The influence of drainage and soil phosphorus on the vegetation of Douala-Edea Forest Reserve, Cameroun*,**

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Abstract

All living trees (≥30 cm gbh) were enumerated in 104 80 × 80 m plots arranged along four transects in the Douala-Edea Forest Reserve Cameroun, a system of low-lying ancient coastal sand dunes interspersed by numerous streams and swamps. The extent of permanent and seasonal swamps was recorded for each plot. Two hundred thirty taxa were recognized of which 63% were identified to species. Mean tree density was 376 ha^{-1}, basal area 31.0 m^2 ha^{-1} and number of species per plot 39. The Olacaceae were the most abundant family in terms of basal area, but the Euphorbiaceae the most frequently represented. The most abundant species was *Coula edulis* (Olacaceae). Twenty-two plots had most of their area permanently or seasonally swamped. Percentage sand, silt and clay ranged between 32–100, 0–64, 0–21% respectively. The ranges for other variables recorded were: pH (2.7–5.4), organic carbon (1.5–12.4%), available phosphorus (7–90 ppm) and potassium (28–188 ppm), and nitrogen (ammonium 4–40 ppm, nitrate 1–12 ppm).

Classification of the plots on the basis of six soil variables provided three large distinct groups: swamp plots and non-swamp plots, the latter divided into plots of low and high available soil phosphorus. Swamp plots were distinguished by high abundances of *Protomegabaria stapfiana* and *Librevillea klainei*, though correspondence ordination of plots in these groups showed *P. stapfiana* associated with more clayey soils and *Librevillea klainei* (and *Gluema ivorensis*) on the very sandy soils. Direct gradient analysis highlighted several species associated with these lower phosphorus soils. Available soil phosphorus is not as low at Douala-Edea as in parts of Korup, and the association of these Douala-Edea soils with the Caesalpinioideae is correspondingly weaker.

* Nomenclature follows Aubréville (1963–1983).

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Introduction

In a previous paper (Gartlan *et al.*, 1985) we reported the results of a multivariate analysis of the vegetation of the Korup Forest Reserve (now Korup National Park) in Cameroun.

We here report the results of a similar study carried out in the Douala-Edea Forest Reserve. The comparison of these two areas is of particular interest as both form part of the coastal forest belt of Cameroun and show some overlap in tree species. However, the history and edaphic environments of these two forests are in marked contrast, the Douala-Edea landscape probably being of comparatively recent origin and based on marine deposits, whilst Korup seems to represent part of a major West African refuge area (Gartlan, 1974) and is based on weathered granite and quartzite soils. For example, whilst Korup has had a long and relatively stable history during recent periods of glaciation, Douala-Edea is likely to have undergone several cycles of drastic changes, ranging from dry periods due to oceanic retreat during glaciation to the present area of the Reserve being inundated during interglacial periods.

Like Korup, the Douala-Edea Reserve contains a large number of rare and endangered animal species, notably the black colobus monkey (*Colobus satanas* Waterhouse) and the African Manatee (*Trichechus senegalensis* Link.). The vegetation of this Reserve has been the subject of a detailed and continuing phytochemical survey which has revealed that it invests very heavily in a wide range of secondary metabolites (Gartlan *et al.*, 1980; Waterman, 1983). The impact of these compounds on food selection and the feeding behaviour of the black colobus monkey has also been investigated (McKey *et al.*, 1981). Although the Reserve has been hunted to a limited extent recently by the local inhabitants, with evidence of old pigmy camps around Lake Tissongo (R. Letouzey, pers. comm.), there is no evidence of any large scale interference with the forest.

The study area

The Douala-Edea Forest Reserve lies on the Atlantic coast of Cameroun from the south of the Nyong River (3°13′N; 9°54′E) north to Souellaba Point (3°49′N; 9°33′E) and extends inland to include a total area of about 130 000 ha (Fig. 1 of Gartlan *et al.*, 1985). The Reserve is divided into two unequal parts by the Sanaga River which, inland, forms the northern boundary for the larger southern part in which the study took place. About 1% of the Reserve is covered by open water, the principal area being Lake Tissongo, the starting point for three of the four transect lines used in this survey.

The entire Reserve lies below 80 m elevation and rarely exceeds 50 m. The area around Lake Tissongo is about 15 to 20 m elevation and slopes gradually toward the coast, the altitude being about 10 m in the area of transect A (Fig. 1 of Gartlan *et al.*, 1985). However, the topography of the Reserve is not flat but is cut by many low-lying streams or swamps through which the water drains north into Lake Tissongo and the Sanaga or south into the Nyong. Toward the coast, where the system of coastal sand dunes is still extant, drainage channels are very tortuous, often running along dune systems parallel to the sea for long distances. Drainage is to a large extent dependent on the levels of the Sanaga and Nyong and in periods of flood water can actually flow back from the rivers into the Reserve, thereby inhibiting drainage and inundating large areas.

The soils found in the study area are very high in sand content which was anticipated as the Reserve lies entirely upon marine sediments built up by north flowing marine currents, a process that probably began during the Cretaceous and still continues today. Analysis of fossil microfauna to a depth of about 2 700 m reveals a continuous marine origin (Gazel, Hourcq & Nickels, 1956). The Precambrian rock that marks the 'true' edge of the African continent lies as much as 60 km inland from the present coast, well inland of the Reserve, with the area of the Reserve built up entirely by marine deposits and preserved by tectonic uplift associated with volcanic activity along the Mount Cameroun–Bioko line (Hori, 1977).

Meteorological data were collected at the base camp by Lake Tissongo from March 1976 to November 1978. Prevailing conditions throughout the area of the Reserve appear to be very uniform and these findings can be related to the whole study area. The total annual rainfall is in the range of 3 000 to 4 000 mm per year. Heaviest rainfall was between August and October, diminishing to the very dry months of December and January. From February onwards rainfall increases steadily with June being the very wet. Thus the rainfall pattern observed appears to be intermediate between the unimodal distribution seen in Douala and in the Korup Forest Reserve and the bimodal distribution seen further south on the coast at Kribi. The mean monthly temperature varied between a maximum of 28.7 °C and a minimum of 24.6 °C with a mean annual diurnal variation of only 8.8 °C.

Methods

Floristic data

Floristic analysis was based on 104 plots, each 80×80 m, ranged along four transects labelled A, B, C and D. The transect cutting and tree numbering was conducted between March 1975 and August 1976. Transects B, C and D were cut from Lake Tissongo roughly at right angles to prevailing physical gradients. Each was intended to be 5 km in length with a total of 34 plots spaced equidistantly along the transects. In practice, transects C and D terminated at lesser distances, after 24 and 12 plots respectively, as at those points they reached permanent *Calamus* swamp. Transect A was cut for a full 5 km from the Lombé Camp site, SW of Lake Tissongo and starting inland about 7 km from the sea. Thus the total area enumerated was 66.56 ha, taken from within the area of the Reserve which spanned 20 km from west (plot A1) to east (plot C24) and 8 km from north (plot D12) to south (plot B34). Within transect A plots were subdivided into 40×40 m subplots as in the Korup study (Gartlan *et al.*, 1985).

