

A structural analysis of rain forest at Korup and Douala–Edea, Cameroon

D. McC. Newbery

Department of Biological & Molecular Sciences, University of Stirling, Stirling
FK9 4LA, Scotland, UK

and

J. S. Gartlan

WWF Cameroon, B.P. 6776 Yaoundé, Cameroon

Synopsis

Diameter frequency distributions (dfds) of 197 tree species in Korup National Park and 118 tree species in Douala–Edea Forest Reserve (based on c. 41 000 and 25 000 trees ≥ 30 cm gbh in 135 and 104 plots along four transects at each site, respectively) were individually classified into four groups of species according to their maximum diameters ($\geq 99\%$ trees < 50 , < 70 and < 90 cm dbh, and $> 1\% \geq 90$ cm dbh), and separated into two abundance classes ($n \geq 50$ and $n = 20–49$ (or $15–49$)). A fifth group, from those species in 3 and 4, was defined by a relative lack of small stems and given detailed attention. Dfd's were evaluated for all species together on a transect and site basis, and compared for individual species across transects, and between sites for those group 5 species in common.

Analysis focussed on three large ectomycorrhizal species in groups 3 and 4, *Microberlinia bisulcata*, *Tetraberlinia bifoliolata* and *T. moreliana* (Caesalpiniaceae), which were restricted to, and dominated, the forest on the nutrient-poor soils of transect P at Korup. *M. bisulcata*, the most abundant, was markedly group 5 in character, with very few small trees, whilst the *Tetraberlinia* species had strong replacement potential. Although there were 27 species (42% of groups 3 & 4) at Korup and 19 (48%) at Douala–Edea in group 5, *M. bisulcata* was unique in its combination of large size, dfd, mycorrhizal habit, spatial distribution and soil association. The potential replacement of this species was contrasted also with a non-ectomycorrhizal caesalp with similar dfd that occurred on nutrient-richer soils, *Erythrophleum ivorense*.

Knowledge of the Caesalpiniaceae-rich *la forêt biafriéenne* of Letouzey (which includes Korup and Douala–Edea) is reviewed, and the distribution, ecology and regeneration of the caesalps discussed. Structure and inferred dynamics of the forest at Korup are discussed with special regard to the ectomycorrhizal species.

Introduction

La forêt biafriéenne, or atlantic coastal forest, of Letouzey (1968, 1985) is a particular and important forest type of western Central Africa. It lies as an arc around the Bay of Biafra, from south-east Nigeria, through Cameroon to the south-west corner, bordering Equatorial Guinea, for some 250 km (Letouzey 1968). Lying inland of the coastal mangrove forest and forming a band 100–150 km wide, it is topographically well-defined by land generally < 300 m elevation, occasionally reaching 500 m. This forest type lies within the Guinea–Congo Region of evergreen rain forest (Schnell 1976; White 1983), which in parts tends towards semi-deciduousness. The underlying geology is varied, being mostly of granites and gneiss, with soils ranging from very sandy to those of high clay content (Letouzey 1968; White 1983). In Cameroon, two subtypes were recognised by Letouzey (1968, 1985): *la forêt littorale*, evidently a form much degraded by man (also Letouzey 1975); and *la forêt*

congolaise, akin to the extensive tracts of the region, eastwards and occupying much of the Congo (Zaire) Basin (Letouzey 1985).

The climate of the atlantic coastal forest is distinctive in two respects. Firstly, the rainfall is higher (>2 m and often >3 m annually) compared with the lower levels for much of West and of Central Africa (typically 1.5–2 m annually), and secondly, there is just one clear dry season (December to February) compared with elsewhere in the region with two less pronounced dry seasons annually. The wettest areas of lowland forest (>5 m rainfall) with the strongest dry season lie inland of Mount Cameroon, into and to the west of the Rumpi Hills, in south-west Cameroon.

Floristically, *la forêt biafrière* has one main feature, its unusually high species richness of trees in the subfamily Caesalpinioideae of the Leguminosae. 'La proportion des Caesalpiniacées est particulièrement remarquable et aucune autre famille semble-t-il ne peut rivaliser en nombre absolu ou relatif d'espèces avec cette famille, ni avec la dimension moyenne des espèces en cause, plusieurs d'entre elles appartenant à la state arborescente' (Letouzey 1968, pp. 125–6). In terms of relative abundance, the Caesalpinioideae are a major, often dominant, family throughout the Guinea–Congo Region (Schnell 1976; White 1983), sometimes forming distinctive near monodominant stands in Central Africa (Lebrun 1936; Germain & Evrard 1956; Devred 1958; Gérard 1960, Hart *et al.* 1989) and in West Africa (e.g. Voorhoeve 1964). However, in the coastal atlantic forests described by Letouzey several caesalps are codominant, and the species representation of this subfamily varies within the forest type (Letouzey 1968, 1985).

Aubréville (1968) estimated that the Guinea–Congo Region had 62 genera and 175 species in the Caesalpinioideae, and of its five tribes 75 and 69 species were of the Detarieae and Amherstieae respectively. Of 157 species of Leguminosae recorded for dense humid forests of Cameroon by Letouzey (1968), 91 were of the Caesalpinioideae and of these 49 (perhaps up to 57) were considered limited to *la forêt biafrière*. Many of the species in the Amherstieae and Detarieae are large canopy and emergent trees (Aubréville 1970; Letouzey 1985) and therefore provide a major contribution to total basal area abundance and forest biomass. *Microberlinia bisulcata* A. Chev. can achieve very large diameters (Letouzey 1985), and the species is characterised by large laterally-extensive buttresses. Large individuals of this species were also noted by Richards (1963) in his study in Southern Bakundu Forest Reserve, Cameroon.

A second interesting characteristic of the caesalpinioideae legumes is their propensity to spatial clumping, to exhibit a gregarious behaviour. Letouzey (1968, 1985) estimated that approximately half of the more common caesalps show clumping. Often the gregarious species showed strong regeneration, with many small-stemmed trees within the clumps. Part of the explanation for clumping at a local level is likely to lie in the limited dispersal of seeds.

During the Pleistocene glacial periods Equatorial Africa was drier and cooler (Hamilton 1976, 1989, 1992) and the extensive interglacial rain forest in the Guinea–Congo Region contracted into three main forest refugia. One such core area was in western Central Africa, in Cameroon and Gabon, where today there is a greater floristic richness and a higher level of endemism than in surrounding forests (White 1983). Climatic and palaeo-ecological data of Maley (1987, 1989, 1991) support the refugium hypothesis. *La forêt biafrière* lies in the coastal and more northerly part of this refugium, whereas the forests inland of this atlantic belt and south towards

Gabon are today relatively drier. The last 10 000 years has seen an expansion of some rain forest tree species back into main Guinea–Congo Region (Hamilton 1989, 1992).

Several authors have sought without success to explain the broad trends in distribution of caesalpiniaceous legumes in equatorial Africa by soil conditions (Lemée 1961; Aubréville 1968; Letouzey 1968, 1983; White 1983). Caesalps, especially those in the Amherstieae, are found on a wide range of edaphic conditions from very wet to dry sites, from sandy to clayey soils. However, these conclusions were based on very descriptive general observations and scarcely any detailed soil chemistry. The question of water balance at sites has received little attention (Letouzey 1983; White 1983; Högborg 1986): rainfall and seasonality are likely to lead to stronger distributional hypotheses than those of nutrients. Many of the present-day distributions of tree species in equatorial Africa are also dependent on Holocene history, and the continuing influence of the last Quaternary glacial and interglacial periods.

Much of the primary coastal atlantic forest in Cameroon has been degraded by man, both in previous centuries of settlement and more recently by timber extraction (Jentsch 1911; Letouzey 1968, 1985). Much of the *Microberlinia bisulcata* (local name—zingana), for instance, will have been removed as it has been a reasonably important commercial species. A strong indication of past human disturbance is an abundance of *Lophira alata* Banks ex Gaertn. f. (Letouzey 1957, 1968). Pockets of unequivocal primary forest are difficult to find but, as Letouzey (1968) speculated and later confirmed (Letouzey 1985), they exist in the south-west of Cameroon.

Letouzey (1968) reported on many relevés throughout Cameroon, undertaken for his large-scale phytogeographical analysis. Single, 'homogeneous', 500 m × 10 m (0.5 ha) units were examined for trees >20 cm dbh. (Letouzey argued that extra species were very rarely present below this limit.) Within the atlantic coastal forest type only two enumerations were made in primary forest: at Yabassi, 90 km inland (centrally on the outer edge of the arc; five plots of 9 ha each) and at Kribi (on the southern tip of the arc; one plot of 1 ha). Full species data are presented for the Kribi site (Letouzey 1968, p. 128), but only stem densities and species richness for Yabassi because the determinations were doubtful. These data were compared with the 15 1 ha plots of Mildbraed (1930) near Limbe (a coastal south-west site), but in Letouzey's opinion Mildbraed's samples were in already much degraded forest. Aside from extensive and valuable herbarium collections there were no reliable ecological data prior to 1975 (i.e. Gartlan *et al.* 1986). Richards (1963) enumerated a 1.5 ha plot at South Bakundu but it was not entirely of primary forest.

In the forest subtype, *la forêt à Lophira alata* Banks, Letouzey (1957, 1968) undertook a major enumeration of 44 000 trees >40 cm gbh (12.7 cm dbh), of 180 species, in 150 ha. The three other abundant and large-stemmed tree species were *Sacoglottis gabonensis* (Baill.) Urb., *Cynometra hankei* Harms and *Coula edulis* Baill. Amongst the smaller stemmed, understorey species, *Crateranthus talbotii* Bak.f. and *Dichostemma glaucescens* Pierre formed 4.9 and 3.9% of the stems respectively. This sampled area was known from reliable historical records to have been populated by man in the late 18th century (Letouzey 1957).

Kaji (1985, 1990) reports on enumerations of trees ≥ 4.5 cm dbh in three belt transects (10–20 m wide) in *la forêt biafriéene* in the Campo Reserve, in southern Cameroon (close to the Equatorial Guinea border, 30 km from the coast; rainfall c.

2100 mm), and in which *Tetraberlinia bifoliolata* (Harms) Hauman was an abundant species (5.6, 2.6 & 2.7% basal area respectively). The associated other abundant species on transects 1 and 2 were *Calpocalyx heitzii*, *Hymenostegia afzelii* (Oliv.) Harms, *Sacoglottis gabonensis*, *Scorodophloeus zenkeri* Harms, *Staudtia stipitata* Warb. and two unidentified Olacaceae, whilst on transect 3 the associated species were *C. heitzii*, *S. zenkeri*, and *S. gabonensis*, with *Erythrophleum sauveolens*, *Brachystegia zenkeri* Harms and an *Anthonotha* sp.

Two sites within the coastal atlantic forest of Cameroon have recently, however, received intensive ecological study: at Korup (Gartlan *et al.* 1986), in south-west Cameroon, close to the Nigerian border; and at Douala–Edea (Newbery *et al.* 1986), coastal and centrally located on the atlantic forest arc. (Details of the sampling are also given later in this paper.) Korup (especially the southern part, and to which this study refers) is almost certainly a primary forest (Gartlan 1986; Gartlan 1992), but Douala–Edea probably only partly primary. The latter also has been under heavy hunting pressure in recent years (Gartlan 1992). Korup National Park is of outstanding scientific and unique conservation value because of its history and location, in one of the wettest and now isolated forests of the atlantic coastal arc. It is undoubtedly the most important remnant of *la forêt biafriéene* (Gartlan *et al.* 1986; Gartlan *et al.* 1992). Korup is contiguous with Oban Forest Reserve in south-east Nigeria with which it has a strong floristic similarity (Hall 1977, 1981; Keay 1989).

In Korup National Park, a group of caesalpiniaceous legumes were found to be strongly associated on low elevation sites with sandy soils of low available phosphorus concentrations, and absent from steeper, higher elevation and nutrient-richer sites (Gartlan *et al.* 1986). These species, largely of the tribe Amherstieae, were shown to be ectomycorrhizal (Newbery *et al.* 1988; Alexander 1989b) and aggregated in their spatial distribution. The six most important species in terms of basal area contributions were *Microberlinia bisulcata* A. Chev., *Tetraberlinia moreliana* Aubrév., *Tetraberlinia bifoliolata* (Harms) Hauman, *Berlinia bracteosa* Benth., *Anthonotha fragrans* (Bak.f.) Exell & Hillcoat and *Didelotia africana* Baill. They appear to have been selected by the poor site conditions and that may, in part, have been due to their ectomycorrhizal status. Other trees in the forest are almost certainly endomycorrhizal (Newbery *et al.* 1988; Alexander 1989b). In Douala–Edea Forest Reserve, on the dry (non-swamp) sites, the association between ectomycorrhizal caesalps and soil nutrients was slight (Newbery *et al.* 1986): one hypothesis for this was that the levels of available soil phosphorus were higher and selection of these species was weaker.

Measurement of long-term population dynamics of these trees is not feasible: trees are long-lived, some maybe 300+ years in age (Jones 1956). Since the end of the last glacial dry period in Africa only some 30–35 complete generation turnovers will have elapsed, the climate changing continuously also over those centuries. However, from an examination of the distribution of tree sizes (aging being impossible) for the principal species, some insights into recent history and likely projections of future population structure are attained. This admits no information on relative mortality, recruitment and growth rates for different species as no data exist.

The main questions addressed in this paper are whether the large ectomycorrhizal caesalpineaceous legumes are regenerating on the sites to which they appear most adapted at Korup, and whether their size distributions are similar to those of other

species at Korup, and at Douala–Edea. The size structure of the forest, or of each species or group of species, will be shown by its *diameter frequency distribution* (abbreviated to *dfd* throughout). Nomenclature follows Hutchinson & Dalziel (1958, 1963), with revisions in Keay (1989); and Aubréville (1970) for the Caesalpinioideae. The term ‘caesalp’ is used here as a contraction of ‘caesalpinoid’.

This paper is presented as a tribute to the late René Letouzey (1918–1989) in recognition of his great contribution to our understanding of the flora and vegetation of Cameroon (Villiers 1989).

Analysis of the data and results

Preliminary treatment of the data

The girths (gbh, measured to the nearest cm) of all trees ≥ 30 cm gbh were converted to diameters (dbh) and stored to nearest cm. Thus the minimum gbh of 30 cm was *c.* 9.7 cm dbh which became rounded to 10 cm. The successive 5 cm dbh classes were defined as 10–<15 (i.e. 10–14 cm), 15–<20 (i.e. 15–19),..., 195–<200, ≥ 200 cm (39 classes). These rounding errors have a negligible effect on the analyses.

Korup. A summary of the enumeration of the four transects P to S is given in Table 1. Each plot was 80 m \times 80 m (0.64 ha in area). The total area enumerated was 86.40 ha (21.76 for P, R and S; 21.12 for Q). Transect Q was compared with the others as if it had the same area, the error being very small.

Douala–Edea. The enumeration on transects A to D is summarised in Table 2; transects B, C and D had 34, 24 and 12 plots respectively and these have been combined. Each plot was 80 m \times 80 m, as at Korup, and the total area enumerated was 66.56 ha (21.76 ha on A, 44.80 on BCD). Transects BCD can be compared with A by dividing tree frequencies by 2 (equivalent to 35 plots), again with little error.

Table 1. Enumeration summary for four transects (P, Q, R, S) at Korup with proportions of trees ≥ 10 cm dbh in five size classes and those accounted for in two abundance classes.

	P	Q	R	S	All
Number of plots	34	33	34	34	135
Number of trees enumerated	10 084	10 157 (10 465)*	10 382	10 045	40 668
Density (ha ⁻¹)	463	481	477	461	471
Basal area (m ² ha ⁻¹)	26.2	23.2	26.7	34.9	27.8
Number of species	241	243	280	312	410
Percentage of trees in dbh class (cm)					
10–<30	81.5	83.7	81.8	76.6	80.9
30–<50	13.0	12.4	12.8	15.1	13.3
50–<70	3.5	2.7	3.4	4.6	3.5
70–<90	1.4	0.8	1.1	2.0	1.3
≥ 90	0.6	0.4	0.9	1.7	1.0
Percentage of trees accounted for by					
134 common species ¹	94.1	94.6	92.3	87.4	92.1
63 less common species ²	3.8	3.5	5.2	7.1	4.9
remaining 213 rare species	2.1	1.9	2.5	5.5	3.0

*Equivalent number on 34 plots.

^{1,2}Species with ≥ 50 and 20–49 individuals respectively.

Table 2. Enumeration summary for four transects at Douala-Edea (A; and B, C and D combined) with proportions of trees ≥ 10 cm dbh in five size classes and those accounted for in two abundance classes.

	A	BCD	All
Number of plots	34	70	104
Number of trees enumerated	6415	18 582 (9026)*	24 997
Density (ha^{-1})	295	415	376
Basal area ($\text{m}^2 \text{ha}^{-1}$)	33.3	29.9	31.0
Number of species	89	216	230
Percentage of trees in dbh class (cm)			
10–<30	69.0	79.2	76.6
30–<50	19.3	12.4	14.1
50–<70	6.1	4.9	5.2
70–<90	2.8	1.9	2.1
≥ 90	2.8	1.7	1.9
Percentage of trees accounted for by			
76 common species ¹	94.2	93.1	93.4
42 less common species ²	4.8	5.0	4.9
remaining 112 rare species	1.0	1.9	1.7

*Equivalent number on 34 plots.

^{1,2}Species with ≥ 50 and 15–49 individuals respectively.

Ordination of tree densities per plot

In the context of the dfd analyses here, the relevant measure of abundance is density. Using logarithmically transformed numbers of trees ($\ln(n+1)$) of each species in each plot, two ordinations by (detrended) correspondence analysis were performed. Correspondence analysis is appropriate because counts per plot are likely to be Poisson-based and the distance metric in CA is χ^2 -based. CA also allows similar weighting to common and less common species which is desirable when comparing distributions of species with different population sizes.

Korup. The first axis ordered transects as P, Q, R then S (Fig. 1). This result showed a strong gradient in vegetation composition and provided the basis for comparing species across the four individual transects.

Douala-Edea. One plot, C19, was a distinct outlier and was removed. On re-analysis, axis 1 discriminated between transect A plots and transects B, C and D plots with the exception that two plots, B30 and B31 (and marginally B29), were grouped with A (Fig. 2). This ordination provided the basis for comparing transect A with transects BCD combined.

Selection of species for dfd analysis

Two abundance classes were defined: common species with ≥ 50 individuals and less common species with 20–49 individuals at Korup, and 15–49 individuals at Douala-Edea. The remaining species may be termed rare and will not be considered here. Fifty trees was considered to be minimal for inspecting a dfd with reliability, but the 20(15)–49 class included many interesting, often large-stemmed, species essential to the discussion of forest composition. Two abundance classes enabled a test of whether features of common species ddfs held for lower abundances.

For each species the numbers of trees in increasing 5 cm dbh classes were found. In order to condense the large quantity of data at each site yet highlight interesting

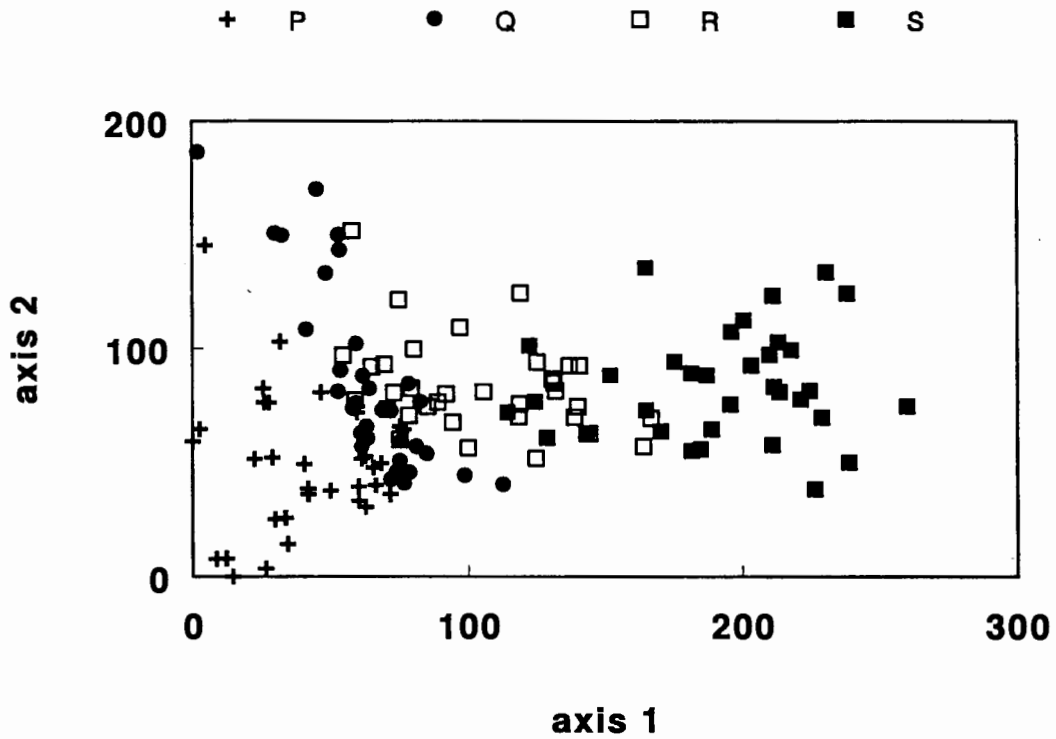


Figure 1. Ordination by detrended correspondence analysis of 135 0.64 ha plots at Korup (trees ≥ 30 cm gbh), labelled according to the four transects sampled. ($\lambda_1=0.320$; $\lambda_2=0.113$; $\lambda_3=0.085$). Lower and upper quartile axis 1 scores: P, 26–61; Q, 53–76; R, 75–131; S, 169–219.

