Chapter 2.

Vegetation.

Introduction.

The natural vegetation of *85%* of the country is lowland rain forest (Caballi!, 1983), although the present extent of forest cover is estimated at 200,000 km2 *(75%)* (Myers, 1991). Areas outside those originally forested are mostly savanna, swamp and mangroves (Caballé & Fontes, 1978). Various authors have commented on tree species distribution in Gabon, and attempted classifications of forest types (Aubréville, 1948; Caballi! 1978, 1983; Catinot, 1978; Chevalier, 1916; Heitz, 1943; Nicolas, 1977; de Saint Aubin, 1963; Schnell, 1976; White, 1983; Wilks, 1990). In the UNESCO classification (White, 1983) Gabonese forests are predominantly either 'hygrophylous coastal evergreen Guineo-Congolian rain forest' or 'mixed moist semi-evergreen Guineo-Congolian rain forest', with patches of 'single-dominant moist evergreen Guineo-Congolian rain forest' characterised by ***Gilbertiodendron*** dewevrei, in the northeast (Wilks, 1990). Letouzey (1968) described Gabon's forests as 'foret dense humide sempervirente de basse et moyenne altitude'. Other classifications have attempted to delimit forest types characterised by one or more species: Schnell (1976) recognised two forest types, with or without ***Aucoumea klaineana*** respectively; and Caballé (1978, 1983) recognised three geographical areas in which the commoner large tree species varied. However, most of the available data were collected on forest inventories with a bias towards large or commercial species (Nicolas, 1977). Few plant collections have been made in the country (Breteler, 1978), and until further data are available, it is pointless to attempt more than the general classifications of White and Letouzey (A. Louis, personal communication).

Reitsma (1988) undertook a detailed botanical inventory of four square 1-ha plots in different regions of Gabon. He reported large differences in species composition and diversity, which were related in part to prevailing environmental conditions in the four sites, and proximity to an area thought to be a Pleistocene forest refuge. The least Species-rich plot was located in the Lopé Reserve, central Gabon, where soil conditions were least favourable and average annual rainfall was low. This chapter describes a larger scale botanical study conducted within Lope, and attempts to explain observed differences in forest structure and composition.

Study Area.

Research was carried out in the Lope Reserve, at the Station d'Etudes des Gorilles et Chimpanzés (SEGC) at 0°10'S, 11°35'E and the Societe Forestier du Gabon (SOFORGA) logging concession (0°25'S, 11°25'E). Lope, which covers 5,000 km2, is the largest of five protected areas in Gabon. Most of the reserve is covered **by** mature semi-evergreen tropical rain forest, but there are 300 km2 of savanna and forest-savanna mosaic along its northern and eastern limits (Figure 2.1). About 2,500-3,000 km^2 of the forest have been selectively logged at low intensity (1-2 trees per hectare), principally for one tree species, *Aucoumea* **klaineana.**

Lopé lies in an area of relatively low rainfall compared to much of Gabon (EDICEF, 1983). Mean annual rainfall at SEGC is 1,536 mm (1984-90), although there is considerable inter-annual variation in the amount and distribution of rainfall: Consistently low rainfall in July and August constitutes a "major dry season", which is a feature of the annual cycle, although the timing of its onset and its duration varies between years; December to February are generally relatively dry months, but no distinct second dry season can be defined (Figure 2.2). Rainfall increases from north to south within the reserve (EDICEF, 1983: p. 35).

Mean relative humidity does not drop below **70%,** even between 13:00 and 15:00 (SEGC, unpublished datal, which compares well with data collected elsewhere in Gabon (see Nicolas, 1977; **de** Saint Aubin, **1963).** Mean relative humidity does not, as might be expected, fall in the long dry season, because cold sea currents at this time of year cause constant cloud cover throughout the country, resulting in reduced temperature, insolation, and evaporation (EDICEF, 1983; Hladik, 1973; Nicolas, 1977). Temperatures vary little over the year, but both mean monthly minima and maxima are lowest during the major dry season, with a range of 20-23°C and 26-33°C respectively over 7 years.

Figure 2.1: Lopé Reserve, with locations of transects and savanna.
Overlay to Figure 2.1: Geological map of Lopé (after Martin *et al.*, 1981).

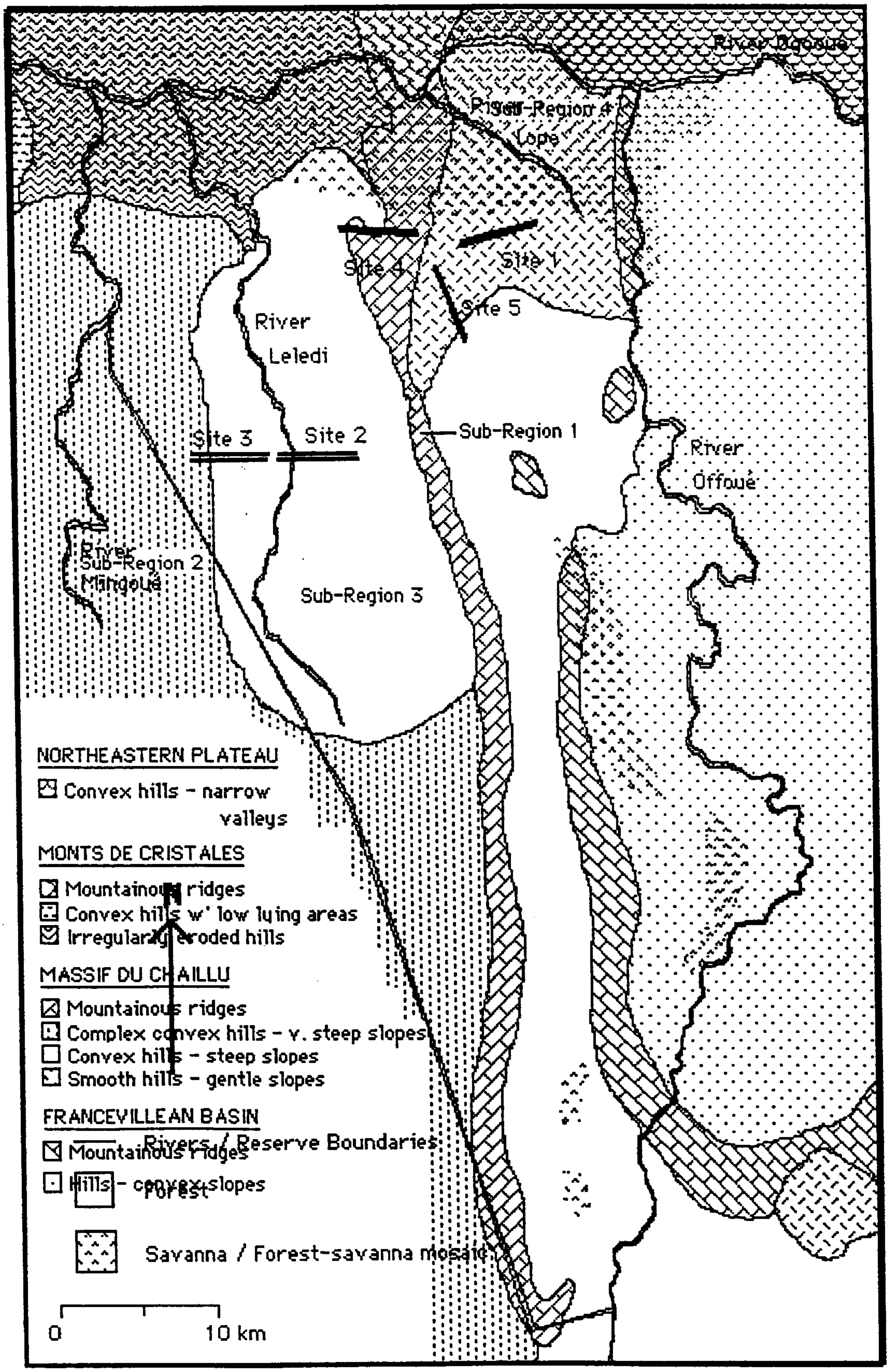
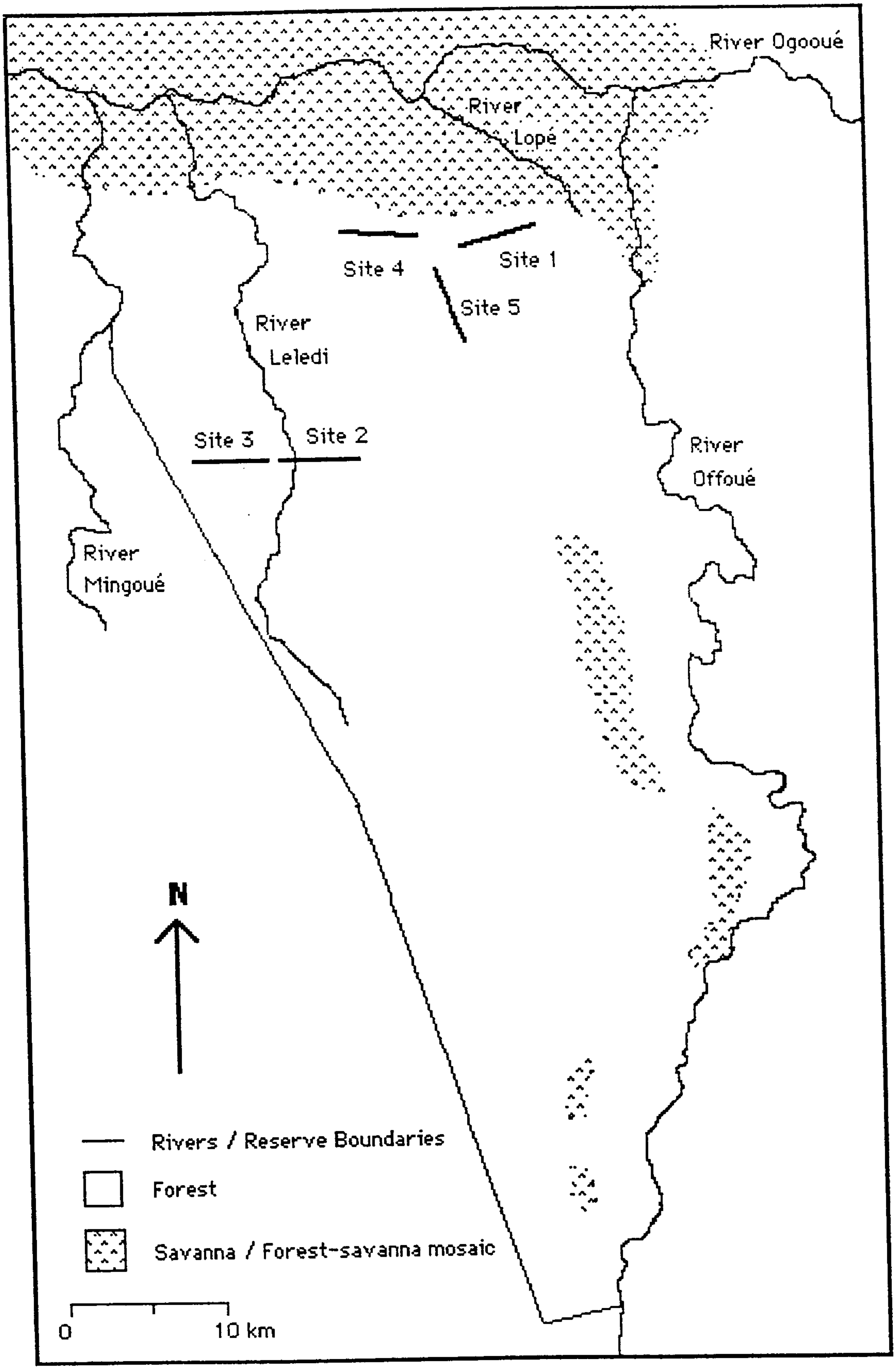