In each quadrat all living trees and lianes with a girth (gbh) at breast height (1.3 m) of 30 cm or more were enumerated. Each living individual was identified or, where this was impossible, collected and assigned a code number for future reference.

Edaphic variables

Soil samples for transect A were taken from a single point within each subplot of a plot, the exact position being decided randomly. Samples were taken from the surface (0–10 cm) and at a depth of 45 cm and separately bulked for each plot. Only the results from surface samples are reported here. For transects B, C and D the samples taken were of a composite nature collected from the top 10 cm of soil after removal of surface detritus at points 20 m N, E, S and W of the centre of the plot. All soil samples were oven dried at 70 °C and stored in airtight polythene bags until their return to the University of Wisconsin for analysis.

Soils were analysed for their mechanical fractions (percentage sand, silt and clay), pH, percentage organic carbon, available phosphorus and potassium and for nitrate-nitrogen in the same way as those in the Korup study (Gartlan *et al.*, 1985). Ammonium-nitrogen was measured by steam distillation.

Descriptive data were obtained for slope and drainage (permanent and seasonal swamps and streams) for each plot using the same criteria as in Gartlan *et al.* (1985).

Floristics

A total of 24 997 trees and 501 lianes with a gbh of 30 cm or more were measured in the course of the enumeration. (Lianes are not considered further here.) From the trees a total of 198 taxa could be recognized to at least the family level (Table 1), leaving only 318 individuals (1.3%) of the total unaccounted for. Thirty-two (14%) taxa have not yet been placed at any taxonomic level but all were rare, being only represented by one or a few individuals.

The two families/subfamilies contributing the greatest amount to the total basal area (Table 2) were the Olacaceae with 22.3% and Legumino-

Table 1. Level of taxonomic identification of trees (≥30 cm gbh) in 104 plots in the Douala-Edea Forest Reserve.

	species	identification to		family unknown
		genus only	family# only	
All taxa (=230)	146	22	30	32
Taxa based on descending order of total basal areas of first				
100 species	93	6	1	–
50 species	50	–	–	–

Also distinguishes the three subfamilies of Leguminosae.

Table 2. Representation of the 12 most abundant families (or subfamilies of Leguminosae) in 104 (80×80 m) plots in the Douala-Edea Forest Reserve in terms of basal area. (1) Number of species; (2) Basal area (m^2 ha^{-1}); (3) Number of stems (ha^{-1}).

Family (subfamily)	(1)	(2)	(3)
Olacaceae	4	7.11	44.7
Leguminosae (Caesalpinioideae)	27	5.19	50.1
Euphorbiaceae	18	3.89	88.2
Ochnaceae	3	2.17	12.6
Humiricaceae	1	2.13	1.0
Ixonanthaceae/Simaroubaceae	3	1.25	1.1
Ebenaceae	11	1.17	36.0
Guttiferae	8	1.02	19.7
Annonaceae	14	0.95	15.2
Anacardiaceae	3	0.68	10.7
Lauraceae	1	0.56	6.1
Rubiaceae	24	0.55	12.4
Other families ($n=33$)	81	4.37	76.2
Unknown families	32	0.85	2.0

sae/Caesalpinioideae (16.3%). In terms of the number of stems, the Euphorbiaceae (23.6%) were the most frequent family. The contributions to the Ochnaceae and Humiricaceae were almost entirely due to the presence of significant numbers of the large emergents *Lophira alata* and *Sacoglottis gabonensis* respectively.

The mean density of trees per plot (with 95% confidence limits) was 376±16 ha^{-1}, the mean basal area 31.0±1.5 m^2 ha^{-1} and the mean number of species per plot 39±2 (0.64 ha).

The most abundant species in the Douala-Edea enumeration was *Coula edulis* (Olacaceae) which formed 18.9% of the basal area and 6.7% of the tree stems (Table 3). The other 19 most abundant species in the enumeration in terms of basal area representation are shown in Table 3 together with their tree densities. They account for 69.7% of the total basal area and 45.9% of the tree stems.

Only one commercially important timber tree was recorded in this enumeration, *Lophira alata*.

Numerical analysis

Ordination of floristic data

Of the total number of taxa, 63% were identified to species (Table 1). The unidentified species were the least abundant and therefore will be of little importance in an ordination (as shown for Korup, Gartlan *et al.*, 1985).

Detrended correspondence analysis (Hill & Gauch, 1980) of all plots and all species, using the basal area of each species per plot, showed three distinct outliers (B30, B31 and C19; see explanations below). These were removed and the data re-ordinated (Fig. 1). Transect A plots, which included most of those in swamps, were dispersed to the positive end of axis 1 and the majority of the plots of transects B, C and D as a cluster of points at the negative end of this axis. No clear division along this gradient is evident that would enable the plots to be reliably classified on the basis of their vegetation.

Table 3. Basal area and density of the 20 most common species, based on their total basal area in the enumeration, in the Douala-Edea Forest Reserve sample of 104 80×80 m plots. (1) Family (subfamily); (2) Basal area (m^2 ha^{-1}); (3) Density (ha^{-1}).

	(1)	(2)	(3)
Coula edulis	Ola	5.87	25.0
Sacoglottis gabonensis	Hum	2.13	1.0
Lophira alata	Och	1.99	3.8
Dichostemma glaucescens	Eup	1.32	42.3
Protomegabaria stapfiana	Eup	1.29	21.4
Cynometra hankei	Leg	1.16	2.7
Strombosia pustulata	Ola	0.83	17.4
Anthonotha macrophylla	Leg	0.82	17.9
Librevillea klainei	Leg	0.78	1.2
Trichoscypha patens	Ana	0.67	10.1
Erythrophleum ivorense	Leg	0.66	0.7
Odyendyea gabonensis	Ixo	0.61	0.7
Klainedoxa gabonensis var. *microphylla*	Eup	0.57	0.4
Beilschmiedia cf. gaboonensis	Lau	0.56	6.1
Mammea africana	Gut	0.44	3.3
Ctenolophon englerianus	Cte	0.41	1.7
Strombosiopsis tetrandra	Ola	0.40	1.6
Leptaulus daphnoides	Ica	0.39	12.5
Berlinia bracteosa	Leg	0.36	0.7
Anthocleista vogelii	Log	0.35	1.9
Total		21.6	172
Remaining (210) species		9.4	204

Families: Ana, Anacardiaceae; Cte, Ctenolophonaceae; Eup, Euphorbiaceae; Gut, Guttiferae; Hum, Humiricaceae; Ica, Icacinaceae; Ixo, Ixonanthaceae/Simaroubaceae; Lau, Lauraceae; Leg, Leguminosae (Subfamily: Caesalpinioideae); Log, Loganiaceae; Och, Ochnaceae; Ola, Olacaceae.