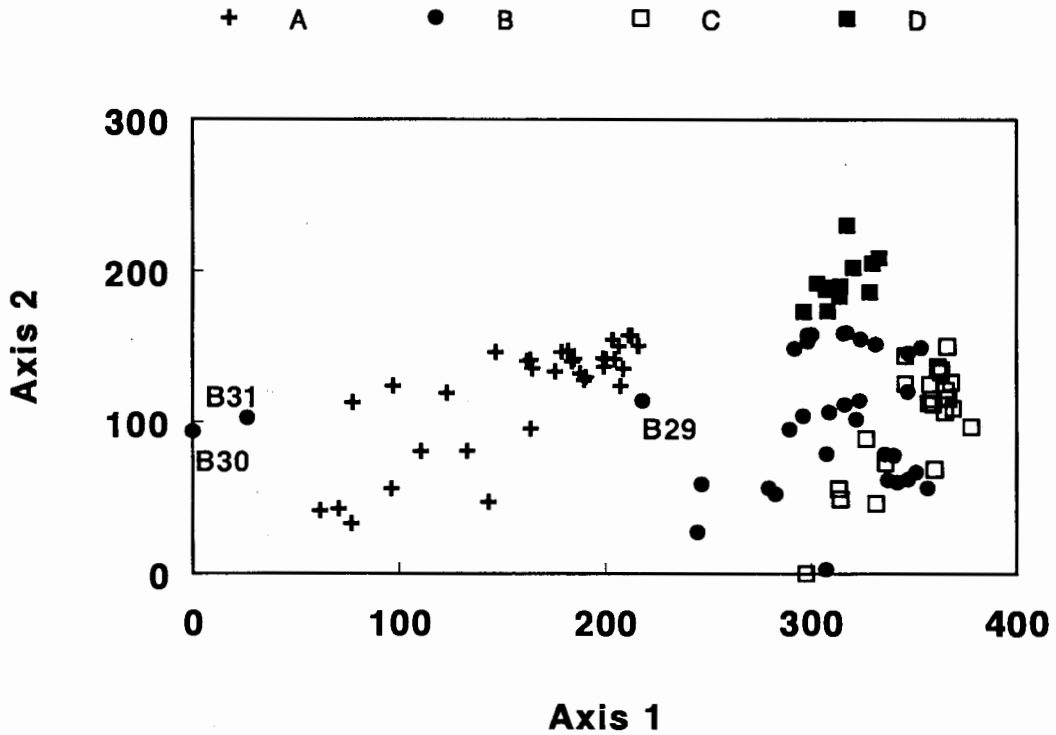


Figure 2. Ordination by detrended correspondence analysis of 103 0.64 ha plots at Douala-Edea (plot C19 removed, trees ≥ 30 cm gbh), labelled according to the four transects sampled. ($\lambda_1=0.489$; $\lambda_2=0.202$; $\lambda_3=0.133$). Lower and upper quartile axis 1 scores: A, 131–201; B, 291–338; C, 336–366; D, 307–326. The three transect B plots grouped with those of transect A are labelled.

Table 3. Common species ($n \geq 50$) at Korup classified according to four types of diameter (dbh) frequency distribution (dfd) and their occurrence and class abundances on transects P to S. Bold values indicate number of species restricted to transects P and S in class 4.

	dfd class				All
	1	2	3	4	
dbh (cm) limit	<50	$\geq 99\%$ trees <70	<90	>1% ≥ 90	
Number of species in total	65	25	21	23	134
with uneven dfds	4	12	12	16	44
percentage uneven	(6)	(48)	(57)	(70)	(33)
Number of species very low/absent on					
P	5	1	1	2	9
P+Q	2	1	3	3	9
P+Q+R	1	0	0	0	1
Q+R	0	0	0	0	0
Q+R+S	1	0	0	2	3
R+S	1	0	0	0	1
S	3	3	2	1	9
Others	2	0	0	0	2
Sum	15	5	6	8	34
Number of trees on transects					
P	5205	2846	656	782	9489
Q	5415	3046	598	549	9608
R	4975	3030	691	882	9578
S	3873	2858	819	1230	8780
All	19468	11780	2764	3443	37455
Density (ha^{-1})	225	136	32	40	434

and unusual features of some species, the dfds were assigned to four structural groups, as follows;

- 1 $\geq 99\%$ of trees < 50 cm dbh
- 2 $\geq 99\%$ of trees < 70 cm dbh
- 3 $\geq 99\%$ of trees < 90 cm dbh
- 4 > 1% of trees ≥ 90 cm dbh

These groups, found separately for common and less common species, represented increasing contributions of large trees to the higher strata in the forest along a continuum from understorey, lower canopy, main canopy and upper canopy/emergent. Most attention was given to groups 3 and 4, the species which could achieve the largest stems.

Korup. Of the 410 taxa recorded, 197 were selected for detailed examination in the two abundance classes (Tables 3 and 4). The smaller-stemmed, common species of groups 1 and 2 are listed in Appendix 1 (less common species are not shown), and the larger-stemmed species in groups 3 and 4 are given in Tables 5 and 6.

Douala-Edea. Of the 230 taxa recorded, 118 were selected (Tables 7 and 8); common species of groups 1 and 2 are listed in Appendix 2, and species of groups 3 and 4 are given in Tables 9 and 10.

Table 4. Less common species ($n=20-49$) at Korup classified according to four types of diameter (dbh) frequency distribution (dfd) and their occurrence and class abundances on transects P to S. Bold values indicate number of species restricted to transects P and S in class 4.

	dfd class				All
	1	2	3	4	
dbh (cm) limit	<50	$\geq 99\%$ trees <70	<90	>1% ≥ 90	
Number of species in total	28	15	7	13	63
with uneven dfds	3	9	5	4	21
percentage uneven	(11)	(60)	(71)	(31)	(33)
Number of species very low/absent on					
P	3	2	1	3	9
P+Q	5	1	0	1	7
P+Q+R	1	1	1	4	7
Q+R	0	0	0	0	0
Q+R+S	0	0	0	1	1
R+S	0	1	0	0	1
S	5	1	0	0	6
Others	2	0	0	1	3
Sum	16	6	2	10	34
Number of trees on transects					
P	181	120	35	48	384
Q	168	107	32	50	357
R	303	147	55	39	544
S	252	143	81	236	712
All	904	517	203	373	1997
Density (ha^{-1})	42	24	9	17	23

Unevenness of dfds across transects

This aspect was investigated for Korup but not for Douala-Edea. At the former site more comparisons (6) were possible than at the latter site (2). The aim was to determine whether species had similar dfds across the forest.

Korup. For each species in the common and less common abundance classes, the cumulative percentage frequency of trees in increasing 10 cm dbh classes was found for each transect. Those species with >20% differences between transects in the 10- <30 cm range of dbh were labelled 'uneven' and indicated as such in Tables 5 and 6 and in Appendix 1. (A transect which lacked trees of the species was omitted from the comparisons.) Sample sizes for most species were too small to similarly compare higher dbh classes.

Approximately one-third of the common and less common species showed unevenness. Closer inspection revealed that for a large majority of species, transects differed in the form of *c.* 20-30% versus *c.* 50-70%. Among the common species only 10/134 had relatively fewer trees in the 10- <30 cm range on P compared with QRS and only one had none; and correspondingly among the less common species 4/63 had fewer in that class on P and two had none. More noticeably, among the nine uneven and less common species in groups 3 and 4, four had no trees in the 10- <30 cm class on transect Q, although for these four cases the total number of trees on Q was in the range 1 to 6 only.

Overall, the relative proportions of trees in the lower size classes was roughly constant: There were no clear cases of species (with sample sizes per transect > 10 trees) having markedly different dfds on different transects.

Distribution of species abundances across transects

Scores of those selected common and less common species from the first axes of the ordinations were transformed to be greater than zero and then rescaled to simpler units for ease of comparison (see note 3, Table 5). A novel complementary graphical approach to ordination was used to identify those species with zero or very low (≤ 2 individuals) abundances on transects and transect combinations. The abundances were logarithmically transformed ($\ln(n+1)$). Those species absent from a transect or combination of transects were clearly revealed, and this approach conversely defined those species restricted to a transect.

Korup. Species with low scores tended to be more abundant on transect P, whilst those with high scores tended to be more abundant on transect S (Tables 5 and 6; Appendix 1). Intermediate-scored species (in DCA) occurred on transects Q and R, but they were more often species of wide and even occurrence over all transects.

To assess the degree of similarity in species composition across transects, the following relationships were examined, for common and less common species separately: number of trees per species on transect P versus the mean number on transects Q, R and S (Fig. 3); mean number per species on transects P and Q versus mean number on transects R and S; and mean number on transects P, Q and R versus the number on transect S (Fig. 4). Transect occurrence is indicated in Tables 5 and 6, and in Appendix 1. Those species restricted to transects P or S are also highlighted in Figures 3 and 4. The middle comparison (PQ vs. RS) is not shown because it differed only marginally from the more extreme first and last comparisons; indicating that very few species occurred on Q and R which were not also on either P or S.

Douala-Edea. Those species with low scores were generally present only on transect A (but there were four exceptions due to the two outlying transect B plots) and higher-scored species had higher abundances on BCD transects (Tables 7 and 8; Appendix 2).

The graphical relationships were limited to the number of trees on transect A versus half of the sum of the number of trees on transects BCD combined (Fig. 5). This highlighted the many species restricted to transect A.

Dfd of all species on transects

Forest structure on each transect can be quantified by the dfd of all species and the different transects compared.

Korup. The numbers of trees enumerated on transects P to S were very similar (Table 1). Taken together *c.* 80% of the stems were < 30 cm dbh, and 1% ≥ 90 cm dbh. The maximum difference was 20 trees ha^{-1} (4.2% of the average transect density). Transect S had a significantly different dfd from P, Q or R ($\chi^2 = 103, 237, 109$, resp.; $\text{df} = 4$; all $P \ll 0.001$), based on the five classes shown in Table 1 (i.e. 10–<30, ..., ≥ 90 cm dbh). Transects P, Q and R did not differ significantly from one another (χ^2 values in a range of 5 to 34, $\text{df} = 4$; all $P > 0.05$). Transects P to R had a greater proportion of trees 10–<30 cm dbh (mean 82%) than S (77%) but a smaller proportion of trees ≥ 90 cm dbh (mean 2.0%) than S (3.7%). For trees ≥ 90 cm dbh, using five classes 90–<110, ..., ≥ 170 cm dbh, none of the transects

differed significantly from one another in the proportions of these largest trees (χ^2 values between 1.15 and 3.62, $df=4$; all $P>0.05$).

Douala–Edea. The density of trees was much lower on transect A than transects BCD (Table 2), with a difference of 120 trees ha^{-1} (33.8% of the average transect density). Taking all plots together, *c.* 77% of the stems were <30 cm dbh and 2% ≥ 90 cm dbh. Transects BCD had a significantly different dfd from transect A ($\chi^2=287$, $df=4$, $P\ll 0.001$; A vs. BCD/2) using the five classes in Table 2. Transect A had fewer small-stemmed trees (10– <30 cm dbh), but more large trees (≥ 30 cm dbh), than transects BCD (Table 2). Transects also differed significantly in their dfds for the five larger dbh classes (90– <110 , etc., as for Korup) ($\chi^2=22.1$, $df=4$; $P<0.001$) with transect A showing a deficiency of stems in the 90– <130 class compared with transects BCD.

Overall dfd at sites

The overall dfd quantifies the structure at each site and enables between-site comparisons.

Korup. Dfd for numbers of trees in increasing 5 cm dbh classes (5– <10 , ..., ≥ 200) showed a smooth decline. Graphs of $\ln(n+1)$ versus mid-class dbh (i.e. 12.5, 17.5, etc) showed a non-linear relationship (concave) for individual transects and all transects combined, indicating that the proportional decrease in successive dbh classes itself decreased with dbh. A close linear fit was achieved (Fig. 6) by graphing $\ln(\ln(n+1)+1)$ versus dbh, especially for the dbh range 10– <110 cm for all transects combined. (Graphs of $\ln(n+1)$ versus $\ln(dbh)$ resulted in convex relationships.)

Douala–Edea. Similar results to Korup were found. The concave log–lin graphs were linearised by the double log–lin relationship (Fig. 7), again especially for the dbh range 10– <120 cm for all transects.

Pierlot (1966) advocated a hyperbolic relationship between frequency and gbh (dbh), but for our data at Korup and Douala–Edea it gave an inferior fit to the double log–lin model.

Characterisation of dfds of species in groups

At the two sites the dfds of species in group 1 were all very similar and so were those in group 2: they lacked large trees and were not subdivided (Appendices 1 and 2).

For each site, dfd histograms were drawn for each of the common and less common species in groups 3 and 4, using 10 cm dbh classes (10– <20 , ..., ≥ 200 cm; 20 classes) and inspected. Those species which were lacking smaller trees, especially those in the range 10– <30 cm dbh, were segregated and labelled additionally as members of a ‘group 5’. (These species were therefore a subset of all species in groups 3 and 4.) Those species without a smoothly declining dfd and for which the frequencies in the first three 10 cm classes were equal to, or less than, those in at least the next three 10 cm classes qualified for group 5 status.

Korup. The dfds of individual group 5 species (common and less common combined) are shown in Figure 8, the characteristics of the group in Table 11 and the overall dfd of group 5 species in Figure 9a. The dfds of common species for the four groups, with group 5 trees removed from groups 3 and 4 (Fig. 10), show a mixture of simple linear declines in numbers on graphs of $\ln(n+1)$ versus dbh for groups 1 and 4 but more convex relationships for groups 2 and 3 (Fig. 11a). The

Table 5. Common species ($n \geq 50$) at Korup with (a) $> 1\%$ of trees > 70 cm dbh [group 3], and (b) $> 1\%$ of trees > 90 cm dbh [group 4] ranked according to sample size (n) with unevenness of frequency distributions across transects (UE), the rescaled ordination axis 1 score (D_1) and indication of absence (or very low abundance) on transects (T). *Indicates species with relatively low tree frequencies in smaller size classes [group 5].

	Fam ¹	n	UE ²	D_1^3	T ⁴
(a)					
<i>Cola lateritia</i> K. Schum.	Ster	356	+	27	
<i>Cola verticillata</i> (Thonn.) Stapf. ex A.Chev.	Ster	244	+	29	
<i>Dacryodes edulis</i> (G.Don) H.J.Lam.	Burs	239		41	
<i>Homalium</i> sp.	Samy	219		52	-P/-PQ
<i>Scytopetalum klaineianum</i> Pierre ex Engl.	Scyt	219		34	
<i>Didelotia africana</i> Baill.	Caes	164		15	
<i>Coula edulis</i> Baill.	Olac	119		16	-S
<i>Acioa barteri</i> (Hook. f. ex Oliv.) Engl.	Chry	114	+	48	-P/-PQ
* <i>Mammea africana</i> Sabine	Gutt	112	+	13	
<i>Julbernardia seretii</i> (De Wild.) Troupin	Caes	108		36	-P
<i>Xylopia aethiopica</i> (Dunal) A. Rich.	Anno	106	+	27	
<i>Azelia bipindensis</i> Harms	Caes	106	+	30	
<i>Fagara tessmannii</i> Engl.	Ruta	92	+	26	
<i>Homalium letestui</i> Pellegr.	Samy	90	+	39	
<i>Endodesmia calophylloides</i> Benth.	Hype	83	+	20	
* <i>Caloncoba glauca</i> (P. Beauv.) Gilg	Flac	77	+	34	
* <i>Tapura africana</i> Oliv.	Dich	73		50	-P/-PQ
<i>Memecylon normandii</i> Jac.-Fél.	Mela	70		22	
<i>Diospyros gracilescens</i> Gürke	Eben	69	+	31	
Indet. sp.	Rubi	53		16	-S
* <i>Mitragyna ciliata</i> Aubrév. & Pellegr.	Rubi	51	+	13	
(b)					
<i>Vitex grandifolia</i> Gürke	Verb	418	+	30	
<i>Irvingia gabonensis</i> (O'Rorke) Baill.	Irvi	389	+	36	
<i>Strephonema pseudocola</i> A. Chev.	Comb	314	+	16	-S
<i>Desbordia glaucescens</i> (Engl.) Van Tiegh.	Irvi	275	+	49	-P
<i>Anthonotha fragrans</i> (Bak.f.) Exell & Hillcoat.	Caes	184	+	33	
* <i>Vitex</i> sp.	Verb	159		41	
<i>Erismadelphus exsul</i> Mildbr. var <i>platyphyllus</i> Keay & Stafleu	Voch	147	+	36	
<i>Berlinia bracteosa</i> Benth.	Caes	146	+	17	
* <i>Coelecarpon preussii</i> Warb.	Myri	141		45	-P
<i>Lophira alata</i> Banks ex Gaertn. f.	Ochn	139	+	49	-PQ
<i>Tetraberlinia moreliana</i> Aubrév.	Caes	125		3	-QRS/-RS/-S
* <i>Scyphocephalum mannii</i> (Benth.) Warb.	Myri	123		54	-P/-PQ
* <i>Staudtia stipitata</i> Warb.	Myri	121		40	
<i>Trichilia heudelotii</i> Planch. ex Oliv.*	Meli	119	+	46	
<i>Tetraberlinia bifoliolata</i> (Harms) Hauman	Caes	106		3	-QRS/-RS/-S
* <i>Araliopsis soyauxii</i> Engl.	Ruta	98		49	-P/-PQ
* <i>Erythrophleum ivorense</i> A. Chev.	Caes	79	+	41	
<i>Discoglypsemna caloneura</i> (Pax.) Prain	Euph	77	+	28	
<i>Syzygium rowlandii</i> Sprague	Myrt	66	+	32	
* <i>Alstonia congensis</i> Engl.	Apoc	61	+	45	
<i>Hymenostegia bakeriana</i> Hutch. & Dalz.	Caes	53	+	21	
<i>Newtonia duparquetiana</i> (Baill.) Keay	Mimo	52	+	25	
* <i>Cleistopholis staudtii</i> Engl. & Diels	Anno	51	+	40	

Table 6. Less common species ($n=20-49$) at Korup with (a) $>1\%$ of trees >70 cm dbh [group 3], and (b) $>1\%$ trees >90 cm dbh [group 4] ranked according to sample size (n). UE, D_1 and T as Table 5; *Indicates species with relatively low tree frequencies in smaller size classes [group 5].

	Fam ¹	n	UE	D_1	T
(a)					
<i>Pachypodanthium confine</i> Engl. & Diels	Anno	44	+	27	
* <i>Guarea thompsonii</i> Sprague & Hutch.	Meli	33	+	41	
*Indet. sp.	Anac	31	+	33	
<i>Microdesmis</i> sp.	Pand	26	+	27	
* <i>Sterculia tragacantha</i> Lindl.	Ster	25		57	-P/-PQ/-PQR
* <i>Anthothona cladantha</i> (Harms) J. Léon.	Caes	24	+	34	
* <i>Pseudospondias longifolia</i> Engl.	Anac	20		53	-P
(b)					
<i>Memecylon</i> sp.	Mela	38		52	-P/-PQ/-PQR
* <i>Klainedoxa gabonensis</i> Engl. var. <i>oblongifolia</i> Engl.	Irvi	36		43	-P
* <i>Piptadeniastrum africanum</i> (Hook. f.) Brenan	Mimo	35		52	-P/-PQ
* <i>Microberlinia bisulcata</i> A. Chev.	Caes	34		0	-QRS/-RS/-S
* <i>Pterocarpus</i> sp.	Papi	33	+	44	
<i>Chrysophyllum delevoiyi</i> De Wild.	Sapo	33	+	57	-P/-PQ/-PQR
* <i>Parkia bicolor</i> A. Chev.	Mimo	28		42	
* <i>Hylodendron gabunense</i> Taub.	Caes	27		56	-P/-PQ/-PQR
* <i>Gilbertiodendron brachystegioides</i> (Harms) J. Léon.	Caes	26		24	-S
* <i>Sapium ellipticum</i> (Krauss) Pax	Euph	23	+	39	-P
* <i>Pycnanthus angolensis</i> (Welw.) Warb.	Myri	20		57	-P/-PQ/-PQR
<i>Milletia</i> sp.	Papi	20		51	-P
* <i>Lecomptedoxa klaineana</i> (Pierre ex Engl.) Dubard	Sapo	20	+	20	

¹Family abbreviations as Table 5 plus: Anac, Anacardiaceae; Pand, Pandaceae; Papi, Papilonoideae (Leguminosae); Sapo, Sapotaceae.

convexity for group 2 was more pronounced among the less common species (Fig. 11b).

