONATO DO CONCEICAO, P., 1977. Alguns aspectos ecofisiológicos de floresta tropical umida de terra firme. *Acta amazonica*, 7(2), 157-178.
- ODUM, H., ABBOTT, W., SELANDER, R., GOLLEY, F. & WILSON, R., 1970. Estimates of chlorophyll and biomass of the Tabonuco forest of Puerto Rico. *In Odum & Pigeon (ed.) : A tropical rain forest*, 113-119. Oak Ridge, U.S.A.E.C.
- RAI, S., 1979. Leaf area of some tropical rain forest species of Western Ghats. *Indian J. Ecol.*, 6(2), 1-6.
- RAI, S.N., 1984. Photosynthetic biomass and leaf area index in tropical rain forests of Western Ghats. *Indian J. Ecol.*, 11(1), 19-26.
- RUTHERFORD, M.C., 1981. Survival, regeneration and leaf biomass changes in woody plants following spring burns in *Burkea africana - Ochna pulchra* Savanna. *Bohalia*, 13(3-4), 531-552.
- TANNER, E.V.J., 1980. Studies on the biomass and productivity in a series of montane rain forests in Jamaica. *J. Ecol.*, 68(2), 573-588.
- TRAPNELL, C.G., FRIEND, M.T., CHAMBERLAIN, G.T. & BIRCH, H.F., 1976. The effects of fire and termites on a Zambian woodland soil. *J. Ecol.*, 64(2), 577-588.
- TROLLOPE, W.S.W., 1982. Ecological effects of fire in South Africa savannas. *In B.J. Huntley & B.H. Walker (eds) : Ecology of Tropical savannas*, Springer Verlag, Heidelberg-New York, *Ecological Studies*, 42, 292-306.

- VAN DER MEULEN, F. & WERGER, M.J.A., 1984. Crown characteristics, leaf size and light troughfall of some savanna trees in southern Africa. *S. Afr. J. Bot.*, 3, 208-218.
- VAN SEVEREN, J.P., 1969. L'index foliaire et sa mesure par photoplanimétrie. *Bull. Soc. roy. Bot. belg.*, 102(2), 373-385.
- MEAVER, P.L., MEDINA, E., POOL, D., DUGGER, K., GONZALES-LIBOY, J.& CUEVES, E., 1986. Ecological observations in the dwarf cloud forest of the Luquillo Mountains in Puerto Rico. *Biotropica*, 18(1), 79-85.
- WHITE, F., 1981. Vegetation map of Africa (scale 1:5000000). Unesco/AETFAT/Unso, Paris.
- WILLIAMS, W.A., LOOMIS, R.S. & ALVIM, P. de T., 1972. Environment of evergreen rain forest on the lower Rio Negro. *Trop. Ecol.*, 13(1), 65-78.

Appendix 1 - Vertical distribution of the number of leaves per species at the Kasapa Miombo (values are for the experimental plot of 1/16 ha, 1 February 1977).

	Total	3909	31183	8794	16663	27674	1995	6545	26287	34261	4788	4071	29535	4178	751	884	3184	7623	1725	575	3714	812
1. <i>Albizia adianthijfolia</i>	0																					
2. <i>Anisophyllea boehmii</i>																						
3. <i>Bauphia bequaertii</i>																						
4. <i>Braechystegia boehmii</i>																						
5. <i>Braechystegia spiciformis</i>																						
6. <i>Diphydryniae condylotropion</i>																						
7. <i>Ficus dekdekensis</i>																						
8. <i>Jublermarthia punctatula</i>																						
9. <i>Miomoties usitaciumus</i>																						
10. <i>Monotes kallangensis</i>																						
11. <i>Ochroma schweinfurthiana</i>																						
12. <i>Pariamia mobola</i>																						
13. <i>Pauetta schumanniana</i>																						
14. <i>Pericopsis ungoleensis</i>																						
15. <i>Pterocarpus angolensis</i>																						
16. <i>Schwarziea madagascariensis</i>																						
17. <i>Syzygium macrocarpum</i>																						
18. <i>Tapinanthus erianthus</i>																						
19. <i>Uapaca kirkiana</i>																						
20. <i>Uapaca nitida</i>																						
21. <i>Uapaca phloea</i>																						

Appendix 2 - Vertical distribution of leaf area in the Kasapa miombo values are given in m^2 for the experimental plot of 1/16 ha., as on 1 February 1977 and taking one side into account).