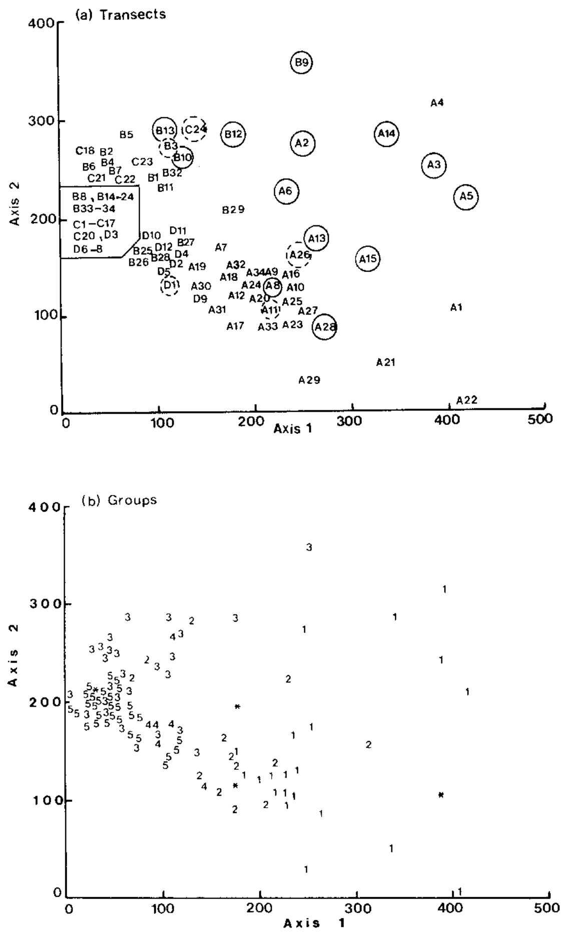

Fig. 1. Detrended correspondence ordination of all plots (n=101), excepting three outliers (B30, B31, C19) using the basal area of trees (≥30 cm gbh) for all species showing the distribution of: (a) transects and plot numbers. Solid and broken circles indicate presence of permanent and seasonal swamps respectively. (b) five soil classes of Fig. 4: 1,poorly-drained plots; 3, well-drained plots (low phosphorus); 5, well-drained plots (high phosphorus), 2 and 4, smaller intermediary classes. * indicates an outlying plot (n=4) from the soils classification.

Classification of soil data

The seven variables, excepting nitrogen (for which there were data only for 67 plots), were each normalized by suitable transformation (usually logarithmic) and then standardized. Since percentage sand, silt and clay are linearly interdependent, one of these variables must be omitted in any multivariate analysis or replaced by orthogonal components (Austin, Ashton & Greig-Smith, 1972). The correlations between sand and silt (r=0.708) and sand and clay (r=0.520) are highly significant (P<0.001) whilst the correlation between silt and clay was insignificant (r=−0.093, P>0.05). Percentage sand was therefore removed and the resulting six variables were used to classify 101 plots – no soil data were collected for plots B30, B31 and C19 – by the 'within-group sums of squares' technique of Orlóci (1967).

Information on drainage (presence of swamps and streams) was not included in the classification because of its presence/absence nature. Sixteen plots (15%) of the total of 104 were recorded as permanently swamped, six (6%) seasonally swamped and 15 plots (14%) had permanent streams present.

Apart from two outlying plots (A1 and A12) and a small group of two plots, the other 97 plots fall into five soil classes (Fig. 2). The first consists entirely of transect A plots and is distinguished from the other classes by its high soil organic carbon percentage (Table 4). The third soil class has transect B plots whilst the fifth class is a mixture of plots from transects B, C and D. Plots in classes three and five have soils with low and high available soil phosphorus concentrations respectively (Table 4). The other two, smaller, classes (two and four, Fig. 2) are intermediate in soil character to the larger classes, and in the interest of detecting the major differences in the vegetation on different soils (highlighted by the main three classes), these smaller soil classes will not be considered further.

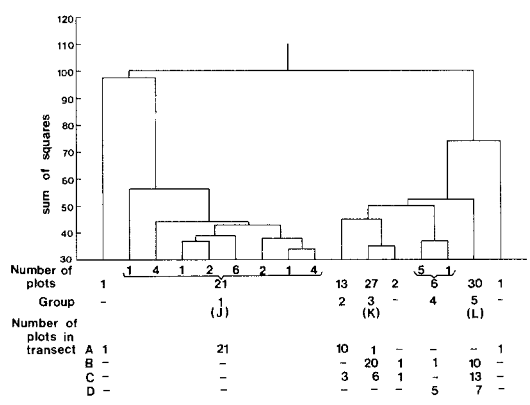

Fig. 2. Agglomerative classification of 101 plots in Douala-Edea Forest Reserve based on six soil attributes (plots B30, B31, C19 excluded).

Table 4. Ranges and medians of nine edaphic variables and the frequency of swamps and streams for plots in five groups from the agglomerative classification of soils in 101 Douala-Edea Forest Reserve plots. The three largest soil groups are designated letters for subsequent reference. (Four plots in three small soil classes are omitted; see Fig. 2).

	Soil group				
	1	2	3	4	5
	J	-	K	-	L
number of plots	21	13	27	6	30
Sand (%)	71 – 100	78 – 97	84 – 95	63 – 80	78 – 93
	84	88	92	74	89
Silt (%)	0 – 28	2 – 19	0 – 5	6 – 16	0 – 9
	10	6	2	10	2
Clay (%)	0 – 11	1 – 6	2 – 11	12 – 21	5 – 13
	3	4	6	15	10
pH	2.7 – 3.9	3.0 – 4.0	3.8 – 4.8	3.7 – 4.0	3.6 – 4.7
	3.4	3.5	4.1	3.8	4.1
Organic carbon (%)	10.0 – 12.5	4.0 – 8.0	1.5 – 3.2	2.7 – 5.2	1.7 – 4.4
	12.5	5.5	2.3	3.4	2.5
Available					
phosphorus (ppm)	7 – 55	8 – 30	7 – 31	9 – 27	30 – 90
	24	15	9	15	53
potassium (ppm)	78 – 188	43 – 88	28 – 50	27 – 40	30 – 63
	133	58	38	38	44
Nitrogen					
ammonium (ppm)	nd	18 – 31	4 – 28	6 – 34	5 – 40
		22	8	24	15
nitrate (ppm)	nd	5.3 – 8.3	1.0 – 7.8	6.0 – 11.5	2.5 – 9.8
		6.3	4.0	8.9	4.4
Drainage (%) plots:					
Swamps:					
permanent	33	15	17	0	0
seasonal	10	8	0	17	3
Streams-permanent	29	15	13	17	0

nd = not determined

Association between vegetation and soils

Axis 1 of the floristic ordination (Fig. 1) is associated with increasing percentage soil organic carbon, percentage silt and the concentration of available soil potassium, and with decreasing percentage clay and the pH value (Table 5). Axis 2 is associated with increasing percentage of sand but decreasing percentage of organic carbon, percentage of silt and the soil concentrations of available potassium and phosphorus, and of nitrogen (Table 5). A similar, but clearer pattern is shown by the distribution of the soil classes on the ordination (Fig. 1b).