After removal of the common group 5 species, 99% of group 3 trees were <80 cm dbh and 99% of group 4 trees were <110 cm dbh. Plotted against the maximum (99%) dbh limit of each of the groups 1 to 3 (i.e. <50 , <70 and <90 cm) the slopes of the $\ln(n)$ -dbh graphs in Figure 11a themselves declined exponentially ($P < 0.05$). The extrapolated group 4 maximum dbh (to include 99% of trees) was 101 cm.

To estimate the lack of trees in the lower size classes of group 5 species combined,

Notes to Table 5:

¹Abbreviations: Anno, Annonaceae; Apoc, Apocynaceae; Burs, Burseraceae; Caes, Caesalpinioideae (Leguminosae); Chrys, Chrysobalanaceae; Comb, Combretaceae; Dich, Dichapetalaceae; Eben, Ebenaceae; Euph, Euphorbiaceae; Flac, Flacourtiaceae; Gutt, Guttiferae; Hype, Hypericaceae; Irvi, Irvingiaceae; Mela, Melastomataceae; Meli, Meliaceae; Mimo, Mimosoideae (Leguminosae); Myri, Myristicaceae; Myrt, Myrtaceae; Ochn, Ochnaceae; Olac, Olacaceae; Rubi, Rubiaceae; Ruta, Rutaceae; Samy, Samydeaceae; Scyt, Scyttopetalaceae; Ster, Sterculiaceae; Verb, Verbenaceae; Voch, Vochysiaceae.

²Unevenness in cumulative % dbh frequencies; + indicates ≥ 2 transects different by $\geq 20\%$ in 10-30 cm class.

³(DCA ordination score +200)/10

⁴'transects(s)' means very low/nil occurrence on transect(s).

*syn. *T. monadelpha*. (Thonn.) De Wild.

Table 7. Common species ($n \geq 50$) at Douala-Edea classified according to four types of diameter (dbh) frequency distribution (dfd) and their occurrence and class abundances on transects A and on BCD combined. Bold values indicate number of species restricted to transects A and 'B to D' in class 4.

	dfd class				All
	1	2	3	4	
dbh limit (cm)	<50	$\geq 99\%$ trees <70	<90	>1% ≥ 90	
Number of species	31	20	12	13	76
Number of species very low/absent on					
A	12	7	2	3	24
BCD	1	1	2	1	5
Sum	13	8	4	4	29
Number of trees on transects					
A	1628	3056	870	491	6045
BCD	8555	5009	1210	2525	17299
All	10183	8065	2080	3016	23344
Density (ha^{-1})	153	121	31	45	351

Table 8. Less common species ($n = 15-49$) at Douala-Edea classified according to four types of diameter (dbh) frequency distribution (dfd) and their occurrence and class abundances on transects A and on BCD combined. Bold values indicate number of species restricted to transects A and BCD in class 4.

	dfd class				All
	1	2	3	4	
dbh limit (cm)	<50	$\geq 99\%$ trees <70	<90	>1% ≥ 90	
Number of species	17	10	6	9	42
Number of species very low/absent on					
A	14	7	4	0	25
BCD	0	2	0	2	4
Sum	14	9	4	2	29
Number of trees on transects					
A	36	79	25	165	305
BCD	442	203	134	150	929
All	478	282	159	315	1234
Density (ha^{-1})	7.2	4.2	2.4	4.7	18.5

the linear relationship expressed by the regression of $\ln(n+1)$ versus dbh for the 10cm dbh classes between 30- <40, ..., 190- <200 cm was determined and used to predict the dfd (Fig. 9b) in the lower classes. The total number of trees predicted was 2251, a difference of +690 (44.2% more) than the observed number 1561. In the dbh range 50- <60, ... ≥ 200 cm observed and predicted sums of trees were similar (727 and 658 respectively; a difference of 69 or 9.5%).

Douala-Edea. Individual common and less common species dfds are shown in Figure 12, the characteristics of group 5 in Table 12 and the overall dfd for the

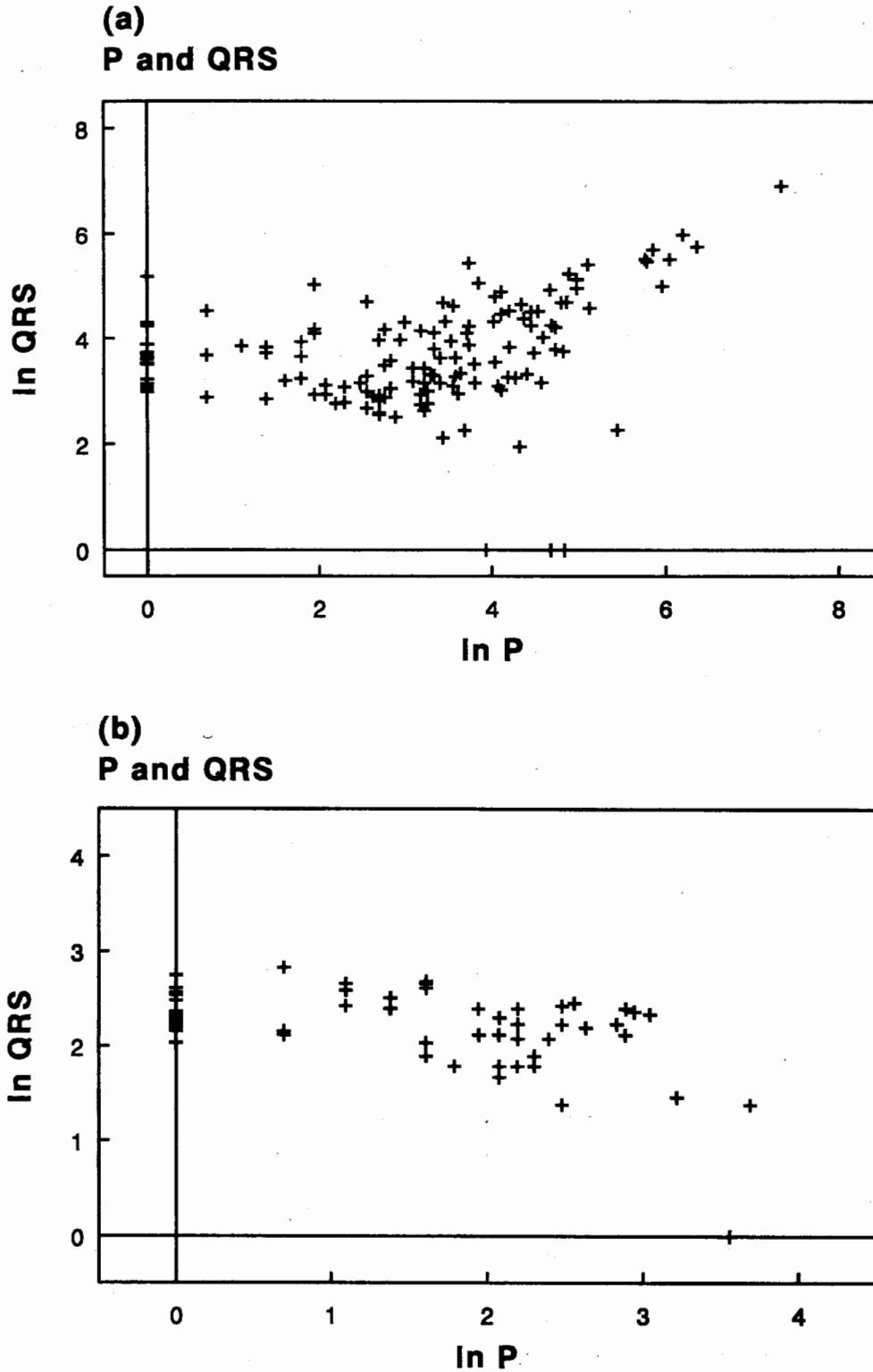


Figure 3. The relationship between the abundances (number of trees ≥ 30 cm gbh; \ln transformed) of (a) common species ($n \geq 50$), and (b) less common species ($n = 20-49$), on transect P and the mean of transects Q, R and S at Korup. (The empty lower left portion of each graph results from the minimum n in each abundance class. Ordinates and abscissae are offset to highlight zero abundances.)

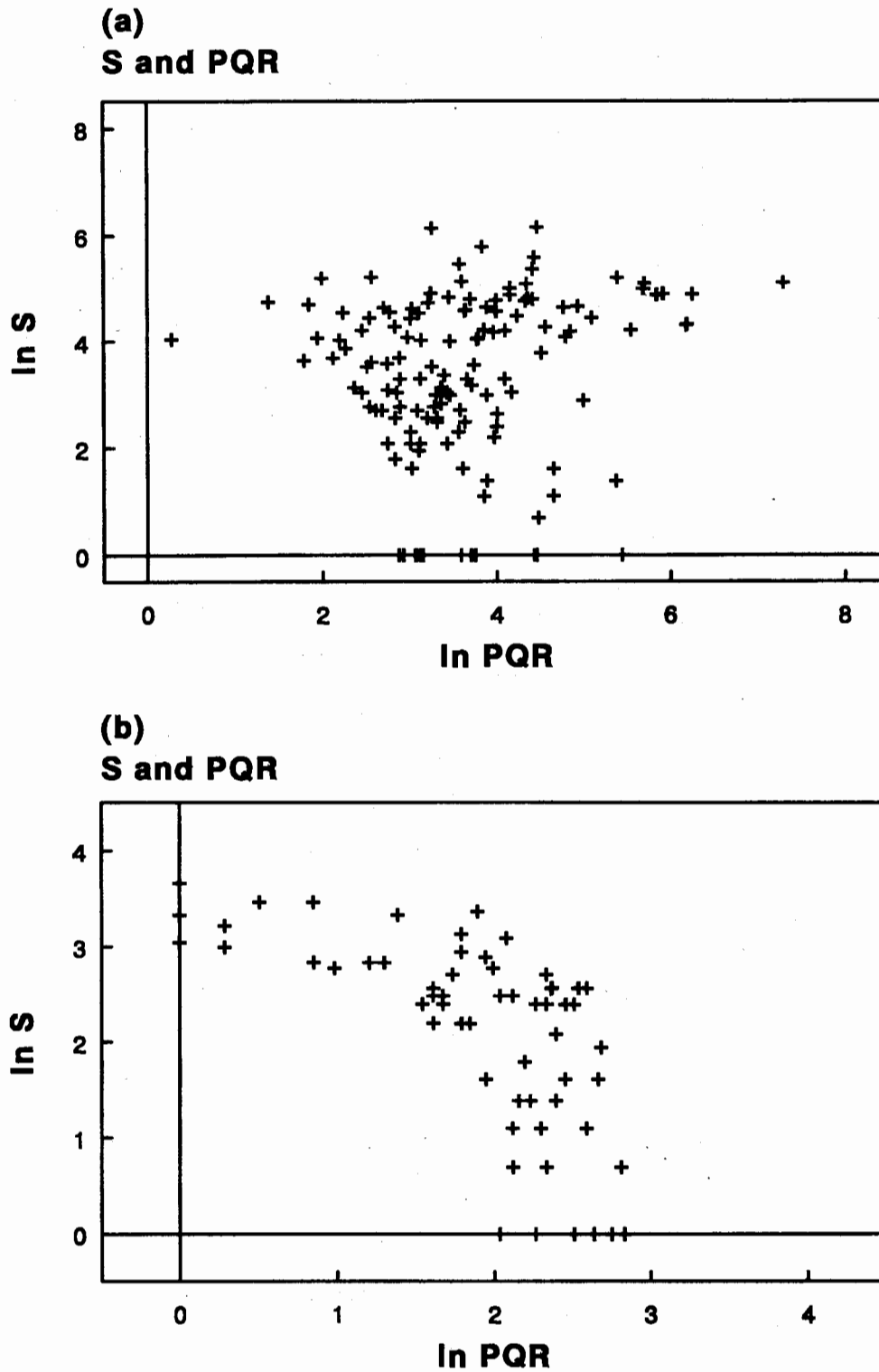


Figure 4. The relationship between the abundances (number of trees ≥ 30 cm gbh, ln transformed) of (a) common species ($n \geq 50$), and (b) less common species ($n = 20-49$), on transect S and the mean of transects P, Q and R at Korup. Comments as Figure 3.

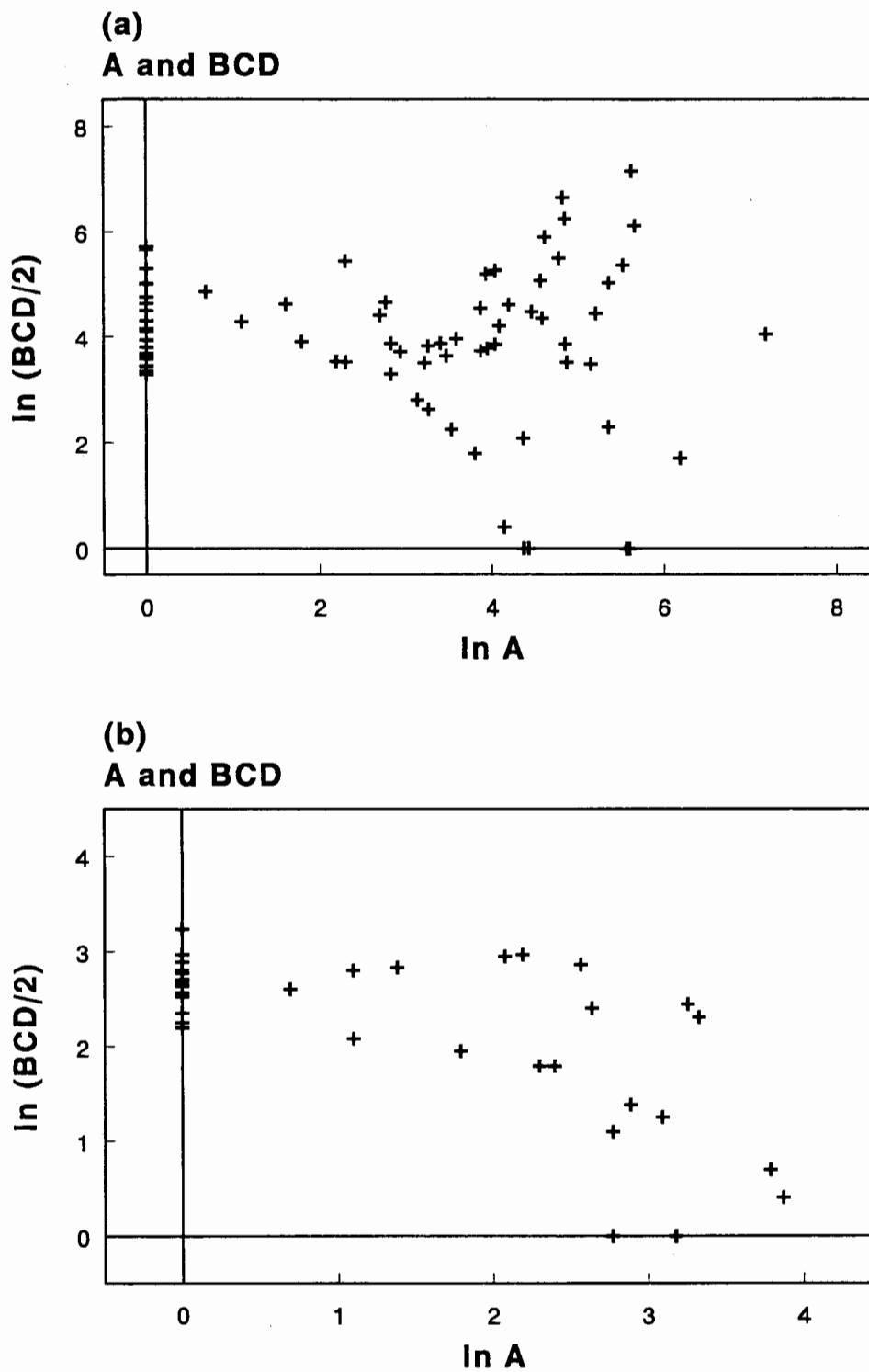


Figure 5. The relationship between the abundances (number of trees ≥ 30 cm gbh, \ln transformed) of (a) common species ($n \geq 50$), and (b) less common species ($n = 15-49$), on transect A and transects BCD/2 at Douala-Edea. Comments as Figure 3.

Table 9. Common species ($n \geq 50$) at Douala-Edea with (a) $>1\%$ of trees >70 cm dbh [group 3], and (b) $>1\%$ of trees >90 cm dbh [group 4] ranked according to sample size (n), with rescaled ordination axis 1 score (D_1) and indication of absence (or very low occurrence) on transects (T). D_1 and T as in Table 5. *Indicates species with relatively low tree frequencies in smaller size classes [group 5].

	Fam ¹	n	D_1	T
(a)				
<i>Beilschmiedia</i> cf. <i>gaboonensis</i> (Meisn.) Benth. & Hook. f.	Laur	407	37	
<i>Pausinystalia johimbe</i> (K. Schum.) Pierre ex Beille	Rubi	264	35	
<i>Gluema ivorensis</i> Aubrév. & Pellegr.	Sapo	260	9	-BCD
<i>Stephonema mannii</i> Hook. f.	Comb	237	12	
<i>Mammea africana</i> Sabine	Gutt	221	29	
<i>Grewia coriacea</i> Mast.	Tili	146	53	-A
<i>Maprounea membranacea</i> Pax & K. Hoffm.	Euph	137	29	
<i>Magnistipula glaberrima</i> Engl.	Chry	124	38	
<i>Anthostema aubryanum</i> Baill.	Euph	115	7	
* <i>Uapaca staudtii</i> Pax	Uapa	63	18	-BCD
<i>Guibourtea demeusei</i> (Harms) J. Léon.	Caes	55	38	-A
<i>Pachypodanthium confine</i> Engl. & Diels	Anno	51	27	
(b)				
<i>Coula edulis</i> Baill.	Oiac	1661	44	
<i>Lophira alata</i> Banks ex Gaertn. f.	Ochn	252	32	
* <i>Cynometra hankei</i> Harms	Caes	178	56	-A
<i>Diospyros gracilescens</i> Gürke	Eben	138	35	
<i>Anthocleista vogelii</i> Planch.	Loga	129	23	
* <i>Ctenolophon englerianus</i> Mildbr.	Cten	111	14	
* <i>Strombosiopsis tetrandra</i> Engl.	Oiac	106	29	
<i>Casearia stipitata</i> Mast.	Samy	89	25	
<i>Strychnos mimifensis</i> Gilg. ex Leeuw.	Loga	78	40	-A
* <i>Librevillea klainei</i> (Pierre ex Harms) Hoyle	Caes	78	12	-BCD
<i>Berlinia craibiana</i> Bak. f.	Caes	75	50	-A
* <i>Sacoglottis gabonensis</i> (Baill.) Urb.	Humi	68	32	
<i>Trichilia zenkeri</i> Harms*	Meli	53	33	

¹Family abbreviations as Table 5 plus: Cten, Ctenolophonaceae; Humi, Humiricaceae; Loga, Loganaceae; Laur, Lauraceae; Tili, Tiliaceae; Uapa, Uapacaceae. *syn: *T. welwitschii* C.DC.

group in Figure 13a. From the smoothly declining dfds in groups 1 to 4 with group 5 species removed (Fig. 14), the graphs of $\ln(n+1)$ versus dbh showed linear relationships for groups 1, 2 and 3, and marginally so for group 4 common species (Fig. 15a). Among the less common species (Fig. 15b) a similar result was found, though less clearly because of the smaller sample sizes.

Removal of the group 5 species led to 99% of groups 3 and 4 trees being <80 and <130 cm dbh respectively. The $\ln(n)$ -dbh slopes for groups 1 to 3 (Fig. 15a) also declined exponentially with maximum group dbh, though not significantly ($P < 0.10$). The extrapolated dbh maximum (to include 99% of trees) for group 4 was 120 cm.

To predict the lacking trees for group 5 species, the linear regression of $\ln(n+1)$ versus dbh for the 10 cm dbh classes from 50- <60 , ..., 180- <190 cm was found (Fig. 13b). The total number of trees predicted was 1802, a difference of +799 (79.7% more) than the observed number of 1003. In the dbh range 50- <60 , ...,

Table 10. Less common species ($n=15-49$) at Douala-Edea with (a) $>1\%$ trees >70 cm dbh [group 3], and (b) $>1\%$ trees >90 cm dbh [group 4] ranked according to sample size (n). D_1 and T as Table 5. *Indicates species with relatively low tree frequencies in smaller size classes [group 5].