Figure 2.1: Lopé Reserve, with locations of transects and savanna.



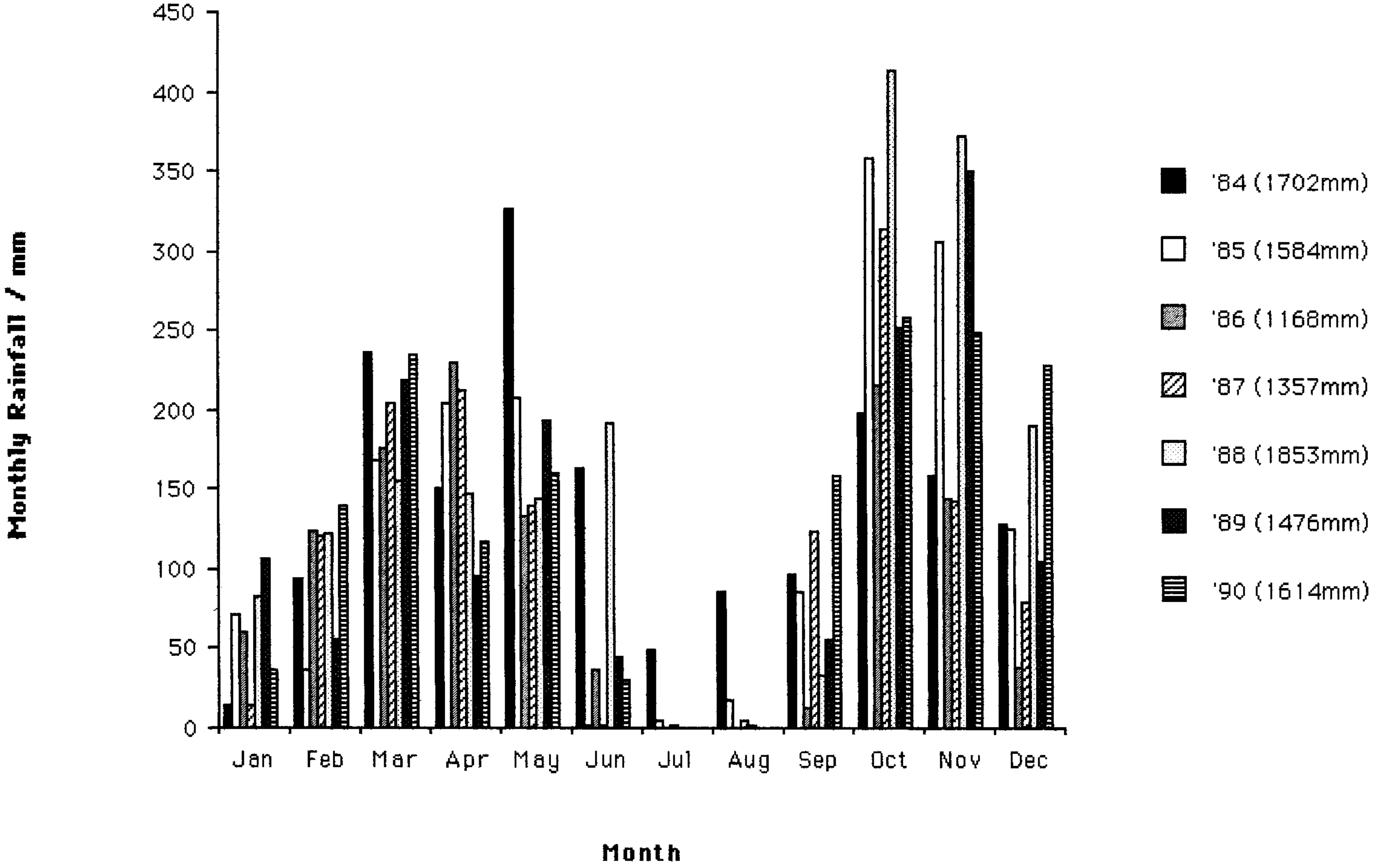


Figure 2.2: Rainfall recorded at SEGC 1984-1990

Gabon can be divided into three geomophological zones (EDICEF, 1983), within which six distinct regions can be distinguished (Fontes, 1975; Martin *et al,* 1981). Lope straddles the border between two of these regions: the central Precambrian mountain range, and the 'Francevillian' sedimentary basin; which meet towards the eastern limit of the reserve. All study sites fell within the 'Massif du Chaillu', one of three Precambrian mountain ranges, which runs from central Gabon southeast into Congo (EDICEF, 1983; Martin *et al,* 1981). Parts of the north of the reserve, outside the study area, fall within the 'Monts de Ndjolé', the second of the three Precambrian mountain ranges. The metamorphic rocks that constitute the range are deeply weathered, forming well-drained, infertile, clay, or sandy-clay ferallitic soils with low pH (>4.5). Within Lopé, four sub-regions can be identified within the Massif du Chaillu, based on topography (Martin *et al,* 1981 - **see** overlay to Figure 2.1):

1) Mountainous ridges (Sub-Region 1)
2) Complex convex hills with very steep slopes (Sub-Region 2)
3) Convex hills with steep slopes (Cub-Region 3)
4) Gently rolling hills (Sub-Region 4)

Aubreville (1967a) described the pattern and distribution of the "strange forest-savanna mosaic" in the Lope area and discussed factors that might have contributed to its formation. Savanna occurs in a band about 10-15 km wide along the river Ogooué in the north of the reserve, and west of the river Offoué along its eastern limit (Figure 2.1 - **see** also aerial photograph in Harrison and Hladik, 1986). Close to the Ogooué, savanna is essentially continuous, interspersed with patches of gallery forest in thalwegs and up some valley sides. Further south the relative proportion of savanna:forest decreases, and further than about 15 km south of the Ogooué, savanna patches are generally isolated within forest on hill-tops about 200-450m in altitude (Plates 2.1 & 2.2). Adjacent hills above about 450m tend to be forested **(IGN,** 1985). Small isolated patches of savanna orrur up to 35 km to the south of the Ogooué.