It is convenient from here on to relabel the soil classes one, three and five, referred to above, by plot groups J, K and L (Fig. 2, Table 4).

The vegetation on group J plots is considerably

Table 5. Coefficients of correlation (Spearman's r_s) between the plot scores from an ordination of all plots in the Douala-Edea Forest Reserve (excepting three outliers) and nine edaphic variables. ($n = 101$, except for nitrogen data where $n = 67$).

	Range	Axis	
		1	2
Eigenvalue		0.64	0.36
Sand (%)	32 – 100	−0.06	0.46***
Silt (%)	0 – 64	0.52***	−0.53***
Clay (%)	0 – 21	−0.59***	0.01
pH	2.7 – 5.4	−0.60***	0.48***
Organic carbon (%)	1.5 – 12.5	0.74***	−0.50***
Available			
phosphorus (ppm)	7 – 90	−0.32**	−0.33**
potassium (ppm)	28 – 188	0.56***	−0.41***
Nitrogen			
ammonium (ppm)	4 – 40	0.11	−0.30*
nitrate (ppm)	1 – 12	0.21	−0.43***

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

different from that on soil groups K and L plots (Table 6) and these latter two groups differ much less from one another. A direct floristic comparison between groups used the procedure developed in Newbery & Proctor (1984) the criteria for which are given in Table 6. Extensive lists of species resulted, and only a portion of them are shown in Table 6. (The full lists are available on request from D.McC.N.). A species ordination (Fig. 3), based on all 101 plots and all species, indicates that species in the lower right part of this figure correspond to those species characteristic of soil group J plots and species of the upper left correspond to those species characteristic of soil group K and L plots (Table 6), and reciprocating the arrangement of plots in Figure 1a. (In Fig. 3 the species scores are corrected so that the lowest values on each axis are just positive for the purposes of illustration.)

Table 6. Mean basal areas per plot ($m^2\ ha^{-1}$) of tree species within soil group J and soil groups K and L combined in Douala-Edea Forest Reserve. Species listed have at least 0.1 $m^2\ ha^{-1}$ in one of the groups. (a) basal group in group J > threefold basal area in groups K and L; (b) basal area in groups K and L > threefold basal area in group J; (c) ≤ threefold difference between groups but basal area in both at least 0.1 $m^2\ ha^{-1}$. In (c), species are ranked in order of decreasing mean basal area over all plots in groups J, K and L. Only the first ten species, out of lists of 22, 20 and 17 species for (a), (b) and (c) respectively, are shown.

	Family (sub-family)	Group	
		J	K+L
number of plots		21	57
(a)			
Protomegabaria stapfiana	Eup	4.12	0.14
Librevillea klainei	Leg	3.07	0.00
Klainedoxa gabonensis	Eup	2.00	0.07
Erythrophleum ivorense	Leg	1.69	0.08
Gluema ivorensis	Sap	1.25	0.00
Mammea africana	Gut	1.22	0.13
Berlinia bracteosa	Leg	1.15	0.00
Anthocleista vogelii	Log	0.79	0.20
Strephonema pseudocola	Com	0.75	0.00
Diospyros dendo	Ebe	0.70	+0.00
(b)			
Coula edulis	Ola	0.61	8.49
Cynometra hankei	Leg	0.00	1.65
Dichostemma glaucescens	Eup	0.37	1.57
Strombosia pustulata	Ola	0.22	1.10
Beilschmiedia cf. gaboonensis	Lau	0.17	0.80
Martretia quadricornis	Eup	0.00	0.43
Diospyros cinnabarina	Ebe	0.00	0.35
Hymenostegia afzelii	Leg	0.00	0.33
Soyauxia talbotii	Med	0.00	0.30
Englerophytum oubanguiense	Sap	0.00	0.27
(c)			
Sacoglottis gabonensis	Hum	2.82	1.97
Lophira alata	Och	2.85	1.45
Anthonotha macrophylla	Leg	0.64	0.87
Odyendya gabonensis	Ixo	0.32	0.76
Trichoscypha patens	Ana	0.64	0.58
Ctenolophon englerianus	Cte	0.73	0.44
Strombosiopsis tetrandra	Ola	0.58	0.35
Leptaulus daphnoides	Ica	0.22	0.45
Pausinystalia johimbe	Rub	0.26	0.25
Diospyros gracilescens	Ebe	0.24	0.23

Families: abbreviations follow those in Table 3. In addition: Com, Combretaceae; Ebe, Ebenaceae; Med, Medusandraceae; Rub, Rubiaceae; Sap, Sapotaceae.

The five most common species in soil group J plots which are also low or absent in soil groups K and L plots are *Librevillea klainei, Klainedoxa gabonensis* var. *microphylla, Erythrophleum*

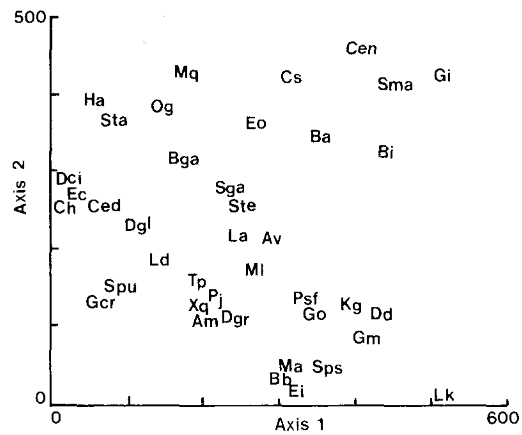

Fig. 3. Species ordinations for all plots (excluding B30, B31, C19). Abbreviations for species: Am, *Anthonotha macrophylla*; Av, *Anthocleista vogelii*; Ba, *Berlinia auriculata*; Bb, *Berlinia bracteosa*; Bga, *Beilschmiedia cf. gaboonensis*; Bi, *Baikiaea insignis*; Ced, *Coula edulis*; Cen, *Ctenolophon englerianus*; Ch, *Cynometra hankei*; Cs, *Casearia stipitata*; Dci, *Diospyros cinnabarina*; Dd, *Diospyros dendo*; Dgl, *Dichostemma glaucescens*; Dgr, *Diospyros gracilescens*; Ec, *Enantia chlorantha*; Ei, *Erythrophleum ivorense*; Eo, *Englerophytum oubanguiense*; Gcr, *Grewia coriacea*; Gi, *Gluema ivorensis*; Gm, *Garcinia mannii*; Go, *Garcinia ovalifolia;* Ha, *Hymenostegia afzelii*; Kg, *Klainedoxa gabonensis* var. *microphylla*; La, *Lophira alata*, Ld, *Leptaulus daphnoides*; Lk, *Librevillea klainei*; Ma, *Mammea africana*; Ml, *Mareyopsis longifolia*; Mq, *Martretia quadricornis*; Og, *Odyendyea gabonensis*; Pj, *Pausinystalia johimbe*; Psf, *Protomegabaria stapfiana*; Sga, *Sacoglottis gabonensis*; Sma, *Strephonema mannii*; Sps, *Strephonema pseudocola*; Spu, *Strombosia pustulata*; Sta, *Soyauxia talbotii*; Ste, *Strombosiopsis tetrandra*; Tp, *Trichoscypha patens*; Xq, *Xylopia quintasii.*