	Fam ¹	n	D_1	T
(a)				
* <i>Cola</i> cf. <i>nitida</i> (Vent.) Schott & Endl.	Ster	35	5	
<i>Hymenostegia</i> sp.	Caes	30	46	-A
* <i>Cleistopholis</i> <i>staudtii</i> Engl. & Diels	Anno	26	51	-A
* <i>Xylopia</i> <i>aethiopica</i> (Dunal) A. Rich.	Anno	26	15	
* <i>Berlinia</i> sp.	Caes	23	31	-A
* <i>Klaineanthus</i> <i>gaboninae</i> Pierre ex Prain	Euph	19	35	-A
(b)				
* <i>Pachypodanthium</i> <i>staudtii</i> (Engl. & Diels) Engl. & Diels	Anno	46	26	
* <i>Erythrophleum</i> <i>ivorense</i> A. Chev.	Caes	45	24	
* <i>Berlinia</i> <i>bracteosa</i> Benth.	Caes	45	23	-BCD
<i>Discoglypemma</i> <i>caloneura</i> (Pax) Prain	Euph	45	43	
* <i>Odyenoyea</i> <i>gabonensis</i> (Pierre) Engl.	Sima	43	39	
* <i>Mitragyna</i> <i>stipulosa</i> (DC) Kuntze	Rubi	33	13	
* <i>Klainedoxa</i> <i>gabonensis</i> Engl. var. <i>microphylla</i> Pellegr.	Irvi	23	16	
* <i>Symphonia</i> <i>globulifera</i> Linn. f.	Gutt	20	9	
* <i>Strephonema</i> <i>pseudocola</i> A. Chev.	Comb	15	21	-BCD

¹Family abbreviations as Table 5 plus: Sima, Simaroubaceae.

Table 11. Proportions of species with group 5 diameter (dbh) frequency distribution (dfd) in four abundance classes at Korup.

Abundance (n)	dfd class		%
	3	4	3+4
Common:			
≥ 200	0/5	0/4	0
$\geq 100 < 200$	1/7	4/11	27
$\geq 50 < 100$	3/9	4/8	41
Less common:			
$\geq 20 < 50$	5/7	10/13	80
Sum	9/28	18/36	42
Number of trees	1146	415	23.0

Table 12. Proportions of species with group 5 diameter (dbh) frequency distribution (dfd) in four abundance classes at Douala-Edea.

Abundance (n)	dfd class		%
	3	4	3+4
Common:			
≥ 200	0/5	0/2	0
$\geq 100 < 200$	0/4	3/5	33
$\geq 50 < 100$	1/3	2/6	33
Less common:			
$\geq 15 < 50$	5/6	8/9	87
Sum	6/18	13/22	48
Number of trees	604	399	18.0

≥ 200 cm observed and predicted sums were very close (620 and 610 respectively; a difference of 10 or 1.6%).

Comparisons between Korup and Douala-Edea

Of the 197 common and less common species at Korup and the 118 at Douala-Edea, 52 were common to both sites. From the total species lists further species are present at both sites but with lower numbers of individuals on one or both; e.g. 19 further common and less common species occurred rarely at Douala-Edea ($n < 15$), and these were too infrequent for comparison.

Without distinguishing changes in abundance class between sites (common at Korup and less common at Douala-Edea, and *vice versa*) the 52 species were classified according to their dfd groups (1 to 4) on both sites (Table 13). Twenty-six (56%) of the species were in the same group at both sites. However, Table 13 displays a clear asymmetry. With one exception, all other species ($n = 22$) are in higher dfd groups at Douala-Edea than they were at Korup. Mostly this is a difference of one group ($n = 17$), but for five species the change was 2 or 3 groups higher. Those species showing large changes in their dfds between sites are named in Table 13. Overall, there was tendency for species to reach larger diameters at Douala-Edea than at Korup.

Four species at Korup and eleven species at Douala-Edea were also in group 5. Three species (*Cleistopholus staudtii*, *Erythrophleum ivorense*, and *Klainedoxa gabonensis*) occurred at both sites, and the one other (*Mammea africana*) was at Korup only. At Douala-Edea eight species showed group 5 dfd (*Berlinia bracteosa*, *Klainianthus gaboniae**, *Pachypodanthium staudtii*, *Strephonema pseudocola*, *Strombosiopsis tetrandra**, *Symphonia globulifera*, *Uapaca staudtii**, and *Xylopia aethiopica* (those marked * being group 2 at Korup but group 5(3 or 4) at Douala-Edea).

From the relationship between the percentage of trees in the 10–<50 cm dbh class (Tables 1 and 2), and the ratio of number of trees in group 1 to those in group 4 (common and less common species combined; Tables 3, 4, 7 and 8), and basal area (Tables 1 and 2) for transects P to S at Korup and A and BCD at Douala-Edea, Figure 16 shows that S with its higher basal area was more similar to A and to BCD, P was very close R and that Q lay at the opposite extreme to S with many smaller and fewer larger trees. Transects Q, P/R and BCD displayed a linear trend, suggesting that P, Q and R were all of a relatively lower basal area due to the fewer very large trees.

Distributions of large versus small trees at Korup

To estimate whether small trees were associated with large trees, the 27 common species (groups 3 and 4) with ≥ 100 trees each (Table 5) were selected. Large trees were defined as individuals with a dbh of ≥ 50 cm and small trees as those with a dbh of < 50 cm. The numbers of plots in which both large and small trees were present, large only were present, small only were present, and neither large nor small were present, were found and the χ^2 -test of association on the 2×2 contingency table (\pm large versus \pm small), with correction for continuity, was calculated for each species. Eighteen species showed significant associations at $P \leq 0.05$ and 15 at $P \leq 0.01$ (Table 14). In all of the significant cases, the proportion of plots with small trees was greater when there were large trees present than when they were absent

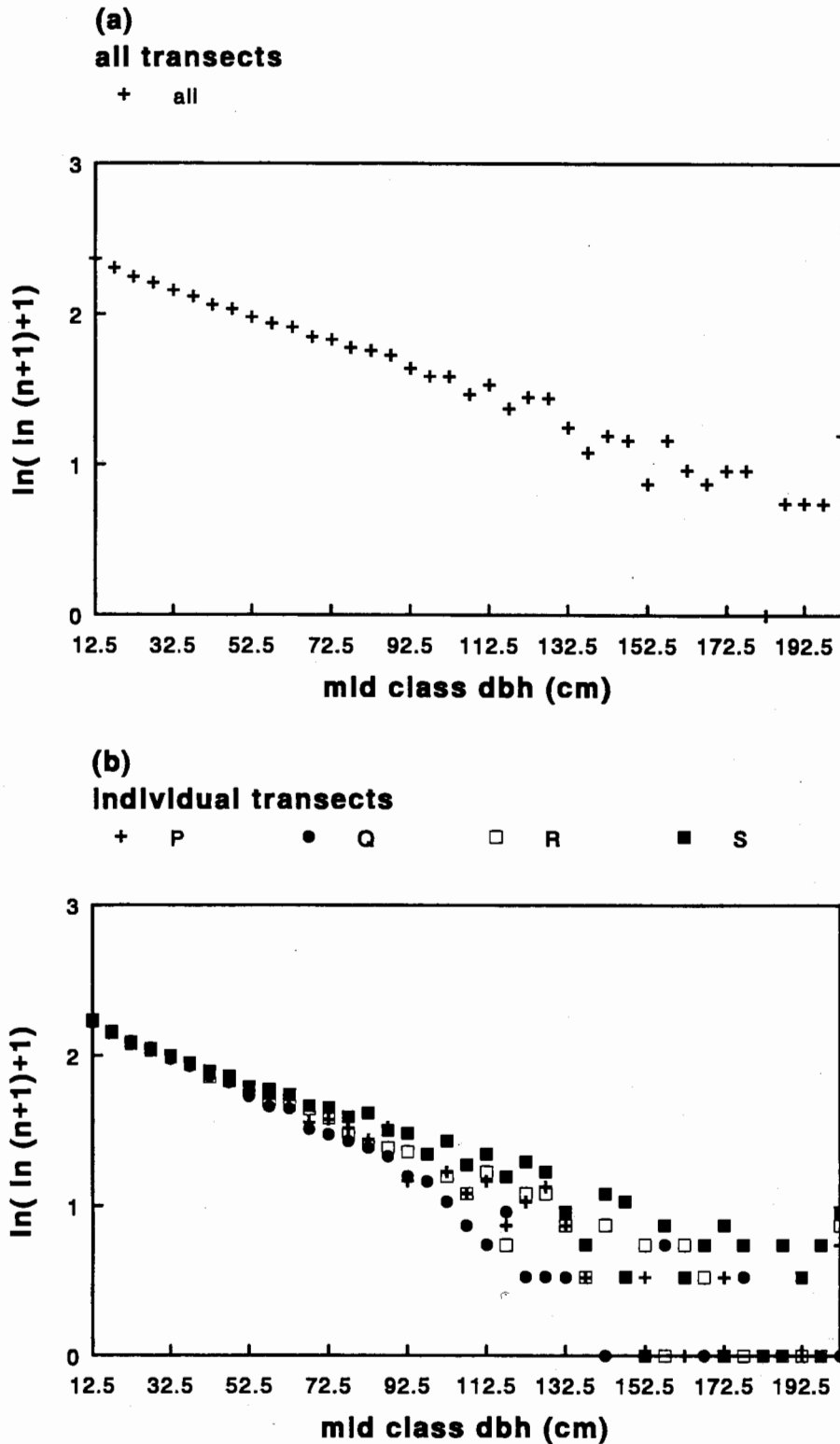


Figure 6. Double log plot of numbers of trees (≥ 10 cm dbh) against mid-class dbh in 5 cm dbh increments (10–<15, 15–<20, ..., 195–<200, ≥ 200 cm) at Korup for (a) all transects (all classes, $n=39$; $b=-0.00907$, $t_{\text{slope}}=-18.2$, $R^2=89.7\%$, $P<0.001$; dbh range 10–<110 cm, $n=20$, $b=-0.00876$, $t=-56.4$, $R^2=99.4\%$, $P<0.001$), and (b) transects P to S individually (all classes, $n=39$, $b=-0.0119$, -0.0124 , -0.0118 , -0.00925 ; $t=-18.1$, -20.8 , -19.2 , -14.6 ; $R^2=89.6$, 91.9 , 90.6 , 84.9% , respectively; all $P<0.001$).

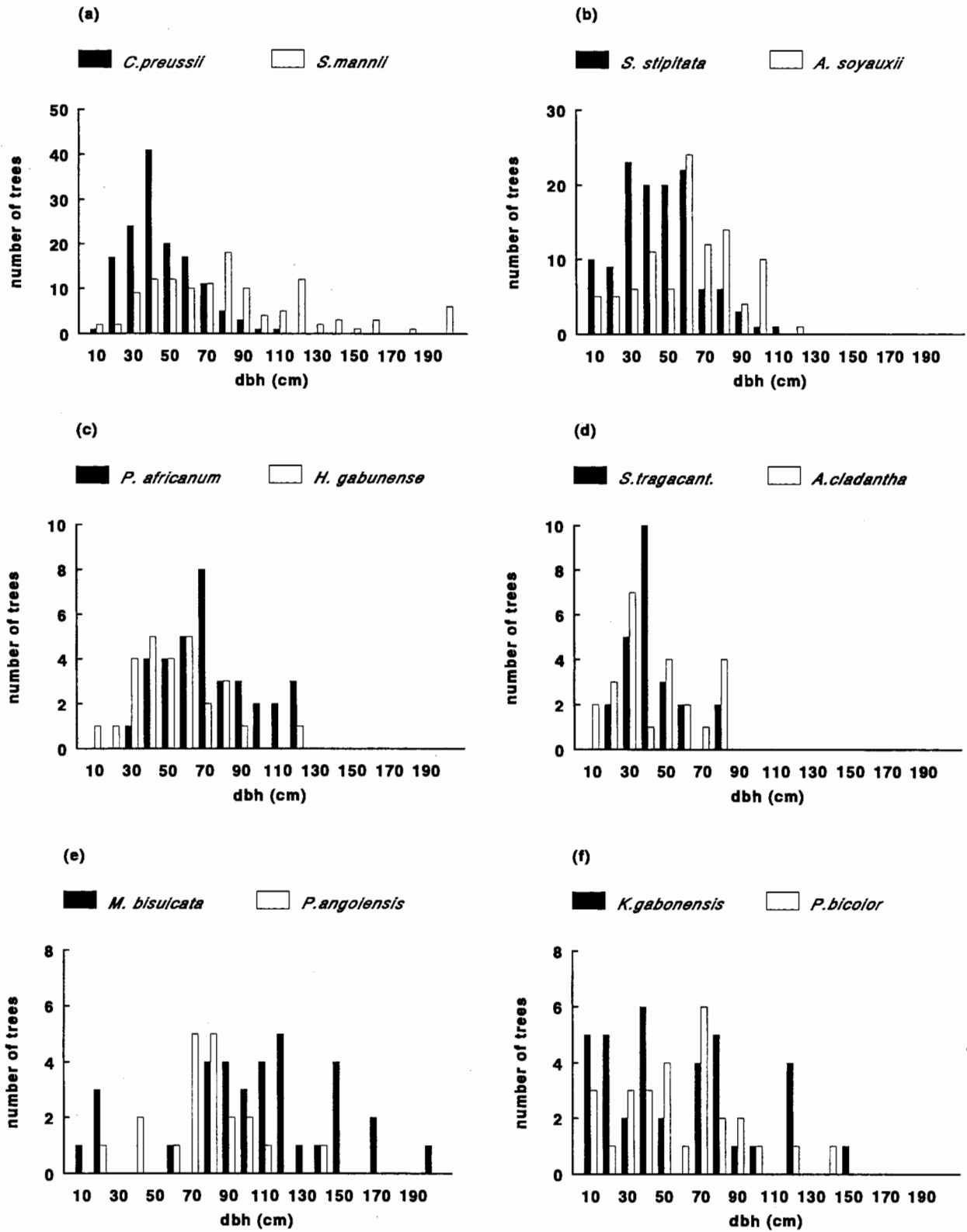


Figure 8.

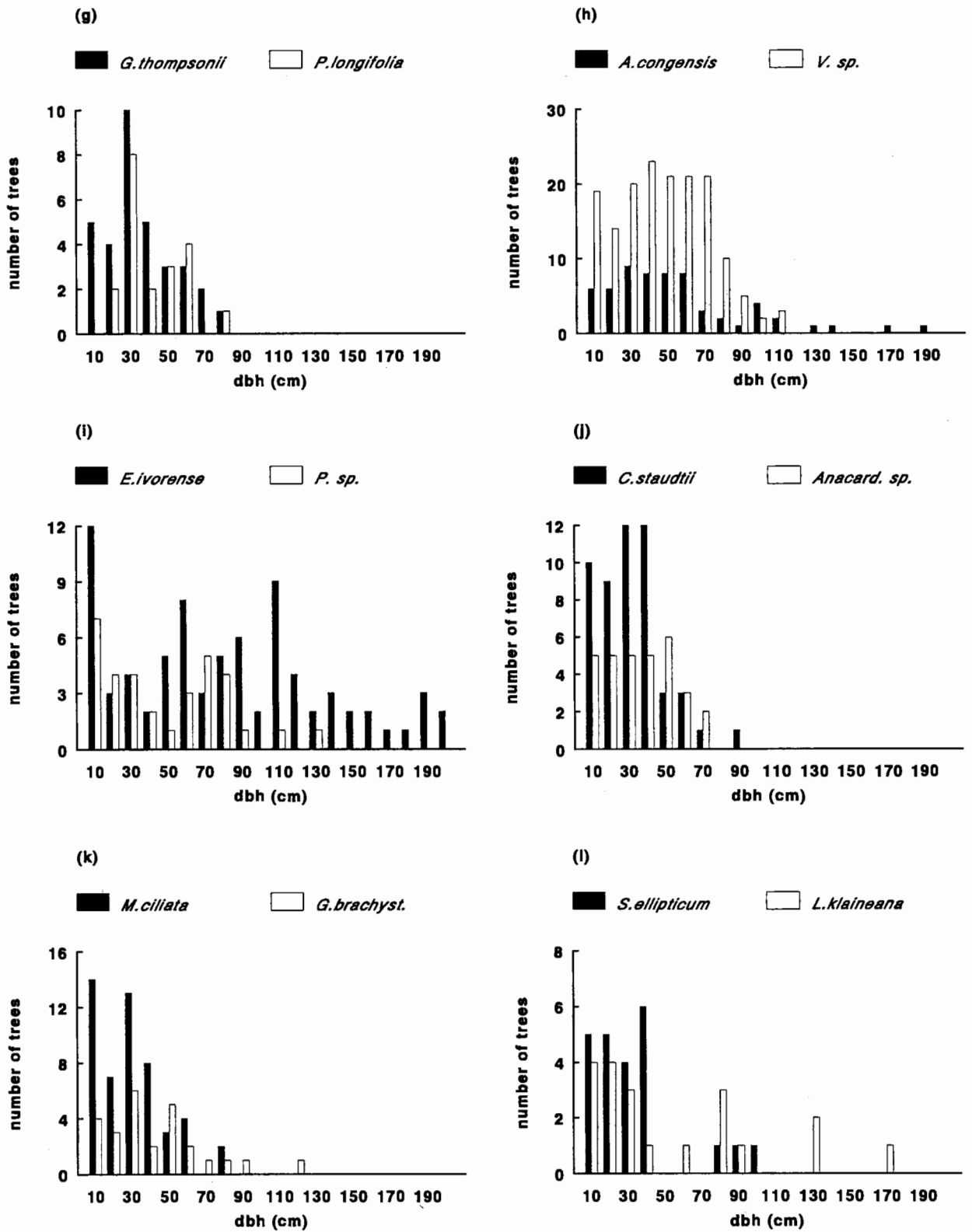


Figure 8.

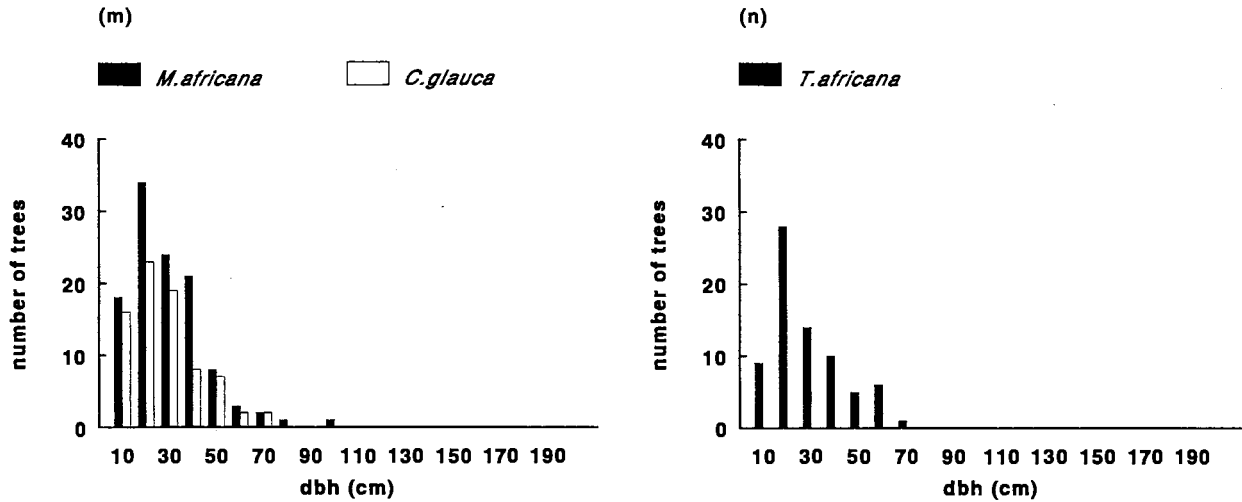


Figure 8. Diameter frequency distributions for 27 species in group 5 at Korup. (a) *Colecaryon preussii*, *Scyphocephalum mannii*; (b) *Staudtia stipitata*, *Araliopsis soyauxii*; (c) *Piptadeniastrum africanum*, *Hyloidendron gabunense*; (d) *Sterculia tragacantha*, *Anthonotha cladantha*; (e) *Microberlinia bisulcata*, *Pycnanthus angolensis*; (f) *Klainedoxa gabonensis*, *Parkia bicolor*; (g) *Guarea thompsonii*, *Pseudospondias longifolia*; (h) *Alstonia congensis*, *Vitex* sp.; (i) *Erythrophleum ivorense*, *Pterocarpus* sp.; (j) *Cleistopholis staudtii*, Anacardiaceae sp.; (k) *Mitragyna ciliata*, *Gilbertiodendron brachystegioides*; (l) *Sapium ellipticum*, *Lecomptedoxa klaineana*; (m) *Mammee africana*, *Caloncoba glauca*; (n) *Tapura africana*. 5 cm dbh classes (10–<15, 15–<20, ..., 195–<200, ≥200).