Savanna vegetation in the north of the reserve has been described in detail **by** Descoings, (1974). **It** is characterised by the grass, Pobeguinea ***arrecta,*** which is dominant, or co-dominant with ***Andropogon pseudapricus, Hyparrhenia diplandra*** or *Schizachyrium* ***platyphyllum.*** Shrubs such as ***Crossoptaryx***

Plate 2.1.

Buffalo (*Syncerus caffer*) in open savanna in the north of the reserve. Note gallery forest in thalweg in the background.

Savanna-forest mosaic, with SEGC (centre). To the right (south) is the beginning of continuous forest cover and the SEGC main study area (Site 1); to the left (north) savanna-forest mosaic extends 12km to the Ogooué.

Plate 2.2.

Looking south towards Site 5 from the savanna edge. Note savanna on hills in foreground.

Forest along the savanna edge. Trees with red canopies are the savanna coloniser *Lophira alata*, with flushes of new leaves.

febrifuga, Bridelia ferruginea, Nauclea latifolia Sarcocephalus esculentus, Psidium guineense and *Psorospermum febrifugum,* occur sparsely throughout the savanna [Descoings, 1974; Fontes, 1978; **Wilks,** 1990).

There is some debate as to whether the origins of these savannas, and equivalent areas in other parts of central Africa, are natural [relicts of a drier period in the Pleistocene when forests receded and were replaced by savannas) or anthropic (left over from periods when the human population of the area was higher). Descoings (1974), after a detailed study of the composition and distribution of savannas in the Lopé area, concluded that the latter was more likely, and Fontes (1978) reached a similar conclusion. Aubreville (1967a) concluded that the pattern of savanna-forest mosaic was due to an on-going process of recolonisation of savanna which had resulted naturally from prehistorical differences in climate, and Nicolas I19771 agreed that the savannas around Lopé were likely to be natural in origin. Recent work in Congo has suggested that savannas in the Oriental Mayombe are natural in origin, although they are maintained today by regular fires started by humans (de Foresta, 1990; Schwartz *et al.,* 1990).

Methods.

Five study sites were established on the basis of their logging history: In Sites 4 & 5 rectangles 5km by 1km were drawn on a map, on a compass bearing crossing the drainage (cf. Norton-Griffiths, 1978), sited such that they were in forest that had been subject to a specified logging regime. A line transect 1m wide and 5km in length was located randomly in the study area (using a random number table to select a number between 0-1000 to signal a starting point along the 1km boundary of the site), and was cut following the compass bearing [Figure 2.1). In Sites 2 & 3 the same procedure was followed, but the sites were continuous and a 10.5km line was cut (transects 2 and 3 were the eastern and western 5km respectively). In Site 1, a 1-km transect established previously (across the drainage, as above) to undertake a botanical survey (Williamson, 1988) was extended to 5 km:

Site 1 was the SEGC main study area, *in* which research on the ecology of apes *(Gorilla g. gorilla* and ***Pan* i. *troglodytes)*** has been underway since 1984 (e.g., Tutin et ***al,*** 1991a). The SEGC study area covers about 40 km^2 along the northern limit of the continuous forest block. The transect was cut at a bearing of 235" and ran parallel to the savanna-forest boundary, about 1km from the forest edge. The entire length of the transect fell within geological Sub-Region 4 (see Figure 2.1). The forest had been logged once, 20-25 years previously, for one tree species, ***Aucoumea klaineana*** which was extracted at an intensity of about one tree ha-'.

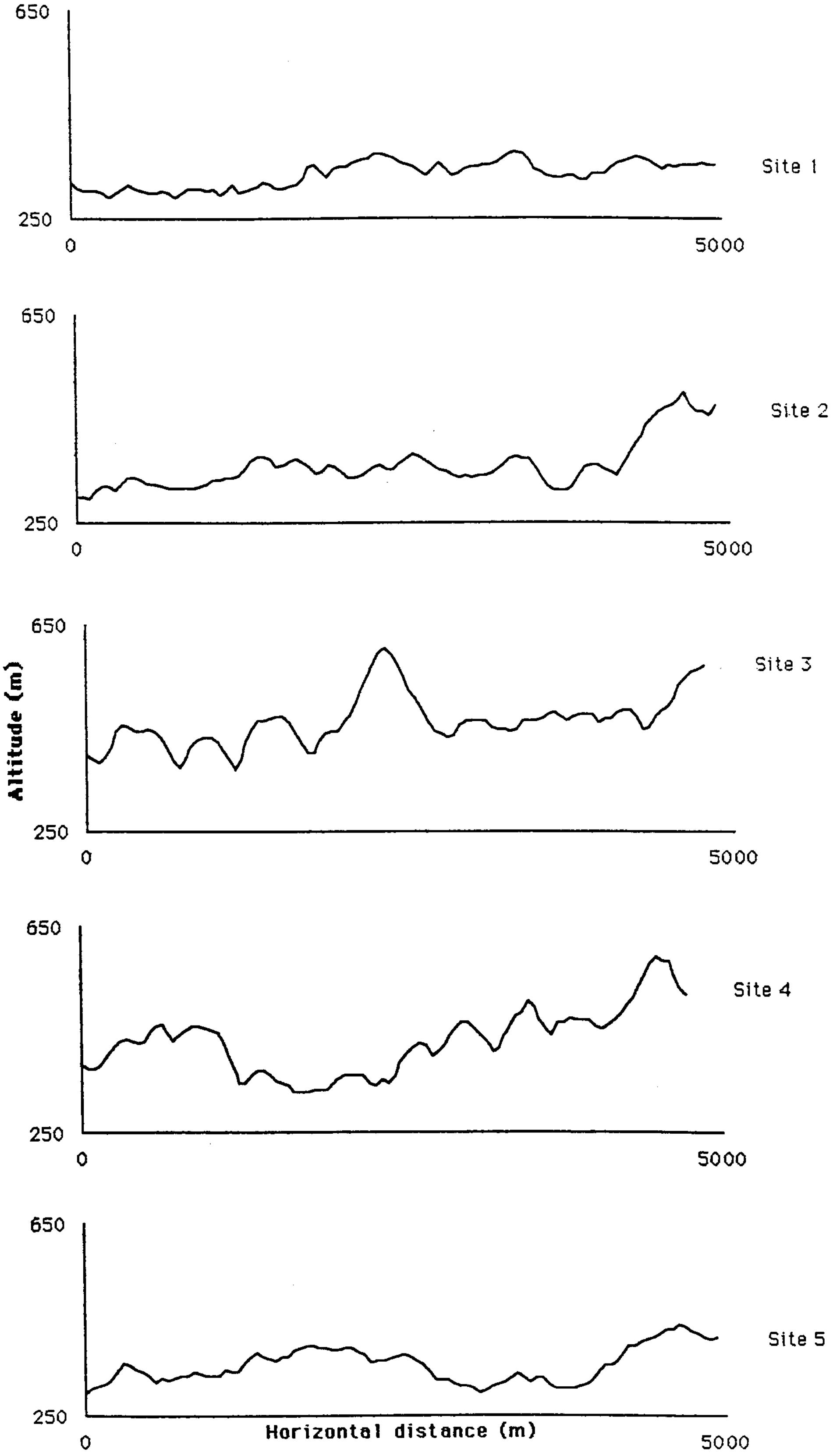
<u>Sites 2 and 3</u> were adjacent to one another, located in the SOFORGA logging concession, 35 km southwest of **SEGC,** with an essentially continuous transect at a bearing of 265°. The first (eastern) 5km (Site *2)* had been logged for ***Aucoumea klaineana,*** and a limited number of other species, at an intensity of i-2 trees ha-1 early in 1986 (3-5 years before this study). The first 9km (Site 2 plus 3.5 km of Site 3) were in Sub-Region **3,** and the final 1.5-km of Site 3 overlapped into Sub-Region 2. **A** river about 20m wide, the Leledi, bisected Site 2 at 3.6 km.