ivorense, Gluema ivorense and *Mammea africana*. Similarly, the five most common species in soil groups K and L combined, which also are lowest or absent from soil group J plots, are *Coula edulis, Cynometra hankei, Dichostemma glaucescens, Strombosia pustulata* and *Beilschmiedia* cf. *gaboonensis*. The species which distinguished soil groups K and L were *Odyendyea gabonensis, Ctenolophon englerianus* and *Hymenostegia afzelii* in soil group K plots and *Martretia quadricornis* and *Grewia coriacea* in soil group L plots. The numbers of species in categories (a), (b) and (c) in an equivalent table (not shown) to Table 6 were 24, 6 and 23 respectively.

The analyses have defined two different forest types on very different soils (Figs. 1, 2): swampy, poorly-drained, high organic matter soils (group J) versus well drained, lower organic matter sandy-loams (groups K and L). Plots in soil groups K and L are more species rich, have a greater density of trees (≥ 30 cm gbh) and a higher proportion of those trees in the 10–20 cm dbh class (though correspondingly fewer very large trees greater than 1 m in dbh) than plots in group J (Table 7).

Outlying plots

Numerical analysis has highlighted five unusual plots. Of the three plots excluded at the ordination stage, C19 is distinctive in its dominance by *Martretia quadricornis* (4.58 m^2 ha^{-1}) and *Pachypodanthidum barteri* (1.09) with all other species in this plot having very low (<0.01 m^2 ha^{-1}) basal areas. Plots B30 and B31 were very similar with high basal areas of *Englerophytum oubanguiense* (2.19), *Acioa chevalieri* (1.49), *Anthostema aubryanum* (1.54) and *Cola* cf. *nitida* (1.42) with other species of basal areas less than 0.7 m^2 ha^{-1}. The vegetation of plot C19 is very similar to that lining the edge of Lake Tissongo and was inundated by moving lake water. Plots B30 and B31 were seasonally-inundated river beds with a deep fine-textured muddy peat layer.

The two most outlying plots (A1 and A12) in the soil classification (Fig. 1) were not so markedly different floristically from the main soil groups' vegetation despite their unusual soil characteristics. Floristically A1 is similar to the soil group J plots (Table 6), whereas A12 is more intermediate between soil groups J and L.

Table 7. Comparison of mean ($\pm 95\%$ confidence limits) tree density, abundance, species richness and dbh frequency distributions between plots in soil group J with plots in soil groups K and L in Douala-Edea Forest Reserve.

	Group	
	J	K+L
number of plots	21	57
Number of species ($plot^{-1}$)	31 ± 2	41 ± 2
Basal area (m^2 ha^{-1})	34.5 ± 5.0	29.8 ± 1.4
Density (ha^{-1})	291 ± 20	406 ± 18
% of tree in dbh class (cm)		
10 – 20	42.7	62.6
21 – 100	54.6	36.4
>100	2.7	1.0

Ordination of groups of plots and their correlation with environmental variables

Plots of soil groups J, K and L were floristically ordinated separately; three outlying plots (B9, B32, B33) of soil group K and two outlying plots (C22, D3) of soil group L were omitted. Soil groups J, K and L were distinct in the relative importance of different environmental variables which are associated with their principal floristic gradients. For soil group J plots, percentage sand and pH were significantly positively correlated, whilst percentage silt and clay were each significantly negatively correlated with axis 1 (Table 8). Available soil potassium was highly negatively correlated with axis 2. Apart from the weak correlation for percentage sand, no variables were highly significantly correlated with axis 1 for the soil group K plots ordination, suggesting that some other variables that we have not measured may be more responsible for this gradient. On axis 2, however, available phosphorus and potassium were significantly positively correlated, as to a lesser degree were percentage clay, pH and nitrate-nitrogen concentration. Soil group L plots did not show the same pattern of strong correlations as soil group K, with percentage clay negatively ($P<0.05$) correlated with axis 1 and ammonium nitrogen negatively correlated ($P<0.01$) with axis 2.

An ordination of the 57 plots in soil group K and L combined was unsatisfactory.

Table 8. Coefficients of correlation (Spearman's r_s) for plot scores of the first two axes of the floristic ordinations of three groups of plots and soil variables in the Douala-Edea Forest Reserve.

	Group					
	J		K		L	
Axis	1	2	1	2	1	2
Eigenvalue	0.63	0.35	0.42	0.24	0.29	0.20
number of plots	21		24		28	
Sand (%)	0.58**	0.02	0.36*	−0.35	0.31	0.27
Silt (%)	−0.48*	−0.03	−0.08	0.10	0.01	−0.21
Clay (%)	−0.80***	0.26	−0.33	0.43*	−0.43*	−0.21
pH	0.50*	0.08	0.18	0.33	0.00	0.28
Organic carbon (%)	−0.02	−0.26	0.13	0.52*	−0.11	−0.29
Available						
phosphorus (ppm)	−0.23	−0.27	0.02	0.67***	−0.39	0.12
potassium (ppm)	0.31	−0.73***	0.26	0.57**	0.14	0.17
Nitrogen						
ammonium (ppm)	nd	nd	0.07@	0.33@	−0.11	−0.52**
nitrate (ppm)	nd	nd	0.01@	0.48*@	−0.38	−0.15

nd = not determined
@ $n = 23$
* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Table 9. Ranges and medians of nine edaphic variables for plots in two subgroups of soil group J, corresponding to low and high soil clay content, and two subgroups of soil group K, corresponding to low and high available soil phosphorus concentrations, in the Douala-Edea Forest Reserve.