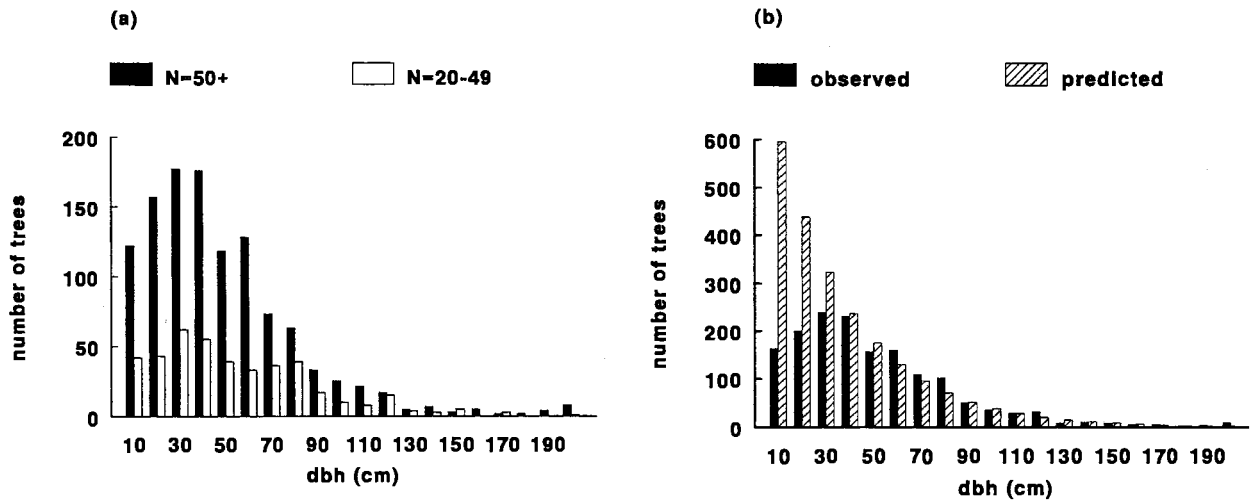


Figure 9. Diameter frequency distributions for (a) group 5 species at Korup in two abundance classes, common ($n \geq 50$) and less common ($n = 20-49$), and (b) those common and less common species combined with the predicted (extrapolated) frequencies based on the regression of observed frequencies in the range 30–<200 cm dbh ($1n(n) = 6.70 - 0.0306 \text{ dbh}$, $n = 17$, $t_{\text{slope}} = -20.6$, $R^2 = 96.4\%$, $P < 0.001$).

(Table 14). Although not as abundant as the species in Table 14, *Microberlinia bisulcata* showed also a strong positive association ($\chi^2 = 29.0$, $df = 1$, $P < 0.001$; proportions, L+ 33%, L– 0%). Small trees are therefore largely associated with large trees.

The wider extent of these large–small tree associations was examined further by

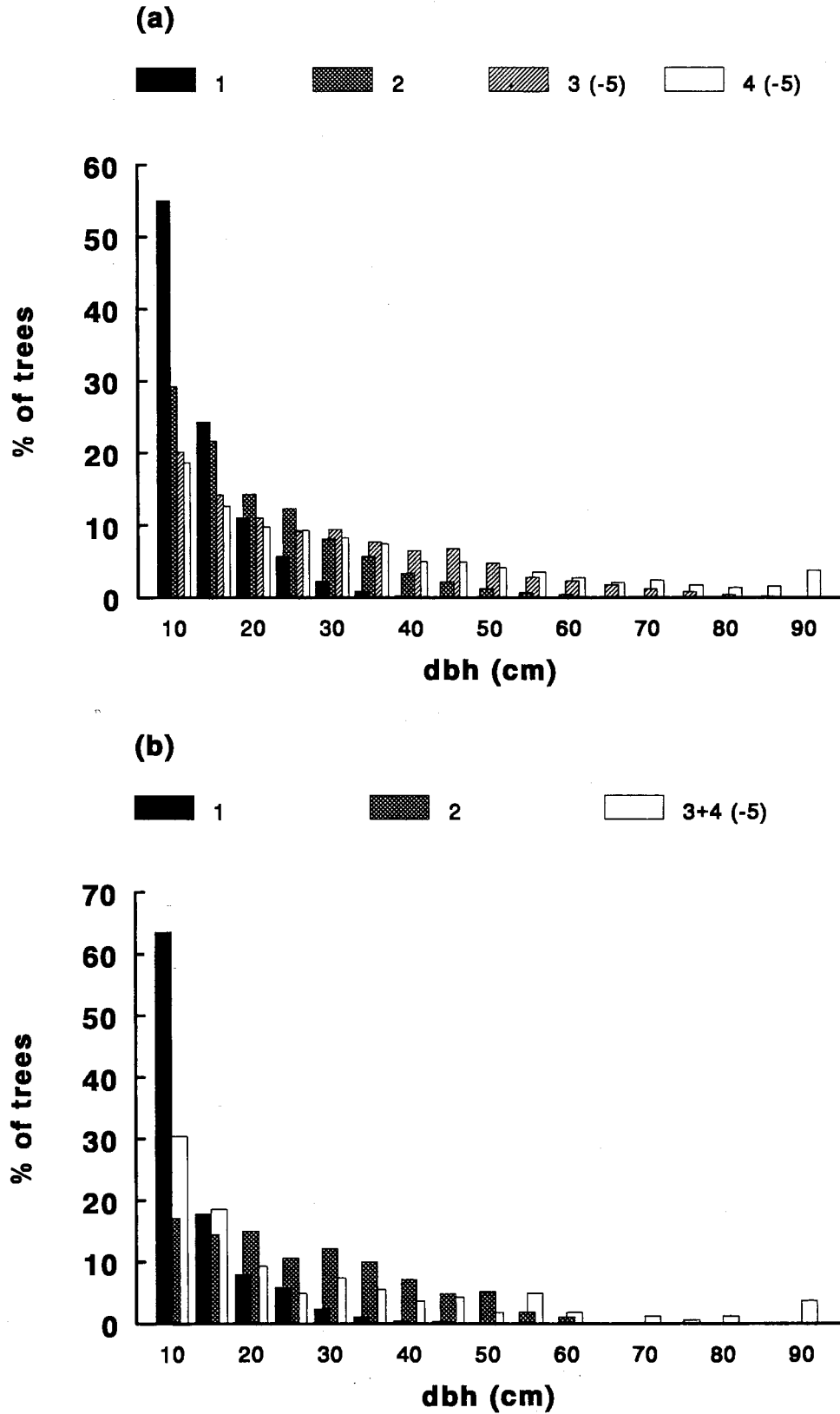


Figure 10. Diameter frequency distributions of trees at Korup in groups 1 to 4 (with group 5 species removed from 3 and 4), expressed as percentages of the totals in each group, in 5 cm dbh classes (10–<15, 15–<20, etc.) for (a) common and (b) less common species.

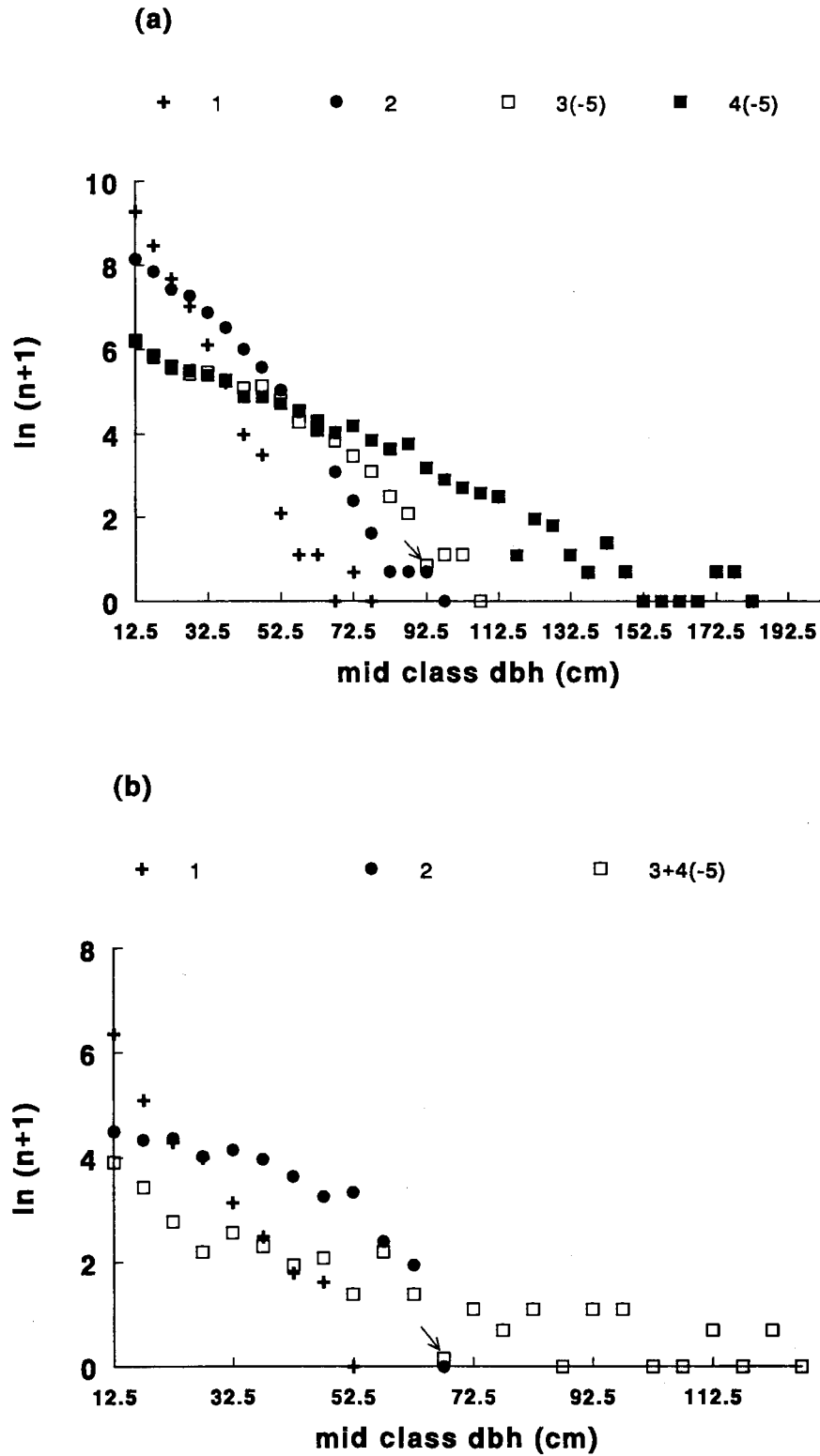


Figure 11. Relationship between logarithm of number of trees at Korup in each of the groups 1 to 4 (with group 5 species removed, as Fig. 10) and mid-class dbh for (a) common and (b) less common species. For common species: dbh range 10- < 50, < 70, < 90, < 110 cm; $n=8, 12, 16, 24$; $b=-0.1702, -0.0884, -0.0514, -0.0363$; $t_{slope}=-32.6, -20.4, -14.7, -31.0$; $R^2=99.4, 97.4, 93.5, 98.1\%$; respectively for groups 1 to 4; all $P < 0.001$). Arrowed values are placed 0.15 \ln units higher to separate overlapping symbols.

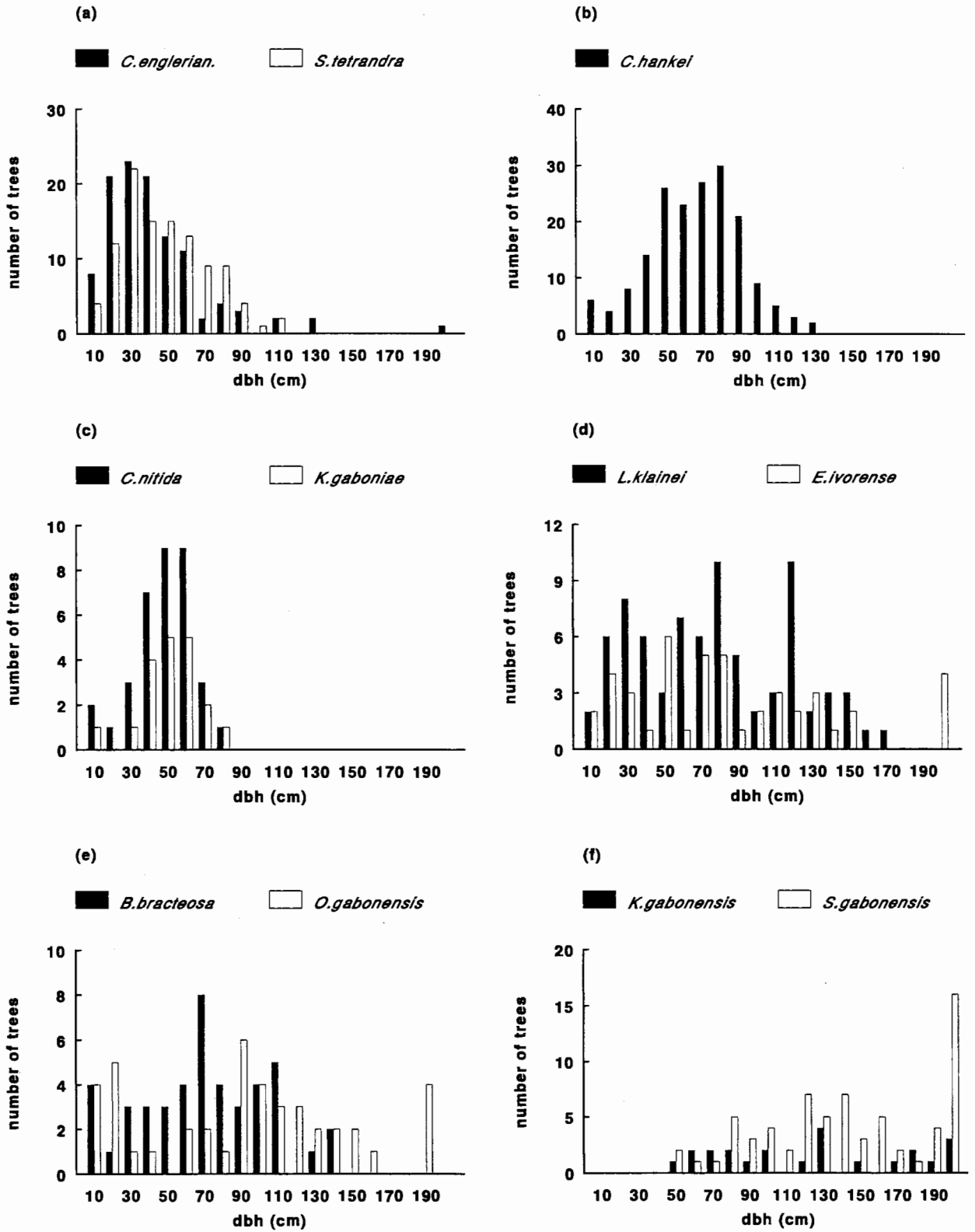


Figure 12.

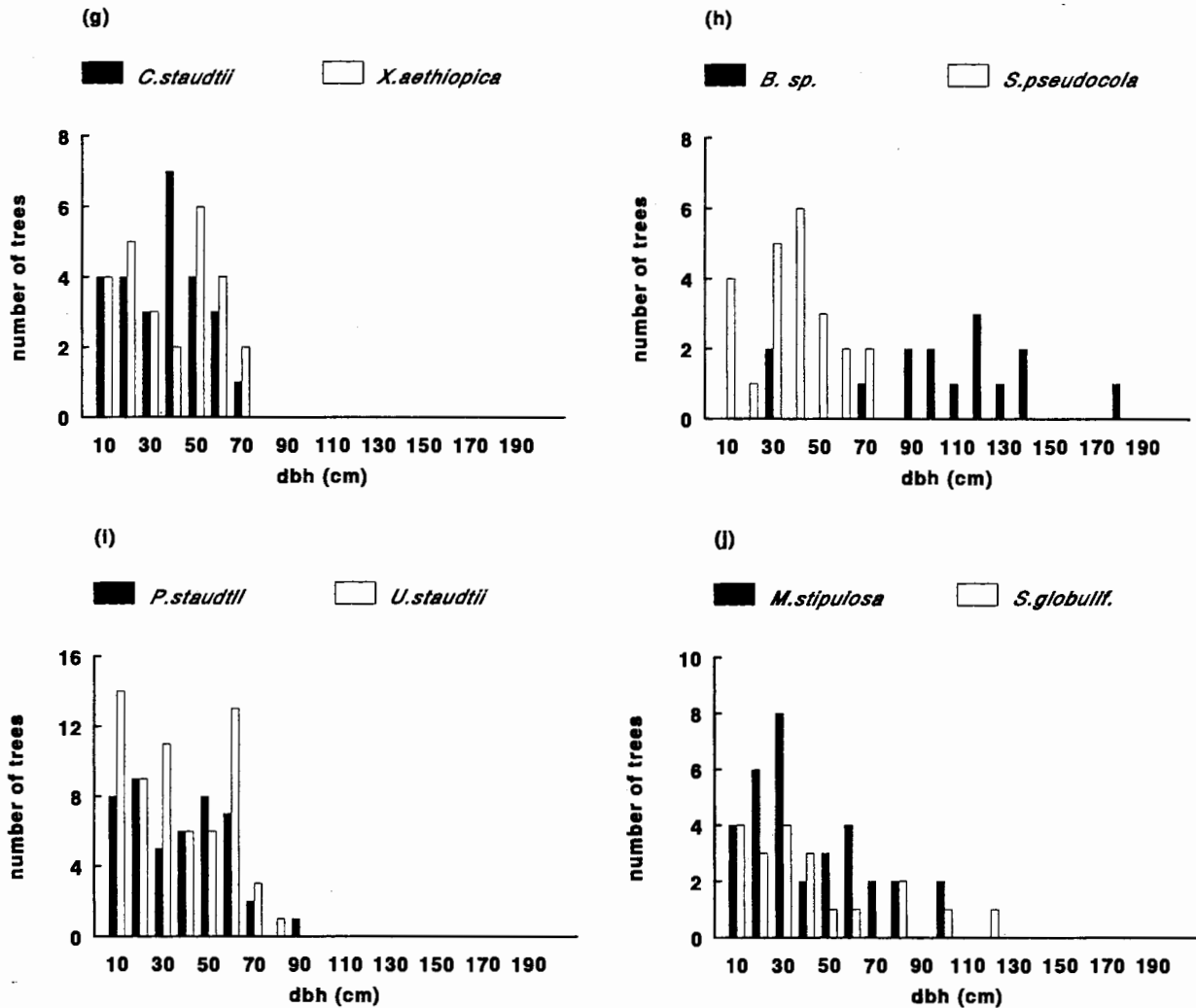


Figure 12. Diameter frequency distributions for 19 species in group 5 at Douala-Edea. (a) *Ctenolophon englerianus*, *Strombosiopsis tetrandra*; (b) *Cynometra hankei*; (c) *Cola nitida*, *Klaineanthus gabonense*; (d) *Librevillea klainei*, *Erythrophleum ivorense*; (e) *Berlinia bracteosa*, *Odyenoyea gabonensis*; (f) *Klainedoxa gabonensis*, *Sacoglottis gabonensis*; (g) *Cleistopholis staudtii*, *Xylopia aethiopica*; (h) *Berlinia* sp., *Strephonema pseudocola*; (i) *Pachypodianthum staudtii*, *Uapaca staudtii*; (j) *Mitragyna stipulosa*, *Symphonia globulifera*. 5 cm dbh classes as Figure 8.

a correspondence analysis ordination of the 135 plots at Korup, using the densities of small and large trees separately (as two pseudospecies) for the 64 common and less common species (Tables 5 and 6). Axis 1 plot scores were strongly correlated with the plots scores from the ordination of all species ($r=0.913$, $df=133$; $P \ll 0.001$), small and large trees together (Fig. 1). Examining the species ordination of this new CA, the absolute differences in scores of the corresponding small and large pseudospecies ($n=64$) in the axis 1-2 plane had a mean of 37 (rescaled) units and 95% confidence limits (based on ± 2 SD of \ln transformed data) of 18 and 68. These values were small when judged against the range of (large and small pseudo-) species scores in this plane: the 95% limits (2 SD) were -146 to 154 and -126 to 128 on axes 1 and 2 respectively. Most small-treed pseudospecies were therefore distributed similarly to the large-treed pseudospecies.