<u>Site 4</u> was about 5km southwest of SEGC, with a transect cut at 270" falling within Sub-Region 1. The forest had been logged for ***Aucoumea klaineana*** at an intensity of about 1 tree ha-', 10-15 years before.

<u>Site 5</u> started about 3km south of SEGC, with a transect at 155°, predominantly located within Sub-Region **4,** but crossing into sub-region 3 in the last (southern) 500m. Two tributaries of the River Lope, each about 10-15m wide, crossed the transect at 3100m and 3800m. This site had not been affected by timber extraction, but logging was known to have occurred within about 1km **of** the end of the transect, and towards the end of the study it was discovered that loggers had (illegally) almost reached the transect at 3700m.

Figure 2.3 shows profile diagrams for the five sites, illustrating their contrasting topographies.

Figure 2.3: Profile diagrams of the five transects.



The diameters of all trees >10cm dbh in a 5 metre strip, 2.5 m either side of each transect (giving a sample of 2.5 ha), were measured at 1.3m above the ground (diameter at breast height, dbh), or immediately above stilt or buttress roots, using a diameter tape. Each tree was labelled with a numbered aluminium tag. Trees were identified using a combination of sterile characters: general form (e.g., buttresses, stilt roots); bark texture; slash colour, smell and exudates; leaf type and shape. Leaves were collected and compared with herbarium specimens, and where possible fertile collections were made. A voucher specimen of each new species encountered was taken, and these are lodged at herbaria in Libreville, Gabon and Missouri, U.S.A., as well as at SEGC and with the author. All trees >70 cm dbh (minimum legal diameter for commercial exploitation for most species) in a 50 metre strip, 25m either side of the transect, were measured (giving a sample of 25 ha), identified and labelled in the same way. In addition, specimens were collected opportunistically from all plant species encountered fertile during the study in any of the study sites, irrespective of size and location. Heights of all trees were estimated visually to the nearest metre.

Canopy cover at three heights (<10m, 10-20m, >20m) was estimated along the length of the transect using a point quadrat method (Greig-Smith, 1983): As most crowns of trees in the Gabonese rain forest do not exceed 5m in diameter (Reitsma, 1488) a sighting clinometer was used to look up vertically at five metre intervals along the length of the transect, and canopy cover was scored as present or absent in each of the three height classes depending on whether or not a point in the sight projected upon vegetation. Thus 1000 points were recorded at each height along each 5000m transect.

Density of herbaceous vegetation of the families Marantaceae and Zingiberaceae was assessed by counting stem densities for each species present in areas of 1m2, displaced one metre off the transect (to avoid any effects of cutting the transect) at five metre intervals along each transect (cf. Rogers & Williamson, 1987). These families were chosen because they were abundant, relatively easy to identify from vegetative material, species composition and abundance varied between habitats, and they were a major component of the diets of gorillas and chimpanzees (cf. Rogers & Williamson, 1987). Other herbs, shrubs, and trees <10cm dbh were not sampled systematically, but collections were made whenever they were encountered with flowers or fruits.

The locations of notable physical features (e.g., streams, marshes, rocky outcrops, old roads, ridges) were recorded, and average gradient was measured for each 50m portion of each transect using a clinometer.

During the course of the study, an attempt was made to identify easily recognised vegetation types, which could be characterised by their species composition, and structure and general appearence. Some of these had been described previously, such as marshes dominated by ***Marantochloa*** spp. (Marantaceae) (Rogers & Williamson, **1987)** and were easily recognised. With experience more subtle variation in vegetation became apparent, and was often associated with particular physical conditions in the area (e.g., rock outcrops, proximity to the savanna edge), but classification of the forest into vegetation categories in this way was subjective, and often based on intuition.

Two types of multivariate analysis were applied to botanical data in order to substantiate these field classifications: Two-way Indicator Species Analysis (TWINSPAN) (Hill, 1979a) and Canonical Community Ordination (CANOCO) (Ter Braak, 1988 - an extension of DECORANA [Hill, 1979b]). Programmes to process the data were written by C. Legg, who also ran data through TWINSPAN and **CANOCO.** TWINSPAN was run for trees > 10 cm dbh, trees > 70 cm dbh, a combination of these two data sets, and for all three sets of data in combination with herb data (using 100m segments of transects as the sample unit in all cases, although 500m segments were also tried for trees >10 and >70). Stem density was the unit of abundance adopted in all cases, and cut levels for pseudospecies were at zero, two, four, and seven individuals, adding 12 as the last cut when herb data was added. CANOCO was run on data for trees >10cm, >70cm, these two data sets combined, and for herb data in 100m segments. It was then re-run incorporating environmental data: altitude; slope angle; canopy cover at <10m, 10-20m, >20m and overall; proximity to permanent water; proximity to seasonal streams or gulleys which act as water courses during periods of heavy rain; proximity to rocky outcrops; nearest logging road; and distance to continuous savanna vegetation. Finally combinations of trees >10 and >70 and herbs (using log of stem density as unit of abundance) were processed with environment data. The indirect gradient analysis **(DCA)** option was selected, using **2nd** order polynomials for detrending, and down-weighting rarities. Both programmes were run for all species, and for only those species which occurred in at least three 100m samples. TWINSPAN uses reciprocal averaging to divide the data set into two groups, and then continues to further divide the resulting sub-groups until they become too small to divide further, or a pre-determined number of divisions have been made. It forms a divisive hierarchy, giving an output in the form of an ordered two-way phytosociological table of species and transect segments. Being divisive, it is prone to mis-classification of borderline points, since there is no ecological basis for making divisions, nor for determining a sensible point at which to stop. Interpretation of the ecological 'sense' (or otherwise) of the output rests with the field observer. CANOCO, on the other hand, performs an ordination of the data, giving an output in which plots and species are ordered continuously in terms of similarity with respect to one another, which can be displayed graphically. In addition, it can incorporate environmental variables, and display these as gradients of increasing correlation in the graphical output. TWINSPAN groupings can be superimposed upon the CANOCO output, and if the clarity of the groupings is maintained this objectively substantiates the two analyses. The merits and pitfalls of these techniques have been widely discussed (e.g., Gauche, 1982; Hill & Gauche, 1980; Kershaw & Looney, 1985).

Results.

Species compostition.

Trees >10 cm dbh.

A total of 4885 trees and lianes > 10 crn dbh, of 327 species, were encountered on transects. In all, 181 (55%) species were fully identified, a further 54 (17%) could be identified to genus, 44(13%) to family, and 48 (15%) could not be identified. In terms of individuals, 4449 (91%) were fully identified, 277 (6%) could be identified to genus, 82 (2%) to family and 77 (2%) could not be identified. Appendix 2.1 lists all plant species >10cm dbh encountered on transects, and gives the number of each species in each site. Appendix 2.2 lists plants not encountered un transects, which were identified to species level from fertile collections made in the five sites, and in savanna close to Site 1.

There were marked differences in species composition both within and between sites, which could be used to classify several vegetation types. Table 2.1 lists all plant species > 10cm dbh ranked in the "top 10" for basal area and/or number of stems, on at least one transect (it summarises Appendix 2.1 for the

Table 2.1: Species ranked in the 'top 10' for basal area or number of stems on at least one transect.