	Group			
	J		K	
subgroup	a	b	a	b
clay (%)	≤1	≥6		
phosphorus (ppm)			≤9	≥16
n of plots	9	7	11	9
Sand (%)	71 −100	74 − 84	80 −94	84 −95
	95	79	92	88
Silt (%)	0 − 28	8 − 20	1 − 6	0 − 5
	5	10	3	2
Clay (%)	0 − 1	6 − 11	2 −14	5 −11
0	0	6	6	9
pH	2.7− 3.9	2.7− 3.6	3.9− 4.3	3.9− 4.8
	3.5	3.0	4.0	4.3
Organic carbon (%)	10.0− 12.5	10.0− 12.5	1.5− 3.2	1.7− 3.2
	12.5	12.5	2.1	3.0
Available				
phosphorus (ppm)	7 − 50	8 − 29	7 − 9	16 −31
	24	20	8	20
potassium (ppm)	95 −188	78 −143	27 −40	33 −50
	140	85	38	40
Nitrogen				
ammonium (ppm)	nd	nd	3 − 9	6 −25
nitrate (ppm)	nd	nd	6	13
			1.0− 6.0	1.5− 5.5
			3.5	4.5

nd = not determined

Table 10. Mean basal areas per plot ($m^2\ ha^{-1}$) and plot frequency of tree species in two soil subgroups of plots with low and high percentage clay content in group J plots, Douala-Edea Forest Reserve. Species listed have a mean basal area of at least 0.1 $m^2\ ha^{-1}$, and a frequency of occurrence in at least four of the plots in one of the subgroups. (a) basal area in subgroup a > threefold basal area in subgroup b, (b) basal area in subgroup b > threefold basal area in subgroup a, (c) ≤ threefold difference in basal areas between subgroup means, both subgroups with basal areas > 0.1 $m^2\ ha^{-1}$. Only the first 10 species out of lists of 16, 8, 16 species for (a), (b) and (c) respectively are shown.

	Family (Subfamily)	Subgroup			
		a		b	
clay (%)		≤1		≥6	
number of plots		9		7	
		b.a.	f	b.a.	f
(a)					
Librevillea klainei	Leg	6.30	7	+0.00	1
Gluema ivorensis	Sap	2.91	4	0.00	0
Ctenolophon englerianus	Cte	1.67	5	0.00	0
Strephonema mannii	Com	1.06	5	0.00	0
Diospyros dendo	Ebe	1.02	9	0.20	7
Baikiaea insignis	Leg	0.47	6	0.07	3
Beilschmiedia cf. gaboonensis	Lau	0.37	8	0.03	2
Drypetes ivorensis	Eup	0.36	5	+0.00	7
Baphia hylophila	Leg	0.25	5	0.00	0
Casearia stipitata	Sam	0.21	4	0.00	0
(b)					
Protomegabaria stapfiana	Eup	0.74	4	6.70	7
Lophira alata	Och	1.00	6	4.52	7
Anthocleista vogelii	Log	0.44	7	1.33	7
Trichoscypha patens	Ana	0.13	4	1.10	7
Strephonema pseudocola	Com	0.34	1	1.09	5
Dichostemma glaucescens	Eup	0.00	0	1.00	4
Anthonotha macrophylla	Leg	0.19	3	0.90	6
Trichillia zenkeri	Mel	0.00	0	0.40	5
Ouratea affinis sens. lat.	Och	0.02	3	0.20	6
(c)					
Sacoglottis gabonensis	Hum	4.36	5	1.94	2
Klainedoxa gabonensis var. *microphylla*	Eup	2.03	5	1.47	3
Mammea africana	Gut	0.70	5	0.94	7
Coula edulis	Ola	0.46	3	1.18	5
Erythophleum ivorense	Leg	0.71	4	0.82	4
Berlinia auriculata	Leg	0.55	8	0.41	7
Garcinia mannii	Gut	0.45	9	0.40	7
Uapaca staudtii	Eup	0.55	5	0.22	4
Garcinia ovalifolia	Gut	0.29	8	0.48	7
Maprounea membranacea	Eup	0.19	4	0.39	6

Families: abbreviations follow those in Table 3. In addition: Com, Combretaceae; Ebe, Ebenaceae; Mel, Meliaceae; Sam, Samydaceae; Sap, Sapotaceae. Baphia: Leg (subfamily Papilionoideae).

Comparison of the vegetation on soils of differing clay content

In soil group J plots percentage clay correlates most highly with the first floristic gradient (axis 1). Two soil subgroups of plots can be defined as Ja, with a soil clay content of 1% or less, and Jb with a clay content of 6% or more. Apart from the silt content (which is also higher on the high clay plots, Table 9) these subgroups are otherwise similar. The five commonest species which have higher basal areas on the very sandy and virtually clay-free soils are *Librevillea klainei, Gluema ivorensis, Ctenolophon englerianus, Strephonema mannii* and *Diospyros dendo* (Table 10a). These species also appear at the positive end of axis 1 of the species ordination of soil group J plots. Of species with much greater basal area on the finer textured soils (Table 10b), the five most common are *Protomegabaria stapfiana, Lophira alata, Anthocleista vogelii, Trichoscypha patens* and *Strephonema pseudocola.* Several common species appear to be indifferent to the sand or clay contents, e.g. *Sacoglottis gabonensis, Klainedoxa gabonensis* var. *microphylla* and *Coula edulis* (Table 10c).

Comparison of the vegetation on soils of high and low phosphorus levels

Available soil phosphorus concentration on axis 2 (although not the principal indirect gradient) is the variable most highly correlated for soil group K plots and these plots can be allotted to two soil subgroups Ka, with 9 ppm or less phosphorus, and Kb, with 16 ppm of phosphorus or more. Table 9 shows a two and a half fold difference between the median phosphorus concentrations of these soil subgroups: organic matter and soil nitrogen concentration are also higher in the high phosphorus subgroup. The important floristic differences between soil subgroups Ka and Kb are shown in Table 11. The five commonest species which show greater basal areas on low phosphorus soils are *Hymenostegia afzelii, Guibourtia demeusei, Strombosiopsis tetrandra, Casearia stipitata* and *Dialium pachyphyllum.* Of the five commonest species which have higher basal areas on the relatively higher phosphorus soils, only four meet the criteria for inclusion in Table 11; *Anthonotha macrophylla, Strombosia pustulata, Diospyros*

Table 11. Mean basal areas per plot ($m^2\ ha^{-1}$) and plot frequency of tree species in two soil subgroups of plots with low and high available soil phosphorus concentrations in group K plots, Douala-Edea Forest Reserve. Species listed have a mean basal area of at least 0.1 $m^2\ ha^{-1}$, and a frequency of occurrence in at least four of the plots in one of the subgroups. (a) basal area in subgroup a > threefold basal area in subgroup b, (b) basal area in subgroup b > threefold basal area in subgroup a, (c) ≤ threefold difference in basal areas between subgroup means, both subgroups with basal area > 0.1 $m^2\ ha^{-1}$. Only the first 5 species (of a list of 15) are shown in (c).