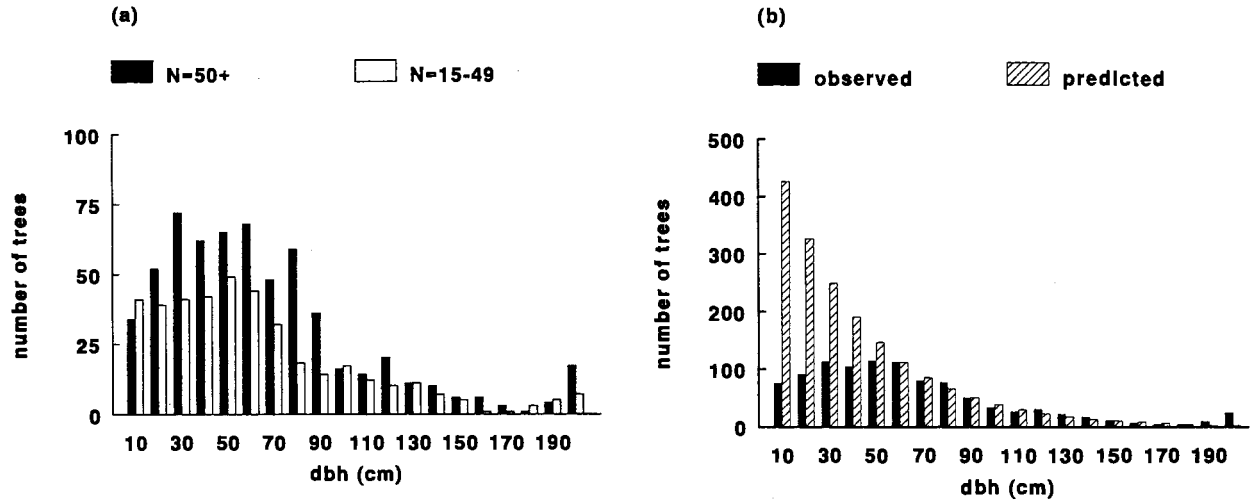


Figure 13. Diameter frequency distributions for (a) group 5 species at Douala-Edea in two abundance classes, common ($n \geq 50$) and less common ($n = 15-49$), and (b) those common and less common species combined with the predicted (extrapolated) frequencies based on the regression of observed frequencies in the range 50- < 190 cm dbh ($1n(n) = 6.32 - 0.0269 \text{ dbh}$, $n = 14$, $t_{\text{slope}} = -19.5$, $R^2 = 96.7\%$, $P < 0.001$).

Discussion

Spatial and diameter frequency distributions at Korup and Douala-Edea

Of the three main ectomycorrhizal species which dominated on transect P (Newbery *et al.* 1988), the most abundant, in terms of basal area, was *Microberlinia bisulcata*, a group 5 species (Fig. 8e). The other two species, *Tetraberlinia bifoliolata* and *T. moreliana*, were in group 4 (Table 5b). The next three most abundant, less spatially restricted, ectomycorrhizal species were *Didelotia africana* (group 3, Table 5a), and *Anthonotha fragrans* and *Berlinia bracteosa* (group 4, Table 5b). That *M. bisulcata* lacked small trees and was not likely to replace the older individuals in time was realised at the time of Newbery *et al.* (1988) and it was the principal motivation for this more comprehensive analysis of the structure of all common and less common species at Korup, and at Douala-Edea. Was *M. bisulcata* an exceptional case, or were there other tree species, not necessarily ectomycorrhizal, with similar group 5 dfds? The results of the analyses showed that indeed this large caesalpineaceous legume was not unique in this respect alone and it was one of 27 species at Korup with a broadly similar dfd which formed 42% of groups 3 and 4 species (Table 11), and a similar pattern at Douala-Edea showed 19 group 5 species forming 48% of the groups 3 and 4 species (Table 12).

A feature of *M. bisulcata* is that it attained very large diameters (Fig. 8e), some over 2+ m dbh. This species should be more closely compared with other species in group 5, which reached a similar maximum size and have the similar 'flat' dfd. *Alstonia congensis* (Fig. 8h) and *Erythrophleum ivorense* (Fig. 8i) were the closest in this respect at Korup, and *E. ivorense* again (Fig. 12d), *Klainedoxa gabonensis* (Fig. 12f), *Odyenoyea gabonensis* (Fig. 12e), and *Sacoglottis gabonensis* (Fig. 12f), were closest at Douala-Edea. If species attaining 1.5 m dbh are also considered then similarly-structured species at Korup were *Klainedoxa gabonensis* (Fig. 8f), *Lecomptedoxa klaineana* (Fig. 8l), and marginally *Parkia bicolor* (Fig. 8f), and at

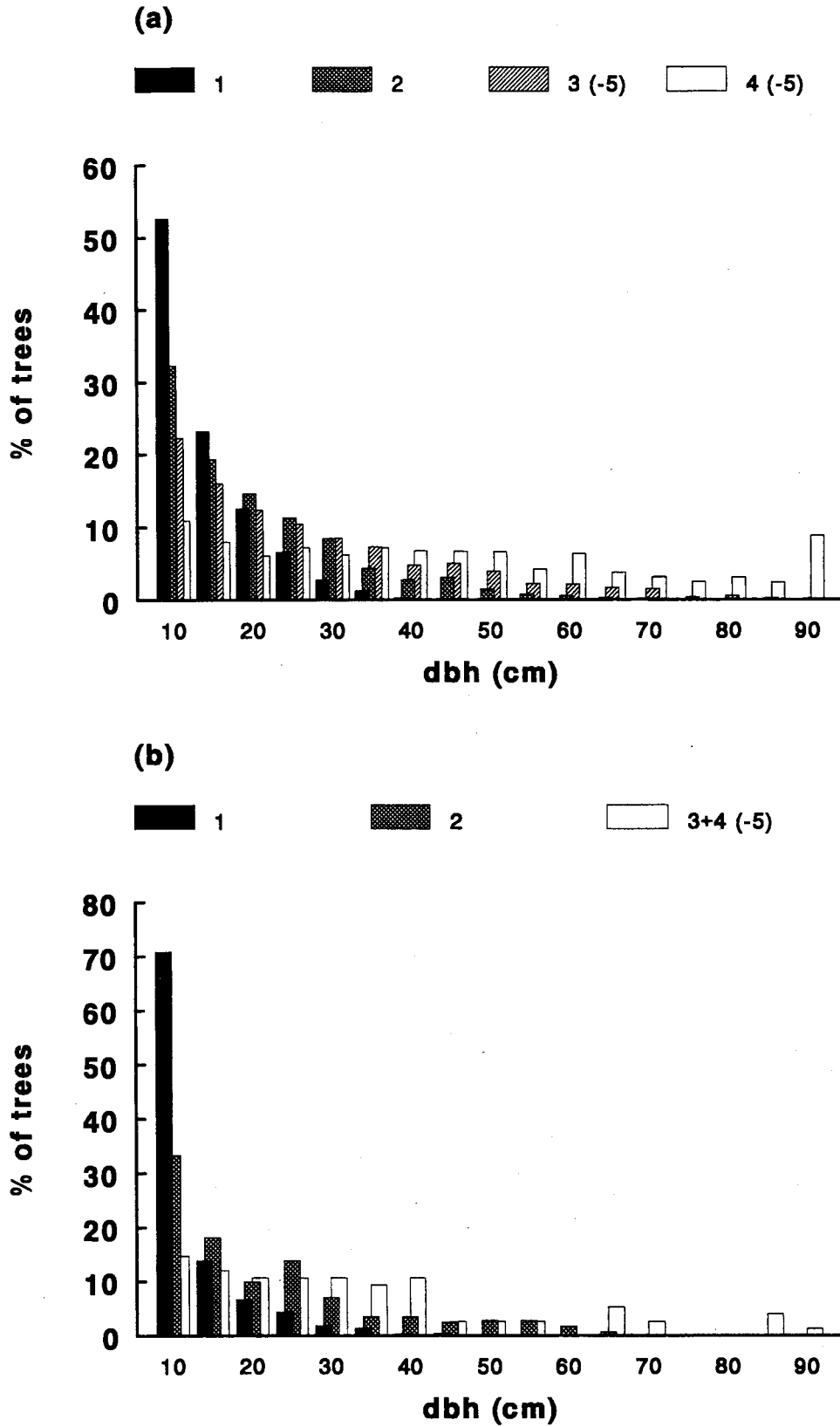


Figure 14. Diameter frequency distributions of trees at Douala-Edea in groups 1 to 4 (with group 5 species removed from 3 and 4), expressed as percentages of the totals in each group, in 5 cm dbh classes (10-<15, 15-<20, etc.) for (a) common and (b) less common species.

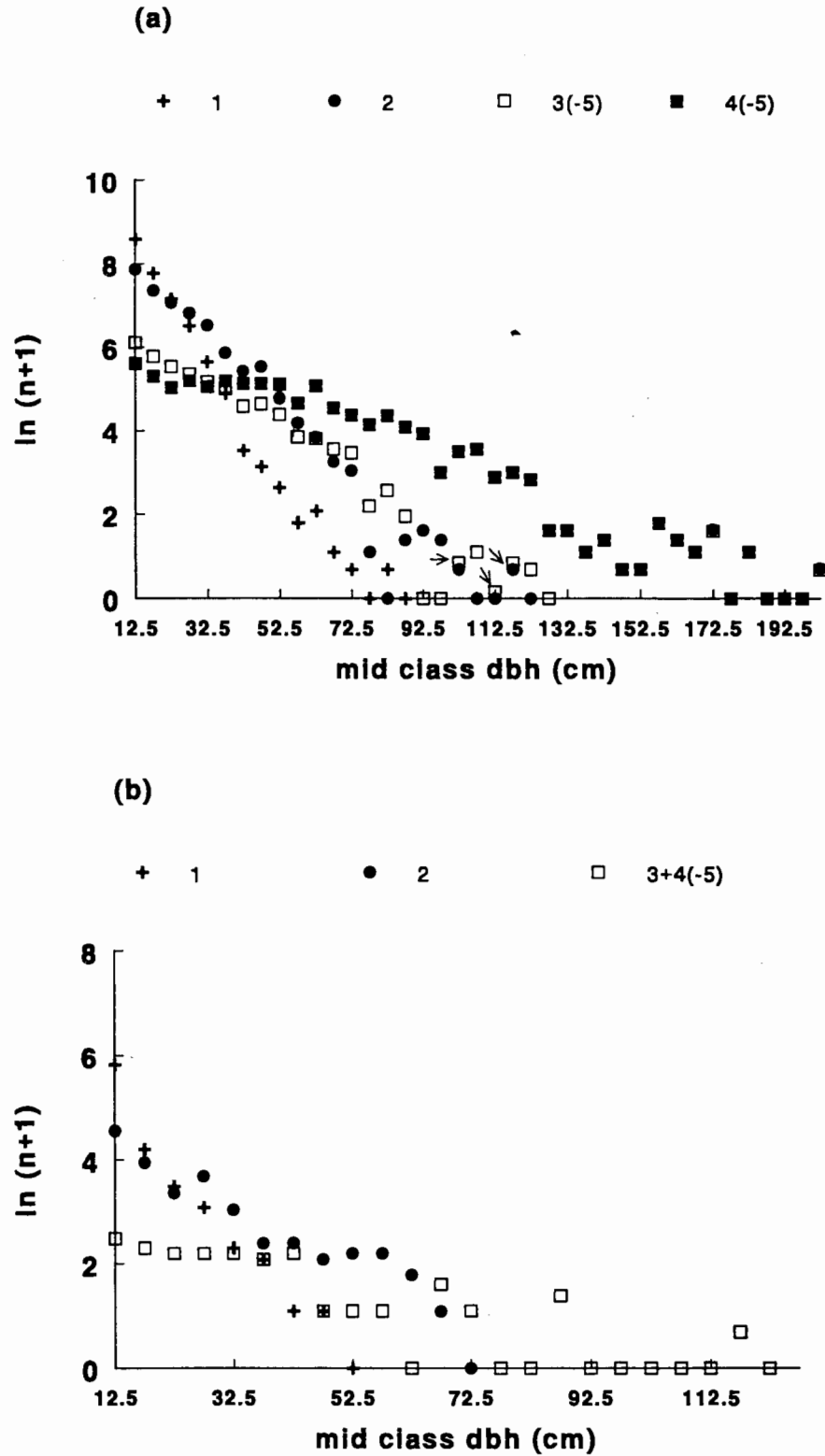


Figure 15. Relationship between logarithm of number of trees at Douala-Edea in each of the groups 1 to 4 (with group 5 species removed, as Fig. 10) and mid-class dbh for (a) common and (b) less common species. For common species: dbh range 10- < 50, < 70, < 90, < 110 cm; $n=8, 12, 16, 24$; $b=-0.1608, -0.0817, -0.0537, -0.0223$; $t_{\text{slope}}=-23.6, -25.4, -17.2, -9.8$; $R^2=98.8, 98.3, 95.2, 83.5\%$, respectively; all $P<0.001$). Arrowed values used as in Figure 11.

Table 13. Numbers of common and less common species (taken together) which occur at both Korup and Douala–Edea classified according to the four dfd groups. (Group 5 species are not removed from groups 3 and 4 here.)

		Korup dfd groups				All
		1	2	3	4	
Douala–Edea dfd groups	1	15				15
	2	9	5			14
	3		6	3	1	10
	4	1 ^a	4 ^b	2	6	13
All		25	15	5	7	52

^a*Berlinia craibiana*

^b*Anthocleista vogelii*, *Pachypodanthium staudtii*, *Strombosiopsis tetrandra*, *Symphonia globulifera*

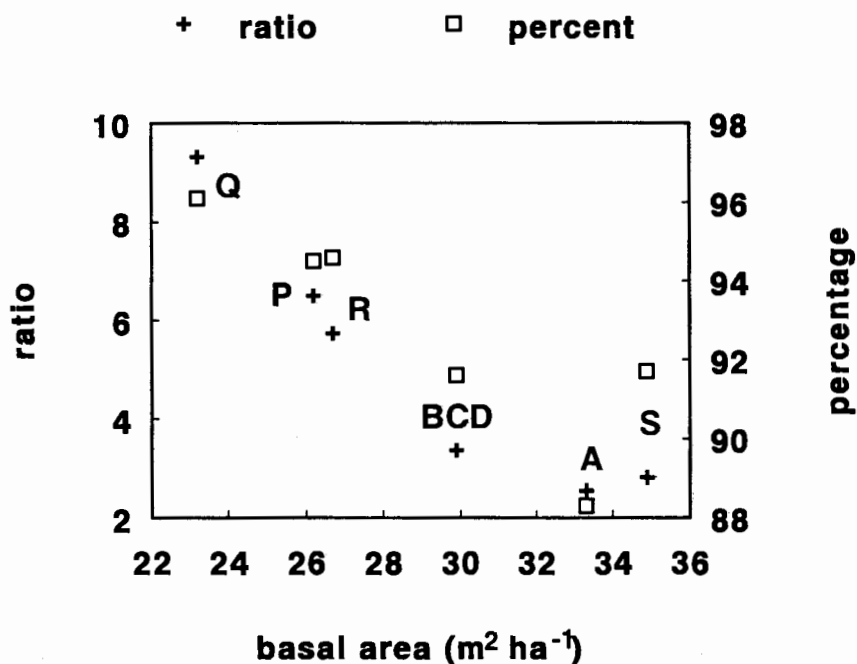


Figure 16. The ratios of the numbers of trees (of common and less common species, in group 1 to those in group 4 (group 5 not removed), and the percentage of trees in 10–<50 cm dbh class out of the total, on the four transects P to S at Korup, and on transects A and BCD combined at Douala–Edea, in relation to basal area of all trees (≥ 30 cm gbh).

Douala–Edea a *Berlinia* sp. (Fig. 12h) and *Librevillea klainei* (Fig. 12d). *Microberlinia bisulcata* had eight like-structured species, two of which occurred at both sites. *M. bisulcata* was absent from Douala–Edea.

At Korup the simple south–north gradient (over *c.* 12 km) was associated with increasing elevation, slope and soil nutrient status, being very similar to the ordination of basal areas in Gartlan *et al.* (1986). Variation existed within transects,

Table 14. The degree of association between small (< 50 cm dbh) and large (\geq 50 cm dbh) trees of 27 common species at Korup ($n=135$ plots) measured by the χ^2 statistic and the proportion of plots with small trees where those plots had large (L+) trees or lacked them (L-). The order of species follows Table 5, where families, authorities and number of trees in total for each species are given.

	χ^2	P	L+	L-
<i>Cola lateritia</i>	7.17	*	94	70
<i>Cola verticillata</i>	2.05		70	53
<i>Dacryodes edulis</i>	0.12		68	61
<i>Homalium</i> sp.	26.03	***	89	20
<i>Scytopetalum klaineianum</i>	0.38		65	57
<i>Didelotia africana</i>	49.1	***	84	15
<i>Coula edulis</i>	7.03	**	76	39
<i>Acioa barteri</i>	4.15	*	57	18
<i>Mammea africana</i>	2.64		57	31
<i>Julbernardia seretii</i>	54.92	***	92	8
<i>Xylopiya aethiopica</i>	1.69		50	30
<i>Azelia bipindensis</i>	0.04		46	48
<i>Vitex grandifolia</i>	4.78	*	89	71
<i>Irvingia gabonensis</i>	1.38		76	65
<i>Strephonema pseudocola</i>	24.99	***	89	38
<i>Desbordia glaucescens</i>	38.09	***	78	16
<i>Anthonotha fragrans</i>	1.33		60	47
<i>Vitex</i> sp.	9.97	**	47	19
<i>Erismadelphus exsul</i>	8.27	**	63	32
<i>Berlinia bracteosa</i>	41.88	***	77	16
<i>Coelecaryon preussii</i>	8.23	**	49	22
<i>Lophira alata</i>	23.12	***	63	16
<i>Tetraberlinia moreliana</i>	93.84	***	94	3
<i>Scyphocephalum mannii</i>	25.83	***	31	1
<i>Staudtia stipitata</i>	0.04		36	48
<i>Trichilia heudelotii</i>	8.38	**	71	29
<i>Tetraberlinia bifoliolata</i>	84.97	***	88	3

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

especially transect P (Newbery *et al.* 1988) but the overall comparison between transects was considered sound. Transects Q and R were overlapping to a larger degree in the basal area ordination but even for the densities P, R and S (Fig. 1) would have shown a strong floristic pattern without Q. (Axis 2 of any DCA is generally unreliable (D. McC. Newbery – review in preparation), so a within-transect interpretation would require re-ordination of each transect.) It is pertinent that transect P plots tended towards the origin of Figure 1. The most important differences were between transects P and S, with Q and R in an intermediate position.

The strong disjunction of plots at Douala–Edea was undoubtedly a swamp–dry ground effect and a similar but less clear result was found with basal area data by Newbery *et al.* (1986). Transect A was of swamp vegetation and to it were added the two separated transect B plots at the extreme of axis 1 (Fig. 2). There was some separation of D from B and C, but for transect comparisons A versus BCD was the most parsimonious. The Douala–Edea B, C and D plots were on much more homogeneous sites than the P to S ones at Korup (Newbery *et al.* 1986). At Korup very little swamp vegetation was sampled and its influence on the ordination was

negligible: only small areas of permanent wetness existed on the lower and flatter parts of transect P where streams drained southwards.

Log-log abundance graphs indicated that only four of the common and less common species (Tables 3 and 4) occurred only on transect P (Fig. 3; T = 'QRS/-RS/-S' in Tables 5 and 6). Three of these, *Tetraberlinia bifoliolata*, *T. moreliana* (Table 5) and *Microberlinia bisulcata* (Table 5, Fig. 8e) were groups 3 and 4; and all those three were the largest-stemmed ectomycorrhizal legumes. The fourth species was indeterminate and in group 1 (but $n < 200$), and also being so small-stemmed was of less consequence. Several species occurred on Q, R and S but were absent or low in abundance on P (Fig. 3). Transect S had five common and less common species (Fig. 4b; Table 4) restricted to it, namely *Chrysophyllum delevoiyi*, *Hyloidendron gabunense*, *Memecylon* sp., *Pycnanthus angolensis* and *Sterculia tragacantha* (T = '-P/-PQ/-PQR' in Table 6), all of five different families. The one caesalp, *H. gabunensis*, is non-ectomycorrhizal (Alexander 1989b). These species were also not the most dominant on S but, whilst *H. gabunense* (Fig. 8c), *P. angolensis* (Fig. 8e) and *S. tragacantha* (Fig. 8d) were group 5, they did not exceed 1.5 m dbh.

Many species on transects BCD at Douala-Edea were absent from transect A (Fig. 5) but relatively fewer were common or less common on A and absent from BCD (Tables 7 and 8; Fig. 5). Plots on transect A were on edaphically extreme sites (swamped ground) in a parallel way to plots on P at Korup which were edaphically extreme in low nutrients. Of those five species which were common or less common (Tables 9 and 10) and absent or very low in abundance on BCD (T = '-BCD'), four, *Berlinia bracteosa* (Fig. 12e), *Librevillea klainei* (Fig. 12d), *Strephonema pseudocola* (Fig. 12h) and *Uapaca staudtii* (Fig. 12i), were group 5 and *Gluema ivorensis* was not. Only *L. klainei* (caesalp; non-ectomycorrhizal) and *B. bracteosa* (caesalp; ectomycorrhizal) reached c. 1.5 m.