Species	**Family**	**Site 1**		**Site 2**		**Site 3**		**Site 4**		**Site 5**	
		a	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**
Aucoumea klaineana	BURSERACEAE	**20.4**	**61**	**8.0**	14	**9.9**	**21**	**8.8**	16	**22.0**	**96**
Augouardia letestui	CAESALPINIACEAE			**3.6**	**34**	1.8	20	**4.2**	**40**		
Ceiba pentandra	BOMBACACEAE									**1.5**	2
Centroplacus glaucinas	PANDACEAE			1.1	**55**	0.8	**37**	1.1	**68**	0.1	5
Cola lizae	STERCULIACEAE	**8.9**	**179**			0.4	7			**8.0**	**194**
Conceveiba africana	EUPHORBIACEAE			**2.3**	**103**	**4.5**	**210**				
Coula edulis	OLACACEAE			**6.5**	**23**	**3.5**	**23**	**5.2**	**44**		
Cylicodiscus gabonensis	MIMOSACEAE							**2.3**	2		
Dacryodes buettneri	BURSERACEAE	**3.5**	8	**6.2**	**29**	**3.9**	9	12	**29**	**3.8**	18
Dacryodes klaineana	BURSERACEAE			1.6	**40**	1.9	**38**				
Desbordesia glaucescens	IRVINGIACEAE	1.0	3	**2.0**	**22**	2.3	15	1.1	12	0.6	12
Dialium soyauxii	CAESALPINIACEAE			0.2	7	0.1	4	**2.1**	**29**		
Diospyros dendo	EBENACEAE	0.3	**29**	<0.1	1	0.2	14	0.1	6	0.5	**28**
Diospyros polystemon	EBENACEAE	**3.0**	**38**	0.7	6	0.4	8	0.1	3	**1.7**	**26**
Diospyros zenkeri	EBENACEAE					0.1	5	<0.1	1	0.7	**40**
Eriocoelum macrocarpum	SAPINDACEAE	0.2	3	<0.1	1	0.1	3	0.2	7	0.6	**23**
Ganophyllum giganteum	SAPINDACEAE	**2.3**	3							0.2	1
Garcinia smeathmannii	GUTTIFERAE			<0.1	3	0.5	**26**				
Hylodendron gabunense	CAESALPINIACEAE	**2.4**	6			0.8	4			1.4	9
Hypodaphnis zenkeri	LAURACEAE	0.8	**18**							0.2	10
Lophira alata	OCHNACEAE	**3.3**	**62**							**7.0**	**75**
Maprounea membranacea	EUPHORBIACEAE	0.3	**17**	0.1	3	<0.1	1	0.4	**25**	0.4	8
Pentaclethra eetveldeana	MIMOSACEAE	**3.5**	14	0.3	1	0.7	4	1.7	6	**3.1**	18
Pentaclethra macrophylla	MIMOSACEAE	**3.6**	14	3.4	7	4.7	16	1.8	11	**3.9**	21

Table 2.1: Species ranked in the 'top 10' for basal area or number of stems on at least one transect / continued.

Species	**Family**	**Site 1**		**Site 2**		**Site 3**		**Site 4**		**Site 5**	
		a	**b**	**a**	**b**	**a**	**b**	**a**	**b**	**a**	**b**
Pycnanthus angolensis	MYRISTICACEAE	**1.8**	4	0.9	2	0.2	1	1.3	3	1.0	3
Sacoglottis gabonensis	HUMIRIACEAE			**4.5**	6					0.1	2
Santiria trimera	BURSERACEAE			**7.6**	**143**	**6.5**	**121**	**3.1**	**54**	0.1	1
Scottellia coriacea	FLACOURTIACEAE	0.2	4							**1.6**	**23**
Scyphocephalium ocochoa	MYRISTICACEAE			1.0	3	**3.4**	10	**8.4**	23	0.6	1
Sindoropsis le-testui	CAESALPINIACEAE			**2.9**	3	1.4	3	**4.1**	11		
Staudtia kamerunensis	MYRISTICACEAE			0.6	1	**2.9**	**21**				
Staudtia gabonensis	MYRISTICACEAE			1.3	6	**3.3**	18	0.5	5		
Strombosia ? zenkeri	OLACACEAE			0.1	1	0.6	20	**3.5**	68		
Strombosiopsis tetrandra	OLACACEAE			1.7	**20**	**3.0**	**38**	**3.6**	**49**	0.1	6
Treculia obovoidea	MORACEAE					0.6	**29**	0.2	5		
Trichilia cf. *prieureana*	MELIACEAE	0.4	11	<0.1	1					0.9	**28**
Trichoschypha acuminata	ANACARDIACEAE	0.4	11	0.9	**32**	0.7	13	0.1	3	0.2	12
Xylopia aethiopica	ANNONACEAE	0.3	**21**	0.1	1	0.4	3	0.8	**36**	<0.1	3
Xylopia hypolampra	ANNONACEAE	0.9	**16**	0.3	2	0.3	2	<0.1	1	0.5	6
Xylopia quintasii	ANNONACEAE	0.8	**38**	0.2	6	0.5	19	0.1	5	**2.5**	**95**
Sum of values for 'top 10' spp.		56.1	528	52.3	531	49.4	617	59.6	494	58.1	687
Top 10 as % of total		76	69	63	56	60	53	60	51	71	67

a = total basal area on transect; b = number of individuals on transect. Values emboldened = species in top 10.

more important species, but does not supersede it). Some species were relatively common in all study sites, notably *Aucoumea klaineana, Dacryodes* ***buettneri,*** Pentaclethra macrophylla Other species tended to be restricted to, or more abundant in Sites 2, 3 & **4,** or Sites 1 & 5, notably: ***Augouardia*** letestui, ***Centroplacus glaucinas, Coula edulis*** **Desbordesia glaucescens,** *Santiria trimera Scyphocephalium ochocae, Sindoropsis* le-***testui,*** *Staudtia* gabonensis and *Strombosiopsis tetrandra* in Sites 2, 3 & 4; and Cola *lizae, Hylodendron gabunense Hypodaphnis* ***zenkeri,*** ***Laphira*** alata, *Trichilia* cf. *prieureana* and *Xylopia quintasii* in Sites 1 & 5. However some species characteristic *of* Sites 2, 3 & **4** occurred at low density in Site 5 (e.g., ***Centroplacus glaucinas,*** Santiria *trimera, Scyphocephalium* ochocoa, *Strombosiopsis tetrandra).* Some species were common in only one site (e.g., *Sacoglottis gabonensis* in Site **2),** or were restricted to any two of Sites 2, 3 & 4 (e.g.,, *Concevaiba africana, Dacryodes klaineana, Garcinia smeathmannii Treculia* ***obovoidea).*** The top ten species in Sites 1 & 5 contributed a greater proportion of the total basal area and number of stems than in the other three sites, showing they were less species diverse.

Table 2.2 summarises the vegetation data for species > 10cm dbh and lists all families ranked in the “top 15” in terms of basal area in at least one site. Burseraceae was the dominant family in all five sites, followed **by** the Leguminosae (separated into sub-families: Caesalpiniaceae, Mimosaceae, Papilionaceae). Families in Sites **1** & 5 obtained similar ranks, as was the case for Sites 2, *3* & 4, but there were some marked differences between these two sets of sites: Olacaceae, Myristicaceae and Euphorbiaceae were more important in Sites 2, 3 & **4;** whilst Sterculiaceae, Ochnaceae Sapindaceae and Ebenaceae were more important in Sites 1 & 5. Sites 2-5 had at least 37-39 families, but Site 1 was less diverse, with 31 families present.

Sites 1 & 5 and Sites 2, 3 & 4 respectively could **be** separated into two sub-units in terms of species composition. Burseraceae dominated Sites 1 & 5 in terms of **basal** area, and trees of the Sterculiaceae were most numerous. *Aucoumea klaineana* accounted for the majority of the stems and basal area of Burseraceae, whilst ***Cola lizae*** was the only Sterculiaceae in the >10cm dbh samples. *Aucoumea klaineana,* Col, *lizae* and *Laphira alata* together represented ***44%*** and 45% of basal area and 39% and *36%* of individuals in Sites 1 and 5 respectively. The abundance of *Cola lizae* is particularly worthy of note as it is a species with a limited distribution that was unknown to science until collected at

Table 2.2: Dominant families >10 cm dbh.