Species	July			August			September			October			November			December		
	1	15	1	15	1	15	1	15	1	15	1	15	1	15	1	15	1	15
1. <i>Albizia adianthifolia</i>	34.25	25.16	21.67	0.0	6.12	18.27	57.67	96.72	90.50	85.98	85.98	85.39						
2. <i>Anisophyllea boehmii</i>	38.43	37.45	36.37	35.34	34.93	41.43	41.12	43.28	44.16	44.42	49.78	53.65						
3. <i>Baphia bequaertii</i>	25.15	24.66	24.14	22.44	13.58	2.00	9.23	24.62	27.34	27.24	27.00	26.94						
4. <i>Brachystegia boehmii</i>	339.46	326.85	310.26	302.38	280.94	89.24	136.17	361.82	414.68	410.95	407.17	404.06						
5. <i>Brachystegia spiniformis</i>	209.49	183.73	161.20	130.24	82.94	200.38	306.27	322.39	319.86	318.17	314.80	312.34						
6. <i>Diplorhynchus condylocarpon</i>	1.32	0.55	0.26	0.17	0.08	0.00	0.00	0.00	4.03	4.16	4.15	4.10						
7. <i>Ficus dekkeneri</i>	0.12	0.12	0.07	0.02	0.01	5.82	12.73	15.79	18.17	21.19	20.49	20.84						
8. <i>Jubaea chilensis</i>	368.60	319.46	261.19	241.43	209.00	46.17	287.25	612.55	688.67	684.04	680.93	676.29						
9. <i>Monotes africanus</i>	28.76	27.52	24.89	23.55	20.59	17.44	0.00	8.59	73.91	96.12	89.58	90.63						
10. <i>Monotes katangensis</i>	9.94	7.09	6.80	6.69	3.75	0.37	9.96	10.13	11.35	13.04	17.51	20.17						
11. <i>Ochna schweinfurthiana</i>	0.37	0.17	0.11	0.02	0.00	0.07	1.38	5.81	7.41	7.39	7.34	7.32						
12. <i>Pavetta schumanniana</i>	1.98	1.14	1.06	0.25	0.16	0.03	0.00	0.00	0.01	0.38	2.47	2.85						
13. <i>Paricopsis angolensis</i>	6.62	2.47	0.44	0.08	0.00	0.16	0.23	3.62	9.80	10.07	10.06	10.02						
14. <i>Farinaria mohola</i>	89.29	82.39	75.48	74.37	59.44	83.00	86.70	80.29	82.63	72.39	87.07	93.61						
15. <i>Pterocarpus angolensis</i>	2.11	0.09	0.01	0.00	0.00	0.00	0.00	0.02	0.59	1.49	1.57	1.57						
16. <i>Schwarziea madagascariensis</i>	3.91	2.33	0.99	0.24	0.00	0.00	0.87	22.48	29.57	29.48	29.39	29.22						
17. <i>Syzygium macrocarpum</i>	16.95	12.15	11.28	8.01	2.81	2.55	5.22	15.98	16.23	16.36	20.98	22.88						
18. <i>Taphrina erianthus</i>	0.08	0.03	0.03	0.00	0.00	0.90	0.94	1.03	1.11	1.11	1.33	1.33						
19. <i>Uapaca kirkiana</i>	4.84	3.63	3.81	3.68	3.50	2.97	2.30	2.61	6.98	7.13	7.17	7.38						
20. <i>Uapaca nitida</i>	9.12	6.79	6.58	6.53	5.49	1.86	15.89	16.61	16.92	17.49	17.86	18.82						
21. <i>Uapaca pilosa</i>	8.28	7.35	7.29	7.25	2.98	2.58	5.70	8.53	10.46	11.92	12.64	12.07						
Total for the experimental plot (1/16 ha)	1199.07	1071.13	953.93	862.69	726.32	515.24	987.63	1656.90	1874.51	1896.00	1905.49	1915.67						
Values per ha	19185.12	17138.08	15262.88	13803.04	11621.12	8243.84	15802.08	26510.40	29921.16	30336.00	30551.84	30650.72						

Appendix 3 - Fortnightly leaf area per species in the Kasapa miombo (1976-1977 climatic year, values are given in m² per 625 m²)