	Family (Sub-family)	Subgroup a		Subgroup b	
phosphorus (ppm)		≤9		≥16	
number of plots		11		9	
		b.a.	f	b.a.	f
(a)					
Hymenostegia afzelii	Leg	1.79	7	0.00	0
Guibourtia demeusei	Leg	0.74	5	0.00	1
Strombosiopsis tetrandra	Ola	0.64	8	0.16	3
Casearia stipitata	Sam	0.44	7	0.00	0
Dialium pachyphyllum	Leg	0.36	6	0.11	2
Berlinia auriculata	Leg	0.27	9	0.04	3
Maprounea membranacea	Eup	0.23	6	0.04	4
(b)					
Anthonotha macrophylla	Leg	0.16	10	2.08	9
Strombosia pustulata	Ola	0.24	8	1.05	8
Diospyros gracilescens	Ebe	0.17	7	0.60	5
Ouratea affinis sens. lat.	Och	0.05	6	0.27	3
(c)					
Coula edulis	Ola	5.82	11	8.90	9
Sacoglottis gabonensis	Hum	2.24	5	1.86	2
Lophira alata	Och	2.40	11	0.82	7
Dichostemma glaucescens	Eup	1.09	10	2.07	9
Odyendyea gabonensis	Ixo	2.11	8	0.86	2

Families: abbreviations follow those in Table 3. In addition: Ebe, Ebenaceae; Sam, Samydaceae. Subfamily: as Table 3.

gracilescens and *Ouratea affinis.* The difference in floral composition between these subgroups is therefore weak.

Direct gradient analysis

All plots in the Douala-Edea Reserve can be placed into eight increasing classes of available soil phosphorus concentration for direct gradient analysis, in a similar manner to that performed for the Korup Reserve species (Gartlan *et al.*, 1985). Since the influence of restricted drainage is so marked on the vegetation, the 19 permanent swamp and stream plots were excluded. Of the 100 common species in the whole enumeration, four were completely restricted to the excluded swampy plots. For the remaining 96 species, the mean basal area was calculated for those plots in each class and these values regressed on the linear and quadratic terms of a polynomial function of phosphorus concentration. Species with a significantly good fit ($P \leq 0.05$) are shown in Table 12. In each significant case the form of the response was ascribed to one of six basic models. These are shown in Fig. 5 of the Korup paper (Gartlan *et al.*, 1985). Models I and VI have high basal area at the lower and upper extremes of the gradient respectively, model III is a Gaussian-shaped response, model IV a U-shaped response and models II and V represent gradually decreasing and increasing basal area response to the gradient respectively.

The frequency distribution of plots with respect to increasing concentrations of available soil potassium was highly positively skewed and therefore unsuitable for direct gradient analysis. The range of potassium in the 85 non-swamp plots was 27–163 ppm and 66 plots had concentrations between 27 and 60 ppm.

Thirty-three species showed a significant response to soil phosphorus concentration, with 7 species having a model III form. Model I responses were the most frequent (17 species) whilst species with models II, IV and VI were relatively infrequent (Table 12). Modal phosphorus concentrations for model III species mostly lay between 21 and 50 ppm.

Comparisons between Douala-Edea and Korup

Floristics

In origin, history and environment the Korup and Douala-Edea Forest Reserves are distinct. Korup is dominated by *Oubanguia alata* and *Scyphocephalium mannii* whereas at Douala-Edea the one main dominant, in our enumeration, is *Coula edulis* (Table 3). Species richness is greater at Korup, with 411 taxa in total in the enumeration (274 to the specific level; Gartlan *et al.*, 1985), than

Table 12. Species with significant response curves for mean basal area per plot on available soil phosphorus concentration in Douala-Edea Forest Reserve, classified according to six basic models. Of the 96 species tested only those with an analysis of variance of regression *F*-ratio significant at $P \leq 0.05$ are listed with the coefficient of determination, $R\%$. The modal concentrations are recorded for model III species.

Model	Species	Family (Sub-family)	R^2	P	Mode (ppm)
I	*Afzelia* sp.	Leg[2]	53	*	
	Anthostema aubryanum	Eup	53	*	
	Baphia hylophila	Leg	53	*	
	Casaeria stipitata	Sam	85	***	
	Cryptosepalum pellegrinianum	Leg[1]	53	*	
	Ctenolophon englerianus	Cte	59	*	
	Gluema ivorensis	Sap	73	**	
	Guibourtia demeusei	Leg[2]	86	***	
	Hymenostegia afzelii	Leg[2]	56	*	
	Klaineanthus gaboniae	Eup	82	**	
	Martretia quadricornis	Eup	82	**	
	Odyendyea gabonensis	Ixo	91	***	
	Pachypodanthium barteri	Ann	76	**	
	Santiria trimera	Bur	55	*	
	Strychnos mimfiensis	Log	65	*	
	Symphonia globifera	Gut	53	*	
	Toubaouate brevipaniculata	Leg[1]	53	*	
II	*Anthonotha lamprophylla*	Leg[1]	63	*	
	Baikiaea insignis	Leg[2]	56	*	
	Maprounea membranacea	Eup	91	***	
III	*Antidesma vogelianum*	Eup	71	*	31 – 40
	Buchholzia coriacea	Cap	76	**	51 – 60
	Diospyros iturensis	Ebe	96	***	41 – 50
	Klainedoxa gabonensis var. *microphylla*	Ixo	57	*	21 – 30
	Mammea africana	Gut	65	*	21 – 30
	Mareyopsis longifolia	Eup	72	**	31 – 40
	Pausinystalia johimbe	Rub	71	*	41 – 50
IV	*Soyauxia talbotii*	Med	87	***	
V	*Afzelia bella*	Leg[2]	56	*	
	Coula edulis	Ste	89	***	
	Garcinia conrauana	Gut	70	*	
	Heinsia crinita	Rub	68	*	
VI	*Balanites wilsoniana*	Zyg	53	*	

Families: Abbreviations follow those in Table 3. In addition: Ann, Annonaceae; Bur, Burseraceae; Cap, Capparidaceae; Ebe, Ebenaceae; Med, Medusandraceae; Rub, Rubiaceae; Sam, Samydaceae; Sap, Sapindaceae; Ste, Sterculiaceae; Zyg, Zygophyllaceae.
Superscripts to Leg (Caesalpinioideae) are the Tribes: 1, Amherstieae; 2, Detarieae.
* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

at Douala-Edea where 230 taxa in total were recorded (198 to the specific level). This difference may in part be due to the area of enumeration at Douala-Edea being c. 25% less than that at Korup. Douala-Edea and Korup differ little in the mean basal area of all trees (≥30 cm gbh), 31 and 28 m^2 ha^{-1} respectively. The mean density of stems at Korup was similar to, whilst that at Douala-Edea much less than, the mean of 487 ha^{-1} for all forest types in Ghana studied by Hall & Swaine (1981).

Three of the five families/subfamilies contributing the most stems at Korup fall within the same category at Douala-Edea, the Leguminosae/Caesalpinioideae, Euphorbiaceae and Olacaceae. However, of the remaining two families that have the highest frequencies at Korup, the Sterculiaceae contributes less than 1% at Douala-Edea and the Scytopetalaceae, the most frequent family at Korup, appears to be completely absent from Douala-Edea.