Family*	Site 1			Site 2			Site 3			Site 4			Site 5		
	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
BURSERACEAE	3	72	9.58 (1)	6	243	9.88 (1)	7	206	9.36 (1)	5	105	9.85 (1)	4	121	10.53 (1)
CAESALPINIACEAE	7	36	2.45 (4)	12	73	4.63 (2)	17	56	4.07 (4)	19	116	6.03 (2)	6	22	1.13 (8)
OLACACEAE	2	4	0.34(15)	7	53	3.84 (3)	7	102	4.35 (2)	8	185	5.66 (3)	3	11	0.82(10)
MIMOSACEAE	6	32	3.47 (3)	3	9	1.72 (7)	4	24	2.84 (5)	5	22	3.17 (5)	4	41	3.00 (3)
MYRISTICACEAE	1	4	0.74(10)	4	12	1.53 (8)	5	51	4.15 (3)	4	40	4.58 (4)	2	4	0.62(12)
IRVINGIACEAE	5	18	1.45 (5)	5	53	2.09 (4)	6	30	2.10 (7)	5	24	1.03 (7)	5	41	1.58 (6)
STERCULIACEAE	2	180	3.62 (2)	2	13	0.10(23)	3	18	0.21(23)	2	5	0.03(35)	2	195	3.34 (2)
EUPHORBIACEAE	5	25	0.54(11)	6	155	1.85 (5)	12	243	2.73 (6)	13	88	1.29 (6)	9	22	0.80(11)
ANNONACEAE	8	90	0.92 (9)	9	53	0.87 (9)	8	52	0.93 (9)	7	62	0.58(10)	8	148	1.65 (5)
EBENACEAE	5	72	1.38 (6)	4	19	0.39(15)	8	53	0.76(10)	7	22	0.35(17)	8	111	1.31 (7)
OCHNACEAE	1	62	1.31 (7)	0	0	0.00 (-)	1	1	0.00(40)	0	0	0.00 (-)	1	75	2.82 (4)
RUBIACEAE	8	37	0.45(12)	6	20	0.22(17)	8	35	0.44(13)	7	45	0.83 (9)	9	18	0.21(18)
HUMIRIACEAE	0	0	0.00 (-)	1	6	1.80 (6)	0	0	0.00 (-)	0	0	0.00 (-)	1	2	0.03(31)
SAPINDACEAE	6	14	1.17 (8)	2	7	0.07(26)	5	8	0.08(27)	1	7	0.07(30)	3	25	0.37(15)
ANACARDIACEAE	4	15	0.44(13)	2	43	0.47(12)	4	19	0.30(19)	3	9	0.15(24)	4	17	0.31(16)
CHRYSOBALANACEAE	1	2	0.12(21)	1	1	0.07(25)	3	9	0.93 (8)	4	10	0.52(13)	0	0	0.00 (-)
SAPOTACEAE	0	0	0.00 (-)	2	3	0.20(19)	5	6	0.47(12)	5	8	0.86 (8)	0	0	0.00 (-)
GUTTIFERAE	1	1	0.15(17)	6	13	0.21(18)	5	40	0.43(14)	3	18	0.53(12)	1	2	0.19(20)
FLACOURTIACEAE	2	13	0.15(18)	1	1	0.02(30)	3	3	0.08(29)	2	6	0.05(31)	6	33	1.10 (9)
PANDACEAE	0	0	0.00 (-)	1	55	0.42(13)	1	37	0.33(18)	1	68	0.46(16)	2	6	0.09(27)
LAURACEAE	2	20	0.37(14)	4	7	0.19(20)	3	9	0.22(22)	3	13	0.30(18)	3	13	0.11(25)
SCYTOPETALACEAE	0	0	0.00 (-)	3	20	0.67(10)	3	18	0.38(16)	1	6	0.08(29)	1	6	0.14(23)
MELIACEAE	1	16	0.16(16)	4	8	0.09(24)	3	7	0.19(25)	1	15	0.18(21)	3	35	0.50(14)
VOCHYSIACEAE	0	0	0.00 (-)	1	2	0.24(16)	1	9	0.66(11)	1	1	0.16(23)	0	0	0.00 (-)
PAPILIONACEAE	1	2	0.10(23)	1	1	0.01(36)	3	10	0.40(15)	2	13	0.18(22)	5	8	0.19(19)
IXONANTHACEAE	0	0	0.00 (-)	1	11	0.60(11)	1	7	0.20(24)	0	0	0.00 (-)	0	0	0.00 (-)

Table 2.2: Dominant families >10 cm dbh / continued.

Family*	**Site 1**			**Site 2**			**Site 3**			**Site 4**			**Site 5**		
	a	**b**	**c**	**a**	**b**	**c**	**a**	**b**	**c**	**a**	**b**	**c**	**a**	**b**	**c**
LUXEMBURGIACEAE	1	1	0.10(22)	0	0	0.00 (-)	0	0	0.00 (-)	1	4	0.55(11)	1	1	0.11(24)
BOMBACACEAE	0	0	0.00 (-)	0	0	0.00 (-)	0	0	0.00 (-)	0	0	0.00 (-)	1	2	0.62(13)
ULMACEAE	0	0	0.00 (-)	0	0	0.00 (-)	1	1	0.04(31)	2	6	0.49(14)	0	0	0.00 (-)
LECYTHIDIACEAE	0	0	0.00 (-)	0	0	0.00 (-)	0	0	0.00 (-)	2	7	0.47(15)	0	0	0.00 (-)
DIPTEROCARPACEAE	0	0	0.00 (-)	1	3	0.40(14)	0	0	0.00 (-)	0	0	0.00 (-)	0	0	0.00 (-)
Undetermined	3	3	0.18	13	19	0.17	18	28	0.8	10	22	0.22	6	6	1.02
Total for top 15 families	65	681	28.24	65	808	31.14	99	926	34.61	89	740	36.43	65	886	30.18
Overall total	84	760	29.59	126	956	33.21	163	1169	38.59	138	974	39.97	108	1026	32.67
Top 15 - % of total	77	90	95	52	85	94	61	79	90	64	76	91	60	86	92
No. families identified		31			39			38			39			37	
Shannon Weaver Index		3.35			3.81			3.97			4.14			3.48	
Simpson's Index		0.08			0.05			0.05			0.03			0.07	
Evenness		0.75			0.78			0.78			0.83			0.75	
Modified Hills Ratio		0.42			0.46			0.35			0.59			0.48	
No. indivs. / No. spp.		8.4			7.5			7.1			6.9			9.6	

a = number of species in 2.5 ha sample; b = number of individuals in 2.5 ha sample; c = average basal area (m^2 ha^{-1}) - with rank

* = ranked in terms of overall average basal area.

SEGC in 1984 (Halle, 1987).

in Sites 2, 3 & 4 species distribution was less skewed towards a few dominant species, as illustrated in Table 2.1, and by the measures of evenness presented in Table 2.2. ***Aucoumea klaineana*** was still most common in terms of basal area but other species attained comparable values (e.g., ***Dacryodes buettneri***, ***Santiria trimera***, *Scyphocephalium ochocoa*). *Santiria trimera* was common in all three of these sites, but parts of Site 2, and particularly Site 3, were characterised by the abundance of ***Conceveiba africana.***

The number of individuals varied between sites, from a minimum of 760 in Site 1 up to 1169 in Site 3. Total basal area varied between sites, between extremes of 29.59 $m^2 ha^{-1}$ in Site 1 and 39.97 $m^2 ha^{-1}$ in Site 4. The total number of species in each site varied from 84 in Site 1 to a maximum of 164 in Site 3. This is illustrated graphically in Figure 2.4, which shows a species-area plot for all species > 10cm dbh in each of the five sites. All five curves are still increasing at 2.5 ha, although this is most marked for Sites 2, 3 & 4. This figure suggests that plant diversity was highest in Site 3 and that Sites 4, 2, 5 and 1 were successive1y less diverse.

Variation in the number of individuals / unit area (site) can mask differences in species diversity (Reitsma, 1988). The ratio of individuals to species given in Table 2.2 demonstrates this, showing Site 5 *to* have been the least diverse in terms of the number of species represented in a given number of individuals, whilst Site **4** was the most diverse. The percentage of species, individuals and basal area accounted for by the top 15 families is a similar index of diversity, and suggests that Site 1 was the least diverse la greater proportion of the total are within the top 15 families) , but is less clear for the other sites. Two widely used indices of diversity are presented in Table 2.2: the Shannon Weaver index (Shannon & Weaver, 1949) and Simpson's index (Simpson, 1949). Both indices rank the sites in a similar order, with Site **4** being most diverse and Cites 5 and 1 ranked fourth and fifth respectively, but Sites 2 and **3** receive different ranks, with Site 3 ranked second by Shannon Weaver, und third by Simpson's index (and vice versa for Site 2). Two measures of species evenness are presented in Table 2: **J'** of Pielou (1975, 1977) and the Modified Hill's Ratio (Alatalo, 1981; cf. Hill, 1973). Both suggest that evenness is greatest in Site 4, but give conflicting information about the other sites.