Species	January						February						March						April						May						June					
	1	1.5	1	1.5	1	1.5	1	1.5	1	1.5	1	1.5	1	1.5	1	1.5	1	1.5	1	1.5	1	1.5	1	1.5	1	1.5	1	1.5	1	1.5	1	1.5				
1. <i>Albizia adianthifolia</i>	85.37	85.32	85.29	84.58	83.53	81.78	75.14	69.55	65.00	55.22	49.63	44.39																								
2. <i>Anisophyllea boehmii</i>	51.48	49.78	48.08	46.58	46.22	44.78	41.99	40.96	40.18	39.93	38.43	38.38																								
3. <i>Baphia bequaertii</i>	26.84	26.79	26.69	26.47	26.33	26.26	26.12	25.99	25.92	25.83	25.67	25.50																								
4. <i>Brachystegia poeppnii</i>	339.82	339.14	339.79	338.07	333.79	330.22	327.94	327.01	326.16	324.09	325.45	325.81																								
5. <i>Brachystegia spiciformis</i>	309.82	306.96	304.25	301.89	298.09	295.67	291.39	285.96	285.72	286.50	244.90																									
6. <i>Diplorenthus condylocarpus</i>	4.04	3.96	3.90	3.88	3.86	3.84	3.81	3.78	3.75	3.73	3.58	2.98																								
7. <i>Ficus dekeleena</i>	20.78	17.50	9.62	8.94	8.24	7.54	6.79	6.61	4.58	2.32	0.47	0.18																								
8. <i>Jubaea chilensis</i>	671.15	659.86	640.50	601.23	574.02	556.28	538.47	511.99	491.79	469.57	426.87	402.11																								
9. <i>Monotes africanus</i>	88.48	86.78	82.12	63.20	61.26	60.58	51.50	49.73	47.17	38.74	32.25	30.05																								
10. <i>Monotes katangensis</i>	20.14	19.91	19.75	18.93	16.86	15.01	13.74	13.43	13.26	13.10	11.08	10.63																								
11. <i>Ochina schwartzfurthiana</i>	7.31	7.29	7.27	7.22	7.12	6.98	6.86	6.73	6.73	3.24	2.00	0.90																								
12. <i>Pavetta schumaniana</i>	2.85	2.78	5.95	5.83	4.04	5.89	6.04	6.09	5.90	5.03	5.00	2.96																								
13. <i>Pericopsis angolensis</i>	9.99	9.95	9.92	9.90	9.86	9.79	9.55	8.88	8.78	8.65	8.50	8.36																								
14. <i>Parinari mobola</i>	93.61	92.62	87.07	102.24	97.43	87.93	87.44	87.31	86.83	85.98	86.45	88.55																								
15. <i>Pterocarpus angolensis</i>	15.75	15.74	15.73	15.73	15.72	15.64	15.35	14.76	14.76	12.71	9.95	5.87																								
16. <i>Schwarztzia madagascariensis</i>	28.93	28.70	28.62	28.43	28.29	27.96	27.42	26.19	26.19	24.11	21.87	19.06	7.61																							
17. <i>Syzygium macrocarpum</i>	22.90	22.92	25.97	25.02	31.17	40.35	36.79	32.05	27.74	25.52	22.55	22.25																								
18. <i>Tapinanthus erianthus</i>	1.32	1.32	1.04	0.86	0.72	0.51	0.14	0.13	0.06	0.01	0.01	0.05																								
19. <i>Upacaria kirkiana</i>	8.24	8.76	7.35	6.94	6.85	6.01	6.44	6.28	6.01	5.97	5.31	5.23																								
20. <i>Upacaria nitida</i>	18.47	17.73	16.65	16.05	12.91	12.67	12.79	11.58	11.34	10.99	10.30	9.87																								
21. <i>Upacaria pilosa</i>	12.35	12.77	14.88	13.12	12.00	12.09	12.88	12.22	10.78	11.41	10.11	9.21																								
Total for the experimental plot (1/16 ha)	1899.64	1873.58	1832.45	1773.11	1728.32	1697.86	1647.88	1591.20	1527.57	1460.41	1370.57	1301.66																								
Values per ha	30394.24	29977.28	29319.20	28369.76	27653.12	27165.76	26366.08	25459.20	24441.12	23366.56	21929.12	20826.56																								