Responses to phosphorus

Thirty-five species are common to both Korup and Douala-Edea enumerations. Of these, 13 occurred in the first 100 most common species in both Forest Reserves and their responses to soil phosphorus gradients were analysed. Bearing in mind that the ranges of phosphorus are different for Korup and Douala-Edea (2–29 and 7–90 ppm respectively in well-drained plots), 6 of 13 species had a significant response in one or both of the Reserves to phosphorus: *Hymenostegia afzelii*, model VI at Korup, model I at Douala-Edea; *Strephonema pseudocola*, model I at Korup, not significant at Douala-Edea; *Lophira alata* and *Strombosiopsis tetrandra*, both model II at Korup, not significant at Douala-Edea; *Klainedoxa gabonensis*, model VI at Douala-Edea, not significant at Korup; *Coula edulis*, model V at Douala-Edea, not significant at Korup. There is no agreement in the response to soil phosphorus for the 6 species compared in the two Reserves.

Of the 22 species characteristic of soil group J swamp plots at Douala-Edea and the 12 characteristic of swamp plots at Korup (Gartlan *et al.*, 1985), only three species are in common. These are *Mammea africana, Mitragyna stipulosa,* and *Symphonia globulifera.*

Discussion

Effect of drainage on forest type

In contrast to Korup (Gartlan *et al.*, 1985) where the plots were arranged along a gradual gradient, at Douala-Edea the forest is clearly divisible into two types. The swamp forest association is dominated by species (Table 6) which are rare or absent in the well-drained plots of soil groups K and L. The swamp plots of soil group J show more variation in their flora and soil characteristics than the tightly clustered plots of soil groups K and L. Of the five most abundant species at Douala-Edea (Table 3), three are clearly characteristic of either forest type.

At Douala-Edea, Letouzey (1975) recognised three forest formations: the littoral forest, riverine forest and high forest of the interior. Our sampling along transect A avoided the true littoral forest and the ends of transects B, C and D connected with the riverine forest. For the large part, however, the present enumeration sampled the interior forest, especially around Lake Tissongo. Letouzey (1968) classifies the interior forest as that being typical of low-altitude, coastal rain forest in the Cameroun, characterised by high abundances of *Sacoglottis gabonensis* and *Lophira alata*, and within it recognizes two types: 'forêt sur sol sec d'une part et forêt marécageuse ou périodiquement inondée sur sol humide d'autre part' (Letouzey, 1975, p. 532). Our results show *Sacoglottis gabonensis* and *Lophira alata* to be approximately equal in abundance in soil group J and soil groups K and L (Table 6), and *Coula edulis*, which Letouzey mentions as being especially abundant around Lake Tissongo, dominates our enumeration. On the well-drained plots of soil groups K and L we found, like Letouzey, important species such as *Cynometra hankei* and *Strombosia pustulata* but the agreement is poor for the swamp plots. Only some of the species typical of the wetter soils referred to by Letouzey (1975) occur more commonly in soil group J plots, notably *Uapaca staudtii, Mitragyna stipulosa* and *Klainedoxa gabonensis*. The dominance of soil group J plots by *Protomegabaria stapfiana* seems to make transect A a special case, though this species is in the Euphorbiaceae which have general associations with wetter soils in the Camerouns (Letouzey, 1968). There are two likely reasons to explain these differences: first, that the periodically inundated vegetation is floristically quite variable at Douala-Edea and Letouzey collected more to the west of the Reserve; and second, that whilst most swamp plots have high levels of soil organic matter (an important criterion in the classification of the soils on which the floristic groups are based) not all high organic plots may have been so regularly inundated in recent years. However, inspection of the ordination of all plots and species (Fig. 3) and noting those plots permanently swamped does not strengthen the comparison with Letouzey's subjective findings.

Variation within poorly drained forest

Not all the plots of soil group J with their characteristically high concentrations of organic matter have permanent or seasonal swamps at present but may have done so in the recent past. The most extreme conditions are found in very sandy soils with permanent streams flowing through the plot and these show an effect in a decrease in available soil potassium concentration (Table 8). In these poorly-drained plots the vegetation does not appear related to soil phosphorus.

Associations between the vegetation and available soil phosphorus in well-drained plots

The dominant vegetation is similar in groups K and L.

No other soil variables separated soil group K and L plots to the same extent as phosphorus and yet for the main ordination phosphorus was only weakly (though significantly) correlated with axes I and II. This presumably is because drainage dominates the main floristic gradient, and phosphorus and drainage are poorly interrelated.

Floristic ordination of the lower phosphorus plots (soil group K) demonstrated that the very lowest phosphorus concentrations in well drained plots were associated with a distinguishable vegetation on the second axis. But the weak correlation with sand on the first axis is not supported by comparisons with soil group J plots.

Direct gradient analysis using all well drained plots without permanent streams showed a predominance of model I responses by species to increasing soil phosphorus concentration. These included several species which have high abundances in soil group K plots, but not soil group L plots.

The association between *Hymenostegia afzelii* (I), *Guibourtia demeusei* (I), *Casearia stipitata* (I) and *Maprounea membranacea* on the low phosphorus soils is further highlighted by a comparison of the selected low and high phosphorus plots of group K (Table 11). In addition, whilst these low phosphorus associated species are almost entirely absent from the high phosphorus plots, the common species associated with high phosphorus are present to some extent in nearly all the low phosphorus plots.

At Korup, Gartlan *et al.*, (1985) showed a strong association of species in the tribes Amherstieae and Detarieae, of the subfamily Caesalpinioideae (family Leguminosae) with soils of low phosphorus concentration. This result is also shown, though less strongly, at Douala-Edea with 8 species of model I and II response in this subfamily. The number of species occurring in each of the five tribes (Polhill & Raven, 1980) are: Amherstieae, 14 (of the genera: *Anthonotha, Berlinia, Cryptosepalum, Didelotia, Gilbertiodendron, Librevillea* and *Toubaouate*): Caesalpinieae, 1 (of the genus *Erythrophleum*); Cassieae, 1 (of the genus *Dialium*); Cercidea, none, Detarieae, 12 (of the genera: *Afzelia, Baikiaea, Cynometra, Hymenostegia, Guibourtia* and *Leonardoxa*). The genera *Baphiopsis* and *Swartzia*, placed in a sixth tribe, Swartzieae, by Aubréville (1963–1983) have been recently made part of the subfamily Papilioniodeae by Polhill & Raven (1980). Malloch, Pirozynski & Raven (1980) have found that species of the two tribes, Amherstieae and Detarieae are commonly infected with ectotrophic mycorrhizae and this in part provides a possible explanation for the floristic gradient associated with available soil phosphorus. Whilst the concentrations of available soil phosphorus at Douala-Edea (7–90 ppm) are generally higher than those at Korup (Gartlan *et al.*, 1985; 2–29 ppm), the principal effect of drainage at Douala-Edea is likely to mask any smaller, more subtle effects of phosphorus. The most important conclusion from the analysis of the Douala-Edea enumeration is that available soil phosphorus levels appear to be too high to select strongly for species in the Casalpinioideae. At Korup (Gartlan *et al.*, 1985) the critical threshold value was 5 ppm phosphorus and the results from Douala-Edea support this finding.

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