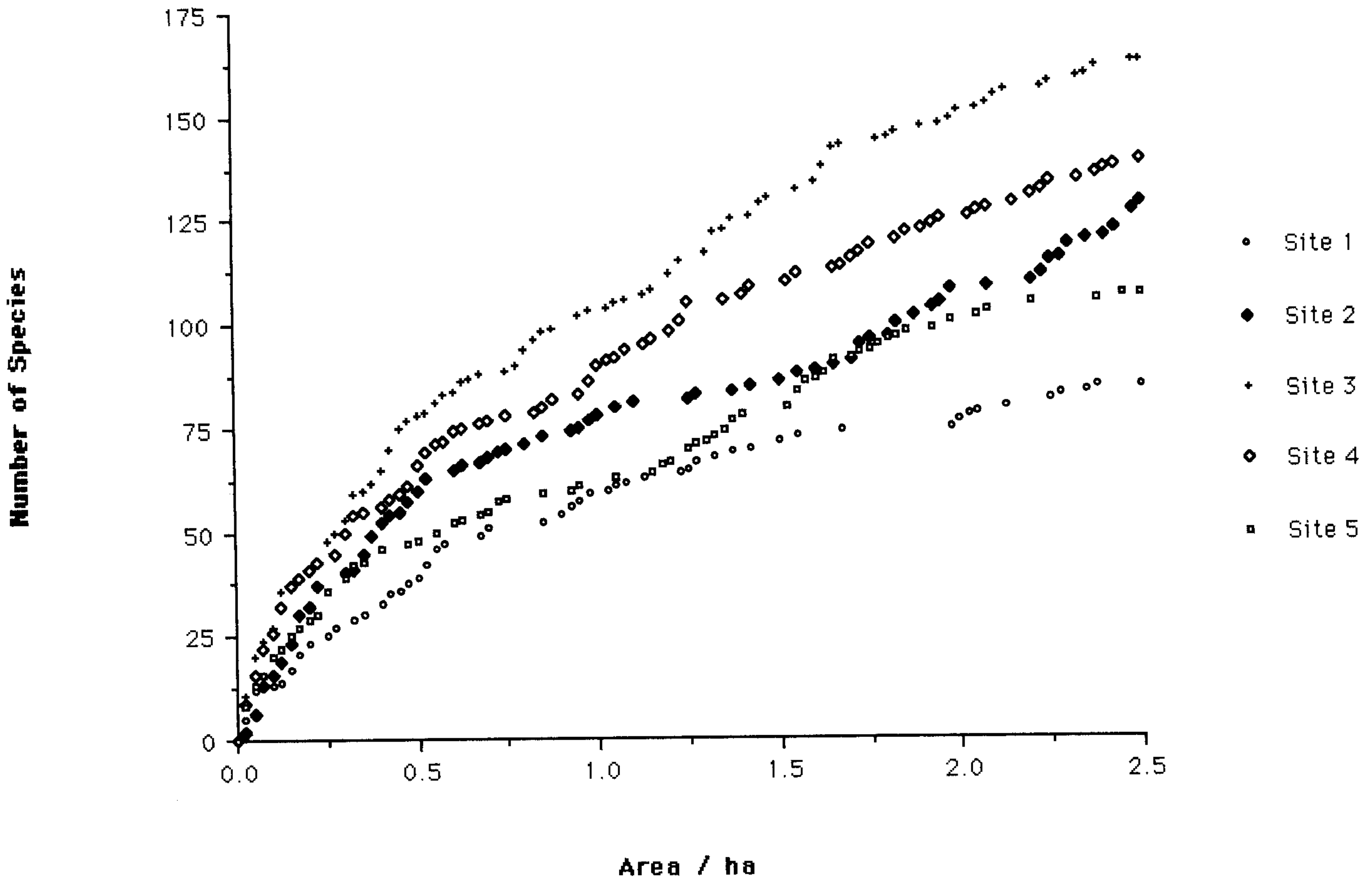


Figure 2.4: Species-area plots for species >10 cm dbh.

In all, 327 plant species > 10cm dbh occurred on the five transects, of which 176 were present in one site only, and 76, 36, 12 and 27 occurred in two, three, four and five sites respectively. Table 2.3 lists the percentage overlap of species between each of the **sites.** This shows that Sites 1 and 5 had many species in common, as did Sites **2, 3** and **4.** Table **2.4** gives the Czekanowski coefficient of similarity (Bray & Curtis, 1457) for the five sites, which takes into account both the number of species in common, and their abundance in each paired comparison. From this table the sites can be ranked in terms of their overlap, with Sites 1 and 5 being most similar, and Sites 1 and 2 most divergent.

Table 2.3: % species overlap between sites for species >10 cm dbh.

	Site 1	**Site 2**	**Site 3**	**Site 4**	**Site 5**
Site 1	- - -	41	48	47	68
Site 2	27	- - -	59	45	32
Site 3	25	46	- - -	43	28
Site 4	29	41	50	- - -	32
Site 5	54	38	43	42	- - -

Table 2.4: Czekanowski coefficient for trees > 10cm dbh.

	Site 1	**Site 2**	**Site 3**	**Site 4**	**Site 5**
Site 1	-	0.16	0.20	0.23	0.69
Site 2			0.63	0.36	0.18
Site 3				0.44	0.23
Site 4					0.19

Trees > 70cm dbh

A total of 1832 trees > 70 cm dbh, of 137 species, were encountered on transects. In all, 109 species **(30%)** were fully identified, a further five **(4%)** to genus, 14 (10%) to family, and nine (7%) could not be identified [Appendix 2.1). Of the individuals, 1797 (98%) were fully identified, a further eight (0.4%) to genus, 16 **(1%)** to family, and **11** *(0.6%)* could not be identified.

Large trees were less useful for quantifying vegetation categories, but some species did show differences within and between sites, as was observed for trees >10cm dbh. Table *2.5* lists all trees > 70cm dbh ranked in the top 10 for basal area on at least one transect. The number of trees differed little in proportion from basal area and so is not shown. *As* for smaller trees, some species were common in all sites, notably *Aucoumea klaineana Dacryodes* ***buettneri*** *Irvingia gabonensis Pentaclethra macrophylla, Pycnanthus angolensis* Other species were characteristic of Sites 2, 3 & **4,** notably ***Coula*** edulis, *Paraberlinia bifoliolata, Sindoropsis le-testui,* or were more common in these three sites (e.g., ***Desbordesia glaucescens,*** *Klainedoxa trilasii),* whilst some species were characteristic **of,** or more common in Sites 1 & 5, notably **Ceiba pentandra,** *Ganophyllum giganteum,* ***Lophira alata,*** and ***Pterocarpus*** *soyauxii* to some extent. The proportion of the basal area accounted for by the top 10 species was greatest in Site *5,* and least in Site 3.

Table 2.6 summarises the vegetation data for trees > 70cm dbh and lists all families ranked in the top 10 in terms of basal area in at least one site. Burseraceae was the dominant family in each site, followed by the Leguminosae. Family ranks were more consistent than for small species, but again some families were more common in Sites 2, 3 & 4 (e.g., Caesalpiniaceae, Myristicaceae) or in Sites 1 & 5 (e.g., Ochnaceae, Sapindaceae), or occurred in only one or two sites (e.g., Humiriaceae, Chrysobalanaceae). The number of families present per site varied between 19 (Site *5)* and 24 (Site **3).**

In Sites 1 & *5* ***Aucoumea klaineana*** was the dominant large tree, representing 40% and 48% of basal area in the two sites respectively. *Lophra alata, Pterocarpus soyauxii* and Dacryodes *buettneri* were also common. In Sites 2, 3 & **4** ***Aucoumea klaineana*** was the commonest large tree, but represented only ***20%,*** 27% and 21% of the respective basal areas. **Dacryodes buettneri** and *Scyphocephalium ochocoa* were common in all three sites, Sindoropsis *le-testui* was common in Sites 2 & 4, and Sacoglottis gabonensis and ***Paraberlinia bifoliolata*** were common in Site *2.* Species overlap between sites was more uniform for large trees than for plants >10cm dbh, but similar trends emerge.