Therefore, whilst *M. bisulcata* was not unique in lacking smaller trees, it was special among the ectomycorrhizal species on transect P. Perhaps the one species of nearly similar dfd (having, however, more trees in the 10- < 50 cm range than *M. bisulcata* at Korup) and maximum dbh was *Erythrophleum ivorense* at both Korup and Douala-Edea and most aptly bears comparison. *E. ivorense* is also a caesalp legume but not ectomycorrhizal (Newbery *et al.* 1988). Structural analysis in terms of the ratio of groups 1 to 4 trees and percentage of trees in the 10- < 50 cm class, showed that transect P was most similar to transect R: On R's nutrient-richer plots *E. ivorense* was dominant (Gartlan *et al.* 1986: Table 5). On an axis of soil nutrient richness (especially of phosphorus) *M. bisulcata* and *E. ivorense* lay at either end with similar dfds.

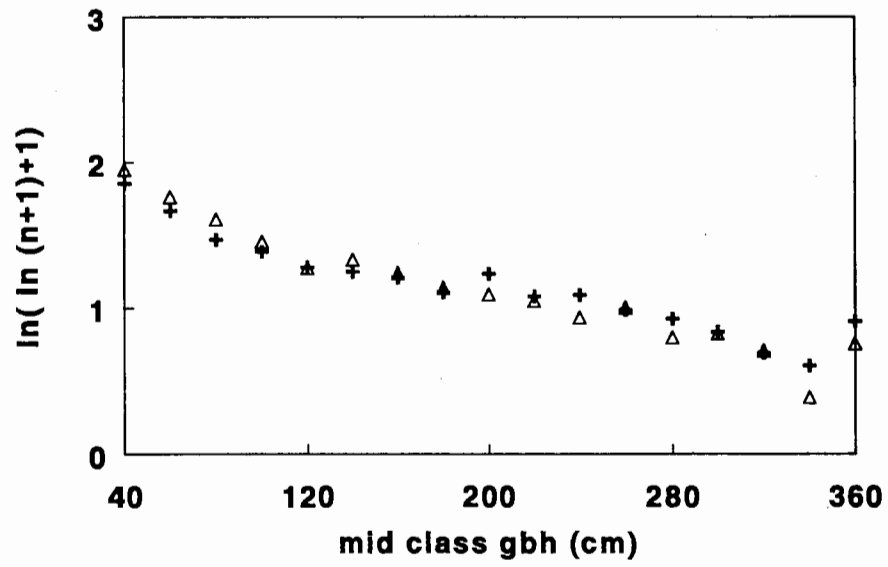
The three ectomycorrhizal species at Korup had a special spatial distribution over the transects combined with their type of dfd. For *M. bisulcata*, the one species that achieved the greatest dbhs and lacked the most smaller trees, it is questionable whether the (older) larger trees will be replaced in time by sufficient smaller individuals to maintain the species in Korup. For the other two species, *T. bifoliolata* and *T. moreliana*, there was evidence of potential replacement. Gartlan *et al.* (1986) and Newbery *et al.* (1988) argued that these three particular species on transect P were adapted to the low soil phosphorus concentrations because of their ectomycorrhizal habit, yet one, the most abundant (in terms of basal area) - *M. bisulcata* - was apparently not regenerating. This problem is considered further later in the discussion.

(a)

G. dewevrei

+ l'Uele

△ Mbole

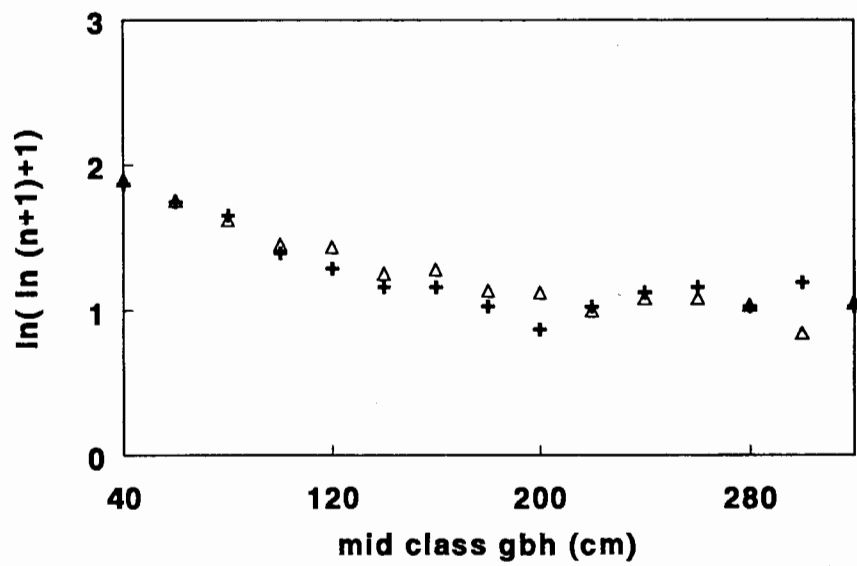


(b)

B. laurentii

+ Yangambi

△ Isangi



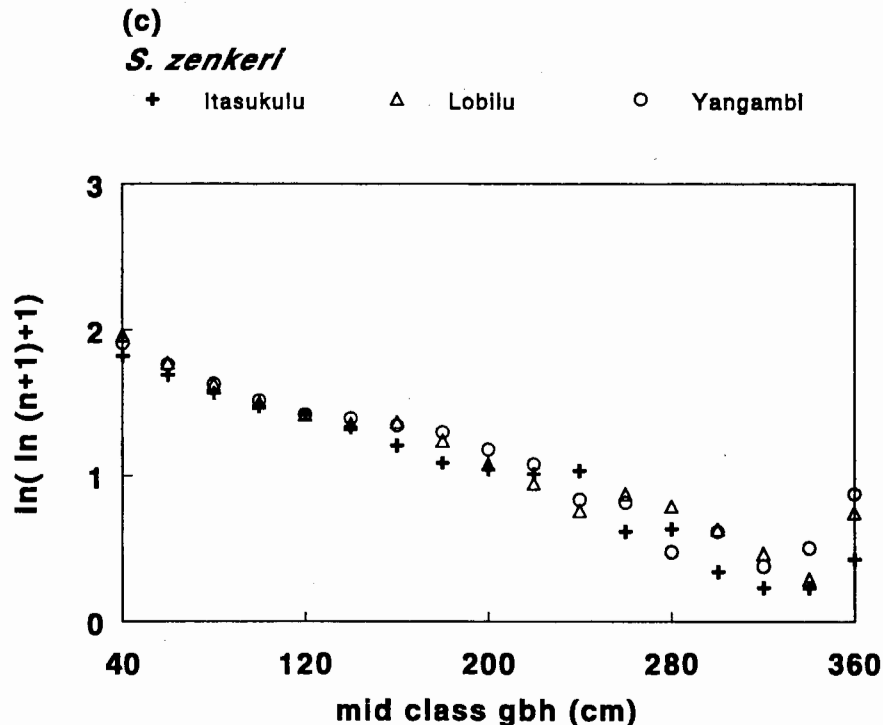


Figure 17. Double log plots of the numbers of trees (≥ 30 cm gbh) against mid-class gbh for 20 cm increasing classes (30–<50, 50–<70, etc.) in Central African stands dominated by (a) *Gilbertiodendron deweyrei* (gbh range 30–<330 cm or dbh 10–<105 cm) at l'Uele (Gérard 1960; $b = -0.0103$, $t_{\text{slope}} = -11.8$, $R^2 = 90.8\%$, $P < 0.001$) and Mbole (Pierlot 1966; $b = -0.0123$, $t = -14.2$, $R^2 = 93.5\%$, $P < 0.001$); (b) *Brachystegia laurentii* (gbh range 30–<230 cm or dbh 10–<75 cm) at Yangambi (Germain & Evrard 1956; $b = -0.0149$, $t = -9.9$, $R^2 = 91.4\%$, $P < 0.001$) and Isangi (Pierlot 1966; $b = -0.0168$, $t = -14.4$, $R^2 = 95.8\%$, $P < 0.001$); and (c) *Scorodophloeus zenkeri* (Pierlot 1966; gbh range 30–<330 cm or dbh 10–<105 cm) at Itasukudu ($b = -0.0164$, $t = -17.7$, $R^2 = 95.7\%$), Lobilu ($b = -0.0152$, $t = -22.5$, $R^2 = 97.3\%$) and Yangambi ($b = -0.0161$, $t = -19.3$, $R^2 = 96.4\%$), all $P < 0.001$. The slopes from the $\ln(\ln)$ transformed plot against gbh, have been multiplied by π , to give equivalence to the Korup and Douala–Edea slopes in Figures 6 and 7.

The similar proportions of species with group 5 dfds at both Korup and Douala–Edea both led to each site's total dfd following the double log–lin model (Figs 6 and 7). This overall dfd was a result of the five groups' dfds (1, 2, 3(-5), 4(-5) and 5) combined together. As higher-numbered groups had trees with larger maximum dbhs they also tended to have relatively fewer smaller trees compared with groups 1 and 2. Hence the proportional decrease from one successive dbh class to the next higher itself decreased. Such a model of dfd for the forests examined was a 'hallmark' of this group 5 effect. If group 5 species, and possibly some others marginal to groups 3 and 4 (and even some overlooked in group 2), had had many smaller trees (to match the shape of groups 1 and 2's dfds) then the forest structure would have been modelled by the simpler single log–lin relationship. It follows also that had group 5 species (Figs 9b and 13b) shown the many more predicted smaller trees, then the numbers of groups 1 and 2 species would have been correspondingly reduced to allow for the same overall density per plot. Removal of group 5 species from the groups 3 and 4 led to a closer fit to a log–lin model for the dfds of each of those groups (Figs 11 and 15). However, at Korup, group 2 less common species showed a convexity in their log–lin relationship (relatively more trees in the 30–50 cm

class than expected in Fig. 10b), which indicated the proportional decrease itself increased with dbh. It is likely that some species of group 2 also tended towards group 5 characteristics by having fewer trees in the 10–<30 cm class than expected from a log–lin model. This convexity is weak for the common species at Korup and absent at Douala–Edea. The dfds of the final groups confirms that the selection of group 5 species from just groups 3 and 4 was largely justified in terms of the models.

Evergreen forests in Central Africa dominated by *Gilbertiodendron dewevrei* (De Wild.) J. Léon. (Gérard 1960; Pierlot 1966) and *Brachystegia laurentii* (De Wild.) Louis ex Hoyle (Germain & Evrard 1956; Pierlot 1966) and semi-deciduous forests at their edge dominated by *Scorodophloeus zenkeri* Harms (Pierlot 1966) all showed a good fit to the double-log lin dfd model for trees up to 2 m dbh, and for forests of *G. dewevrei* and of *S. zenkeri* up to 3 m dbh (Fig. 17). This confirms that the fit, in preference to the log–lin model, is common to other African forests besides Korup. The sources for these comparative sites presented data only in gbh classes and therefore slopes for dbh classes were derived by a conversion (see Fig. 17). The slopes for all of these sites were steeper than those for Korup and Douala–Edea (Figs 6 and 7), for reasons that remain unclear.

Group 5 species were concentrated in the less common abundance class: 80 and 87% of groups 3 and 4 species were in group 5 at Korup and Douala–Edea respectively (Tables 11 and 12). Smaller trees were in general more abundant than larger ones in the forest, so even though group 5 less common species had small sample sizes (of mostly large trees), the power of detection of the small replacing trees was not necessarily diminished. Where small trees were lacking these cases were strongly contrasting to other group 3 and 4 species which had ‘sufficient’ individuals according to the $\ln(n)$ –dbh model. Within group 5 there was a considerable range in the degree to which the species lacked smaller trees (Figs 8 and 12): the definition served to highlight the most deficient species but many others fell short of the $\ln(n)$ –dbh line. Small samples were reflected, however, in the scatter of the dfds and the $\ln(n)$ –dbh graphs for the less common species (Figs 10b and 11b; 14b and 15b).

Although the total areas enumerated at Korup and Douala–Edea (86.4 and 66.7 ha respectively) were appreciable, a doubling of them for instance, would have had two effects. Firstly, if that extra area had been a two-fold intensity of transect lines, another line between P and Q would have missed the large patch of ectomy-corrhizal trees. Secondly, the increased total sample would have brought into view many more group 5 species, recorded in this analysis as rare ($n < 15$ or 20). To investigate species such as *M. bisulcata* further requires more intensive local sampling and this is presently in progress.

Attention has been directed here towards the species which formed large trees of the main canopy (groups 3 and 4) because lack of replacement could be detected from the dfds based on all trees over 10 cm dbh. Within the lower canopy and the understorey there are many more species (groups 1 and 2), and several very abundant ones characterised the two forests (Appendices 1 and 2). But to determine the degree of potential replacement for these smaller trees species would have required enumeration to a much lower minimum dbh. At Korup the most common species (in terms of numbers of individuals) was *Oubanguia alata* Bak.f. (group 2) forming 11.2% of all stems (53 ha^{-1}), followed by *Dichostemma glaucescens* Pierre (group 2) with 4.2% (20 ha^{-1}). Among the group 1 and 2 species with ≥ 500 stems (Appendix 1),

the caesalps *Hymenostegia afzelii* (Oliv.) Harms (non-ectomycorrhizal, Newbery *et al.* 1988) achieved 2.5% of stems (12 ha^{-1}) and *Gilbertiodendron demonstrans* (Baill.) J. Léon. (probably ectomycorrhizal, Alexander 1989b) 1.6% (8 ha^{-1}). *Dichostemma glaucescens* Pierre was the dominant species at Douala–Edea with 11.3% of all stems (42 ha^{-1}) followed by *Protomegabaria stapfiana* Beille with 5.7% (21 ha^{-1}) (Appendix 2). *Anthonotha macrophylla* P.Beauv. and *Berlinia auriculata* Benth. (both ectomycorrhizal caesalps, Alexander 1989b) accounted for 4.8 (18) and 2.1% (8 ha^{-1}) of stems respectively.

Regeneration and replacement in central African and Cameroonian forests

Several authors have commented on the apparent lack of replacement of some canopy and emergent tree species in African tropical forests. Aubréville (1938, p. 132) was one of the first to express this general phenomenon. 'On peut observer fréquemment dans les forêt primaires – peut-être vierges – qu'il existe une grande différence entre la composition du peuplement principal et la nature des plants sous-jacents appelés plus tard à la remplacer. Souvent une espèce abondante dans le peuplement n'a pas de régénération dans le sous-bois'. Richards (1963, p. 123) tried to throw '... some light on the puzzling and frequently noted fact that in many African rain forests seedlings and saplings of most of the larger dominant tree species are scarce or even apparently quite absent'.

Aubréville (1938, loc.cit.) implied a reciprocation in young/old tree spatial distributions: 'Inversement, on rencontre des parcelles envahies par les semis et des jeunes plants d'espèces de grands arbres qui n'existent pas dans l'étage supérieur'. In some cases the problem was seen as one of recruitment by Jones (1955, 1956): 'Even when young individuals of these emergent species are present enumerations have shown that there is often a great deficiency of medium-sized trees' (1956, p. 565). Letouzey (1968) did not record the understorey (sous-bois; trees $< 20 \text{ cm dbh}$) systematically.

There are two major difficulties in interpreting these observations, borne out in each author's case by examples from their studies. Firstly, to what extent does the phenomenon occur, given that often small sample areas were studied? What do 'fréquemment' and 'souvent' (Aubréville 1938), 'frequently noted' and 'most of' (Richards 1963) and 'often' (Jones 1956) exactly mean in quantitative terms? Secondly, Jones (1955, 1956) and Richards (1963) worked in old secondary forest, not primary forest, whilst Aubréville (1938) was influenced in his impressions by both types of forest.

Aubréville cites as his main example one 1.4 ha enumeration in primary forest in which seven out of eight of the large-stemmed species lacked small individuals, but several other species, which achieved larger sizes elsewhere, had many small trees in the plot. Aubréville also mentioned a 80 ha survey in which *Piptadeniastrum africanum* (Hook.f.) Brenan showed a distinct bell-shaped dfd with very few small trees. 'Ils donneraient à penser que dans la forêt équatoriale la notion statique d'association et celle dynamique de climax sont plus que confuses' (Aubréville 1938, p. 135). This led to the idea of a 'cyclic mosaic' (Richards 1952) in which species regenerated away from where they were established in the canopy. The concept, applying to a homogeneous block of forest (Aubréville 1938), implied a negative relationship between the densities of small and large trees across sample plots. From the Korup data analysed here ($n=135$ plots) there is no support for Aubréville's concept of a mosaic – small trees grew with larger ones, although this positive

association may in part have been due to some confounding heterogeneity over the transects, to one or two of which some species were restricted at Korup. On the larger scale of a block of 10–100 ha, with suitable sampling to avoid bias due to single plots, an overall (total) dfd should indicate whether there is potential replacement for that canopy species. The enumeration at Korup provided such a large objective sample, which averaged out the effects of small plot-to-plot local variations.

Swaine & Hall (1988) examined the dfds of common species in eight 0.25 ha subplots (of two 1 ha plots) at Kade in Ghana. *Celtis mildbraedii* Engl. was abundant among the large trees but poorly represented in the smaller (sapling) classes; and conversely, *Strombosia glaucescens* Engl. was found as many small trees and very few large ones. *Piptadeniastrum africanum* also lacked small trees (as Aubréville had found) and had a dfd of similar shape to that of *M. bisulcata* and *E. ivorensis* at Korup (Fig. 8). The sampling at Kade (as with Aubréville's 1.4 ha plot) was perhaps too limited to check objectively whether these cited species had different (reciprocal) dfds elsewhere. No mechanism for the phenomenon has been tested: perhaps seedlings suffer less direct competition when they are away from the large trees of their own species. A more likely explanation lies in stochastic variation in dispersal and recruitment.

Letouzey (1968) drew attention to three striking examples of lack of replacement of large canopy/emergent species in Cameroon. From the large enumeration at Douala–Edea (Letouzey 1957, 1968) and an examination of the frequency distributions of tree girths (i.e. dfds) of large-stemmed species, only two showed the equivalent to what are labelled as group 5 in the present study. *Lophira alata* (Ochnaceae) showed a distinct bell-shaped dfd in his large census of littoral forest, indicating few replacing trees. This species' known requirement for open, fully-lighted conditions for establishment suggested that its large trees originated from times of earlier human settlement and forest clearance (Letouzey 1968). *Sacoglottis gabonensis* (Humiricaceae), in the same forest, had a similar dfd: the reduction in animal dispersers may have been part of the reason for the demise of this important coastal indicator of *la forêt biafriéene*. One further species, *Coula edulis* (Olacaceae) had a truncated, bell-shaped dfd, with relatively few small stems but not completely lacking in them. In our analyses *S. gabonensis* was clearly group 5 (Table 9; Fig. 12f), but *L. alata* and *C. edulis* were not (group 4; Table 9). It is difficult to ascertain from Letouzey's (1958) schematic presentation whether all (common) species were tested and what proportion of the forest's species were of the 'group 5' type. The third example, based upon general observations by Letouzey (1968, 1985) was *Baillonella toxisperma* Pierre (Sapotaceae) forming large stands in *la forêt congolaise*, but lacking everywhere small stems by which to regenerate. Letouzey speculated, that its specialised edaphic niche, at a raised river confluence, was being lost with time through erosion. In summary, it is remarkable that Letouzey's extensive study of the Cameroon flora and vegetation produced only these three prominent cases.

At Douala–Edea, *L. alata* was relatively common in our studies (Table 9) but it did not show a bell-shaped dfd and it was in group 4 which indicated many small trees as well as a few over 90 cm dbh. It is likely that a portion of the sampled area was part of that larger one inferred by Letouzey (1968, 1975) to have been affected by man in the past. At Korup, *Lophira alata* was very rare on transects P and Q. (Three of the 139 trees of these species in the Korup enumeration (Table 5), were in plots P7, 29 and 31, with dbhs of 16, 18 and 53 cm respectively; and transect Q

had no trees.) The large trees of *L. alata* were on transects R and S and followed a group 4 dfd indicating that if there had been disturbances (not necessarily anthropogenic) they were north of transect Q.

Where species of trees in tropical West and Central Africa form (near) monodominant stands they also show very strong regeneration and high potential replacement. Extraordinarily, they are nearly all ectomycorrhizal Caesalpinoideae (Alexander 1989a; Connell & Lowman 1989) and include *Gilbertiodendron dewevrei* (Gérard 1960; Hart *et al.* 1989), *Brachystegia laurentii* (Germain & Evrard 1956), *Tetraberlinia tubmaniana* J. Léon. (Voorhoeve 1964, 1965), *Tetraberlinia bifoliolata* (Kaji 1985, 1990), and *Gilbertiodendron preussii* (Harms) Leon. (Voorhoeve 1965; H.-J. Wöll & D. McC. Newbery, in prep.). Within relic patches of *G. dewevrei* forest in *la forêt congolaise* in south-east Cameroon, Letouzey (1968, 1985) also commented on this species' high degree of potential replacement. Stands of *Monopetalanthus pellegrini* A. Chev., another caesalp reaching over 2 m dbh, formed large monodominant tracts in eastern Cameroon and small patches within *la forêt biafriéne* which consistently had vigorous regeneration (Letouzey 1985).

For the species-richer forests of *la forêt biafriéne*, Letouzey (1968) listed 49 caesalpiniaceous species of which 17 were labelled with 'un tempérament grégaire'. These spatially aggregated species include *Microberlinia bisulcata*, *Tetraberlinia bifoliolata* (also clearly clumped on transect 2 of Kaji (1985)) and *T. polyphylla* (Harms) Leon. (but not *T. moreliana*, a species limited to SW Cameroon and little known to Letouzey). Of these gregarious species '...plusieurs Césalpiniacées ... se présentaient par taches sinon pures, du moins relativement denses avec des individus de tous diamètres et une régénération nettement vigoureuse ...[dans]...la zone de forêt où elles se localisent' (Letouzey 1968, p. 127). In other words, good regeneration was not the general rule: some caesalps lacked it. The only quantitative data come from two 0.5 ha plots, dominated by *T. bifoliolata* (8.0 and 20.4% of total basal area, and 13 and 20% of the stems ≥ 1.3 m high) of Kaji (1985) who found strong regeneration and many small stems of that caesalp. Letouzey (1985) updated his assessment, commenting that *c.* 30% of caesalps were gregarious but not all regenerated vigorously. He remained elusive as to which species lacked regeneration, and one supposes that regeneration of any one gregarious species varies from location to location. There are no clues about *M. bisulcata* by him, nor by Richards (1963).

In Gabon, within forest generally dominated by *Aucoumea klaineana* Pierre, large distinct patches of the caesalp *Paraberlinia bifoliolata* Pellegr. have been observed, with numerous small stems and good regeneration (Saint-Aubin 1961; Gloriod 1974; L. White, personal communication). As an interesting contrast Voorhoeve (1965) recorded *Cynometra ananta* Hutch. & Dalz. in Liberia as being gregarious, sometimes forming near monodominant forests. In a 16.2 ha enumeration of a stand in Sapo National Forest, where *C. ananta* formed 25% of trees of ≥ 61 cm dbh, regeneration was common but saplings rarely grew over 2 m in height.

Gregariousness is not limited to the Caesalpinoideae, however: the Sapotaceae provide several examples, most prominently in the genus *Lecomptedoxa* (Letouzey 1983). In Korup, *c.* 3 km east of the start of transect P stands a distinct clump of *L. klaineana* (Pierre ex Engl.) Dubard (authors' personal observations). Of comparative relevance, in Kaji's (1985, 1990) three transects and two plots only one species, attained a maximum dbh over 2 m, *Erythrophleum sauvolens* (260 cm), and it was lacking small stems.

Replacement of species and inferred dynamics at Korup

M. bisulcata, *T. bifoliolata*, and *T. moreliana* are aggregated as a large stand, straddling transect P, for *c.* 1.5 km of its central length and *c.* 1 km wide at its centre (D. McC. Newbery, unpublished data from a recently completed large 82.5 ha enumeration). These species declined in abundance south of transect P and did not reach transect Q northwards. In the Park this forest association appeared to be singular though recently one other smaller patch has been discovered on the southern boundary (J. J. Green, personal observation in 1995). Within the main stand the species were clumped at smaller scales (Newbery *et al.* 1988). Outside of Korup *M. bisulcata* and *T. bifoliolata* have been recorded in the atlantic coastal forest (Richards 1963; Letouzey 1968; Aubréville 1970) and *M. bisulcata* at Oban (Hall 1977) in Nigeria. *T. moreliana* is restricted to Korup. Letouzey (1968) indicated that *M. bisulcata* and *T. bifoliolata* were gregarious.

Three other ectomycorrhizal caesalps – *Anthonotha fragrans*, *Berlinia bracteosa* and *Didelotia africana* – are also important species at Korup. They were more widely distributed in the forest and at similar densities within and outwith the large stand dominated by *M. bisulcata*, *T. bifoliolata* and *T. moreliana*, and were not found to be gregarious by us or by Letouzey (1968). They were much less restricted to the nutrient-poorer soils: none showed a lack of replacement potential. All three were widely distributed in the forest type outside of Korup, occasionally forming small aggregations, but apparently not forming large near-dominant stands (Letouzey 1968, 1985). Their tolerance to edaphic and climatic conditions seems wide, and they are not selected strongly by the poorest soil conditions. They and other smaller caesalps (Appendix 1) contribute to the high species richness of *la forêt biafriéne*.

Data on population dynamics are presently lacking though some general observations throw light on the *M. bisulcata* recruitment problem on transect P. (There are no comparable data yet on seedlings and saplings of *E. ivorensis* or *Alstonia congensis* on transect R.) *M. bisulcata* produces plentiful viable seed in most years which gives a dense carpet of seedlings (G. B. Chuyong & J. A. Rother, unpublished data). Dispersal is very poor, most seeds falling beneath the tree canopy. The general impression is that there are very few saplings and small poles (1–10 cm dbh) of this species. (D. McC. Newbery & N. C. Songwe, in preparation.) The number of new large ground gaps from tree fall, based upon observations *c.* 50 m to either side of transect P in 1988–92, was two (i.e. 1 per 25 ha in 5 years). This is a very approximate estimate. None of the plots P3 to P20 examined in 1984, for the first time since the original enumerations in 1975, had new major tree falls. Therefore, the frequency of gaps is very low, though it is possible that very occasionally a small tree of *M. bisulcata* may be released towards the canopy.

The lack of small trees (10–50 cm dbh) at Korup in species such as the ectomycorrhizal *M. bisulcata*, and the non-ectomycorrhizal *E. ivorensis* and *A. congensis*, does not necessarily mean that these species will fail to maintain populations of some size in the future, though it does appear less likely that their populations are in equilibrium. If an approximate annual diameter increment of 0.25 cm is taken (from Jones 1956), a tree of 30 cm dbh would need 400 years to increase to 1.30 m dbh. Growth rates may be lower on transect P because the soil is so phosphorus-poor, and the time to attain large diameters perhaps even longer. Continuous replacement of these large trees would therefore require not only higher growth

rates than other species, but also a very high survival rate of those trees through the poorly-represented (but not absent) medium size classes. Access to the putative fungal network (Newbery *et al.* 1988; Alexander 1989a) for the ectomycorrhizal species on the nutrient-poor site (transect P), or efficient exploitation of higher nutrient levels on the richer site (transect R), might allow these species to attain faster growth rates. A network might also confer greater survival on the dominant *M. bisulcata*. The 'flat' dfds showed very wide ranges in the sizes of the larger trees (> 90 cm dbh) – of unknown ages – perhaps as a result of very varying growth rates. These emergent species once free of light competition in the main canopy could then dominate below-ground resources and, depending on their individual locations, achieve greater sizes. This hypothesis of differential survival and growth can only be answered by studies of forest dynamics. Jones (1955) remarked on the relatively low abundances of medium sized trees in old secondary forest in Nigeria, when small and large trees were present. The idea that medium sized trees grew faster, and therefore moved up into the canopy more quickly was tested, but no supporting results were obtained (Jones 1956).

An alternative, and generally more plausible, view is that forest composition is not in equilibrium and that all group 5 species are decaying populations. Several of the less pronounced cases could be a reflection of long-term fluctuations in low and high replacement, and the relatively slight lack of small stems recorded is a temporary phenomenon. However, the great deficiencies in numbers of small trees of species such as *M. bisulcata*, would suggest that these species are going locally extinct in Korup, at least in the next 400–500 years. Two non-equilibrium hypotheses can be erected, though they are not mutually exclusive. Firstly, a change in environmental conditions, especially climatic in the last decades, could have led to a loss in adaptation and what has been observed is the tail of a population established more than *c.* 300 years ago. *T. bifoliolata* and *T. moreliana* appear better suited to present and recent past edaphic and climatic conditions (and the interaction between these especially) and are set to replace *M. bisulcata* as the main caesalps on transect P. This might be a response to the gradual drying of the continent and *M. bisulcata* is an indicator of that process. Similar interactions, possibly competitive, might be occurring between *E. ivorensis* and, for instance, *Vitex grandifolia* on transect R. Secondly, a major disturbance in the past, e.g. lightning and storm damage, could have formed a large, open patch along transect P and created a more lighted environment which allowed a large cohort of *M. bisulcata* to establish by recruitment from the seedling bank. But this mechanism cannot be invoked to explain other group 5 species which are not gregarious in their distribution in the forest. Under lighted nursery conditions all three caesalps responded well to increased light levels (I. Alexander, D. McC. Newbery & J. A. Rother, unpublished data) so *M. bisulcata* is not special in this respect. A particularly strong intolerance of shade is the most likely proximate explanation for the recent lack of small trees of *M. bisulcata*. Of the nearly 200 species examined in this paper for their dfds at Korup, it is extraordinary that only one, *M. bisulcata*, should show such a special combination of characteristics: ectomycorrhizal, gregarious, spatial uniqueness, very large size and an extreme group 5 dfd.

Ecophysiological experiments are clearly needed, which compare the response of the three main ectomycorrhizal caesalps on transect P with one another, and with the non-ectomycorrhizal *E. ivorensis*, *A. congensis* (poor regenerators) and

V. grandifolia (good regenerator) on the richer soils of transect R, to low light, phosphorus limitation and absence of mycorrhizas. These must then be set in the context of seedling demography and growth in the forest under manipulated conditions. Relative growth rates of pole-sized trees would test the hypothesis of differential onward recruitment to the canopy.

The replacement of *M. bisulcata* by the two *Tetraberlinia* species may depend not only on differences in ecophysiology between the saplings of these tree species but also on the ecophysiology of their associated mycorrhizas at this stage. The regeneration problem comes down to why saplings of *M. bisulcata* do not survive and grow whilst those *T. bifoliolata* and *T. moreliana* do. The function of mycorrhizas will be different for a sapling in the shaded understorey as opposed to a tree in the lighted canopy. The extent of host–fungus specificity in tropical ectomycorrhizal caesalps is not known, but there are probably both specialists and generalists operating in Korup (Alexander 1989a). In contrast to the monodominant stands of caesalps elsewhere in Africa, for which Connell & Lowman (1989) have assumed the ectomycorrhizal species are specialist and this is the reason for their dominance, the forest in Korup (*la forêt biafriéene*) has a mixture of caesalps in the canopy, albeit not all in equilibrium. If all three of the main species (and the other less abundant ectomycorrhizal caesalps) largely shared just one or more generalist fungi, then on the assumption that ectomycorrhizas are essential to survival and growth, *M. bisulcata* should regenerate as well as the other two species. One subsidiary hypothesis then is that in such mixed stands specialism is present and *T. bifoliolata* and *T. moreliana* in recent times have selected for fungal species which, for that stage in tree growth (i.e. understorey conditions), enable them to survive well whereas *M. bisulcata* either lacks specialists or its specialists are now of less advantage. Information on the fungal flora of the roots of these species is much needed, and whether fungal species change in abundance as their hosts age.

Ectomycorrhizal habit is, however, only one of a suite of characters that these caesalps are expected to display on the nutrient-poor soils in Korup (Newbery *et al.* 1988; Alexander 1989a,b); others which are presently being investigated are high nutrient withdrawal (especially of phosphorus) before leaf fall, slow decomposition of litter (perhaps controlled by high polyphenol levels) and access to organic phosphorus sources by trees via ectomycorrhizas (Newbery *et al.* 1988). Forest dynamics of the ectomycorrhizal–legume dominated stand on transect P in the near future is made more complex by the realization that whilst *M. bisulcata* is not replacing itself over time, the litter from its emergent and large canopy trees will continue to contribute substantially to nutrient cycling processes for many decades. This appears to be of little selective advantage to its own seedlings.

Conclusion

The presence of species with group 5 ddfs forming a substantial component of the main canopy and emergent trees is a common feature to many African rain forests. It has been recorded in primary and old secondary forests, and appears to increase with increasing richness of the forest. Forests are in continual flux of species proportions with considerable variation spatially and temporally in abundances of both large and small trees of the different species: the more species-rich the forest the greater the flux. Many tropical rain forest tree species have wide tolerances to site

conditions and the role of interspecific competition is likely to be small and slow in effect. Some species may well have decaying populations at some sites, or throughout a forest type, leading to local or wider extinction due to long-term changes in the environmental conditions such as warming in the Holocene. *M. bisulcata* may be an important indicator of recent change. Others are progressing through cycles of low and high abundance which contribute to high diversity. Static observations, expressed as dfds, provide a brief window in time from which dynamics can only be tentatively inferred. Chance, in terms of seeding, dispersal and recruitment events, must play an important role on the scale of recent decades, perhaps centuries, not ignoring the major influence of the last major dry period in Africa. A considerable problem is our inability to age tropical trees and, because of the very long turnover times in their populations (on the scale of centuries), to measure changes demographically. Hypotheses can be put forward for particular species, or guilds of species such as the ectomycorrhizal legumes discussed in most detail here, in the light of their autecology and dynamics, but different explanations for population size structures need to be sought for other species. Where generalities are sought they are inevitably found wanting. The ectomycorrhizal caesalps are an example: their distributions, degrees of dominance or diversity and their potentials for replacement have no clear pattern with respect to climatic and edaphic factors in present-day Africa. Explanations for their occurrence and habit almost certainly lie mainly in the past.

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Appendix 1

Common species ($n \geq 200$; $\geq 0.05\%$ of all trees) at Korup with $\geq 99\%$ of individuals (a) < 50 cm dbh, and (b) < 70 cm dbh, each followed in parenthesis by family abbreviation*, sample size (n), unevenness (UE) in frequency distributions of dbh classes across transects shown by +, the rescaled axis I DCA score (D_1), and distinctive lack of transect occurrence (T). For explanation see notes to Table 5 and text. (Species with $n = 50 - < 200$ omitted.)

(a) *Dichostemma glaucescens* Pierre (Euph,1690,22); *Cola rostrata* K.Schum. (Ster,1526,20); *Strombosia glaucescens* Engl. [syn: *S. pustulata* Oliv.] (Olac,1244,24); *Diospyros gabunensis* Gürke (Eben,1164,24); *Hymenostegia afzelii* (Oliv.) Harms (Caes,1035,26); *Diospyros iturensis* (Gürke) Let. & White (Eben,835,21); *Soyauxia gabonensis* Oliv. (Medu,834,29); *Rinorea oblongifolia* (C.H. Wright) Marquand ex Chipp (Viol,730,41); *Crateranthus talbotii* Bak.f. (Lecy,694,7,-S); *Gilbertiodendron demonstrans* (Baill.) J.Léon. (Caes,649,10); *Diogoa zenkeri* (Engl.) Exell & Mend. (Olac,571,27); *Tabernaemontana brachyantha* Stapf. (Apoc,516,40); *Calpocalyx dinklagei* Harms (Mimo,459,18); *Dasylepsis blackii* (Oliv.) Chipp (Flac,444,25); *Maesobotrya dusenii* (Pax) Hutch. (Euph,365,33); *Enantia chlorantha* Oliv.

(Anno,341,36); *Antidesma vogelianum* Müll. Arg. (Euph,319,38); *Piptostigma morteliana* De Wild. (Anno,316,15); *Baphia leptostemma* Baill. (Papi,292,34); *Garcinia staudtii* Engl. (Gutt,256,6,-RS); *Aulacocalyx talbotii* (Wern.) Keay (Rubi,255,37); *Diospyros zenkeri* (Gürke) F.White (Eben,217,47,-P); *Trichoscypha patens* (Oliv.) Engl. (Anac,211,22); *Octoknema winkleri* Engl. (Olac,210,+,42); *Tabernaemontana crassa* Benth. (Apoc,208,44); *Hunteria* sp. (Apoc,206,40,-P); *Memecylon memecyloides* (Benth.) Exell. (Mela,202,+,24).

(b) *Oubanguia alata* Bak.f. (Scyt,4544,18); *Klaineanthus gaboniae* Pierre ex Prain (Euph,1063,23); *Pausinystalia macroceras* (K.Schum.) Pierre ex Beille (Rubi,536,+,52,-P); *Baphia laurifolia* Baill. (Papi,519,28); *Santiria trimeria* (Oliv.) Aubrév. (Burs,462,+,46); *Strombosiopsis tetrandra* Engl. (Olac,458,39); *Uapaca staudtii* Pax (Euph or Uapa,454,29); *Carapa procera* DC. (Meli,353,37); *Anisophyllea* aff.*purpurascens* Hutch. & Dalz. (Rhiz,339,46); *Scottellia coriacea* A.Chev. ex Hutch. & Dalz. (Flac,336,38); *Dialium pachyphyllum* Harms (Caes,315,26); *Pausinystalia talbotii* Wern. (Rubi,278,37); *Monopetalanthus* sp. (Caes,262,+,13,-S); *Amanoa* sp. (Euph,250,+,5,-S); *Hypodaphnis zenkeri* (Engl.) Stapf. (Laur,246,+,39); *Anisophyllea* aff.*laurina* R.Br. ex Sabine (Rhiz,207,40).

Appendix 2

Common species ($n \geq 125$; $\geq 0.05\%$ of all trees) at Douala-Edea with $\geq 99\%$ of individuals (a) < 50 cm dbh, and (b) < 70 cm dbh, each followed in parenthesis by family abbreviation, sample size (n), unevenness (UE) in frequency distributions of dbh classes across transects shown by +, the rescaled axis I DCA score (D_1), and distinctive lack of transect occurrence (T). For explanation see notes to Table 5 and text. (Species with $n = 50 - < 125$ omitted.)

(a) *Dichostemma glaucescens* Pierre (Euph,2816,44); *Leptaulus daphnoides* Benth. (Icac,830,43); *Soyauxia talbotii* Bak.f. (Medu,608,45,-A); *Diospyros hoyleana* F.White (Eben,604,35); *Diospyros zenkeri* (Gürke) F.White (Eben,576,51,-A); *Garcinia mannii* Oliv. (Gutt,493,16); *Rinorea welwitschii* (Oliv.) Kuntze (Viol,470,48); *Ouratea affinis* (Hook.f.) Engl. (Ochn,412,32); *Diospyros cinnabarina* (Gürke) F.White (Eben,397,55,-A); *Englerophytum oubanguiense* (Aubrév. & Pellegr.) Aubrév. & Pellegr. (Sapo,297,3 -A!); *Diospyros iturensis* (Gürke) R.Letouzey & F.White (Eben,230,18); *Barteria fistulosa* Mast. (Pass,223,45); *Hua gabonii* Pierre & De Wild. (Huac,206,52); *Azelia bella* Harms (Caes,204,54,-A); *Maesobotrya dusenii* (Pax) Hutch. (Euph,192,35); *Polyceratocarpus parviflorus* (Bak.f.) Ghesq. (Anno,178,59,-A); *Ouratea flava* (Schum. & Thonn.) Hutch. & Dalz. (Ochn,176,49); *Antidesma vogelianum* Müll.Arg. (Euph,149,33); *Buchholzia coriacea* Engl. (Capp,146,61,-A); *Diospyros longiflora* R.Letouzey & F.White (Eben,125,29,-A!).

(b) *Protomegabaria stapfiana* (Beille) Hutch. (Euph,1424,18); *Anthonotha macrophylla* P.Beauv. (Caes,1192,36); *Strombosia pustulata* Oliv. (Olac,1156,44); *Trichoscypha patens* (Oliv.) Engl. (Anac,675,36); *Berlinia auriculata* Benth. (Caes,514,26); *Mareyopsis longifolia* (Pax) Pax. & K.Hoffm. (Euph,440,40); *Garcinia ovalifolia* Oliv. (Gutt,352,22); *Martretia quadricornis* Beille (Euph,299,43,-A); *Diospyros dendo* Welw. & Hiern (Eben,269,15,-BCD); *Baikiaea insignis* Benth. (Caes,260,20); *Enantia chlorantha* Oliv. (Anno,257,54,-A); *Xylopia quintasii* Engl. &

Diels (Anno,233,35); *Hymenostegia afzelii* (Oliv.) Harms (Caes,230,54,-A); *Garcinia conrauana* Engl. (Gutt,195,25).

*Family abbreviations in Tables 5 and 9, also: Huac, Huaceae; Lecy, Lecythidaceae; Medu, Medusandraceae; Pass, Passifloraceae; Rhiz, Rhizophoraceae; Viol, Violaceae.

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