Table 2.5: Species >70 cm dbh in 'top 10' for basal area on at least one transect.

Species	**Family**	**Basal Area**[1]				
		Site 1	Site 2	Site 3	Site 4	Site 5
Aucoumea klaineana	BURSERACEAE	**86.3**	**65.8**	**81.1**	**51.2**	**103.4**
Ceiba pentandra	BOMBACACEAE	0.6				**4.3**
Coula edulis	OLACACEAE		**14.3**	3.4	**8.3**	
Dacryodes buettneri	BURSERACEAE	**11.3**	**35.5**	**32.2**	**49.6**	**14.2**
Desbordesia glaucescens	IRVINGIACEAE	1.4	**8.4**	**9.3**	**7.4**	1.8
Ganophyllum giganteum	SAPINDACEAE	**4.3**				3.6
Hylodendron gabunense	CAESALPINIACEAE	**6.2**		1.1		1.3
Irvingia gabonensis	IRVINGIACEAE	3.4	3.8	3.0	0.6	**4.1**
Klainedoxa gabonensis	IRVINGIACEAE	**5.8**	2.7	**10.9**		**5.7**
Klainedoxa trilesii	IRVINGIACEAE	0.5	**7.3**	**8.0**	4.0	1.1
Lophira alata	OCHNACEAE	**14.0**	0.9		1.7	**14.2**
Maranthes glabra	CHRYSOBALANACEAE			5.4	**9.4**	
Paraberlinia bifoliolata	CAESALPINIACEAE		**28.8**	**7.7**	**4.1**	
Pentaclethra macrophylla	MIMOSACEAE	**5.0**	**12.0**	**11.0**	**5.8**	**5.3**
Piptadeniastrum africanum	MIMOSACEAE	**6.7**	2.1	1.4	3.5	**3.7**
Pterocarpus soyauxii	PAPILIONACEAE	**22.3**	7.0	5.6	**4.1**	**11.0**
Pycnanthus angolensis	MYRISTICACEAE	**7.2**	6.3	**10.6**	3.6	**8.3**
Sacoglottis gabonensis	HUMIRIACEAE		**39.2**			
Scyphocephalium ochocoa	MYRISTICACEAE		**20.5**	**18.8**	**29.7**	1.7
Sindoropsis le-testui	CAESALPINIACEAE		**17.7**	**6.6**	**16.1**	
Total basal area for 'top 10' species		169.1	249.5	196.2	185.7	174.2
Top 10 as a % of total		79	77	65	75	81

[1] - m^2 in 25 ha sample. Emboldened species in top 10.

Table 2.6: Dominant families >70 cm dbh.

Family*	Site 1			Site 2			Site 3			Site 4			Site 5		
	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
BURSERACEAE	3	137	3.96 (1)	4	142	4.15 (1)	5	148	4.71 (1)	3	151	4.16 (1)	3	189	4.76 (1)
CAESALPINIACEAE	7	27	0.66 (3)	9	66	2.09 (2)	14	46	1.32 (4)	16	45	1.30 (3)	8	13	0.42 (6)
MYRISTICACEAE	1	8	0.29 (7)	4	45	1.14 (4)	5	57	1.43 (2)	2	50	1.33 (2)	2	17	0.40 (7)
IRVINGIACEAE	5	18	0.54 (6)	6	36	0.99 (5)	6	45	1.33 (3)	4	16	0.51 (5)	5	22	0.54 (4)
MIMOSACEAE	6	23	0.62 (4)	6	27	0.73 (6)	6	29	0.93 (5)	8	25	0.66 (4)	6	24	0.57 (2)
PAPILIONACEAE	1	21	0.89 (2)	1	9	0.28(10)	1	6	0.22 (9)	2	6	0.19 (8)	1	13	0.44 (5)
OCHNACEAE	1	21	0.56 (5)	0	0	0.00 (-)	1	1	0.04(16)	4	21	0.47 (7)	1	24	0.57 (3)
HUMIRIACEAE	0	0	0.00 (-)	1	32	1.57 (3)	0	0	0.00 (-)	0	0	0.00 (-)	0	0	0.00 (-)
OLACACEAE	2	6	0.20 (8)	3	26	0.65 (7)	3	18	0.44 (6)	0	0	0.00 (-)	1	3	0.07(14)
SAPOTACEAE	2	2	0.10(12)	3	5	0.33 (8)	6	12	0.38 (7)	3	4	0.11(11)	2	2	0.09(12)
CHRYSOBALANACEAE	1	1	0.02(22)	0	0	0.00 (-)	3	13	0.31 (8)	3	20	0.48 (6)	0	0	0.00 (-)
ANNONACEAE	0	0	0.00 (-)	2	11	0.29 (9)	1	1	0.04(15)	0	0	0.00 (-)	1	1	0.02(18)
SAPINDACEAE	1	6	0.18 (9)	0	0	0.00 (-)	0	0	0.00 (-)	0	0	0.00 (-)	1	4	0.14(10)
MORACEAE	2	2	0.04(15)	0	0	0.00 (-)	0	0	0.00 (-)	1	1	0.02(20)	2	3	0.18 (8)
RUBIACEAE	2	2	0.06(14)	1	1	0.02(22)	0	0	0.00 (-)	3	6	0.15 (9)	0	0	0.00 (-)
ULMACEAE	1	4	0.07(13)	1	2	0.05(16)	1	1	0.02(22)	1	7	0.13(10)	0	0	0.00 (-)
VOCHYSIACEAE	0	0	0.00 (-)	1	2	0.06(12)	1	7	0.17(10)	1	2	0.04(16)	0	0	0.00 (-)
BOMBACACEAE	1	1	0.02(19)	0	0	0.00 (-)	1	1	0.02(24)	0	0	0.00 (-)	1	2	0.17 (9)
EUPHORBIACEAE	4	6	0.15(10)	1	2	0.06(14)	2	6	0.16(11)	1	1	0.02(20)	2	4	0.10(11)
Undetermined	2	3	0.05	1	1	0.02	3	3	0.08	1	1	0.03	2	2	0.04

Table 2.6: Dominant families >70 cm dbh / continued.

	Site 1			**Site 2**			**Site 3**			**Site 4**			**Site 5**		
	a	**b**	**c**	**a**	**b**	**c**	**a**	**b**	**c**	**a**	**b**	**c**	**a**	**b**	**c**
Total for top 10 families	31	273	8.05	39	399	12.22	50	381	11.24	46	347	9.38	30	311	8.19
Overall total	47	297	8.61	55	427	12.9	70	408	12	62	370	9.97	42	330	8.65
Top 10 - % of total	66	92	93	71	93	95	71	93	94	74	94	94	71	94	95
No. families identified		20			25			24			23			18	
Shannon Weaver Index		2.64			3			3.27			2.99			2.26	
Simpson's Index		0.18			0.08			0.08			0.1			0.27	
Evenness Index		0.69			0.75			0.77			0.72			0.61	
Modified Hills Ratio		0.35			0.58			0.45			0.48			0.32	
No. indivs. / No. spp.		6.3			7.8			5.8			6			7.9	

a = number of species in 25 ha sample; b = number of individuals in 25 ha sample; c = average basal area (m^2 ha^{-1}) - with rank

* = ranked in terms of overall average basal area

As for transects of smaller trees, the number of individuals, species and total basal area, for trees >70cm dbh, differed in the five sites, indicating that there were differences in vegetation structure as well as composition. Sites 1 and 2 had least and most individuals, with 297 and 427 respectively, and were also ranked last and first respectively in terms of total basal area. Site 3 had most species, and Site 5 had fewest, with 70 and 42 respectively. Figure 2.5, showing species - area plots for the five sites, illustrates the differences in species number between sites. Curves for Sites 2, 3 and 4 continue to increase, whilst those for Sites 1 and 5 seem to be levelling out. Diversity of large tree species was highest in Site 3, with Sites 4, 2 and then 1 and 5 together, successively less diverse.

The ratio of individuals to species was lowest (most diverse) for Site 3, and highest for Cite 5. The percentage of species, individuals and basal area accounted for by the top 10 species are relatively uniform in the five sites. Shannon Weaver and Simpson's indices ranked the sites in the same order for diversity: Site 3 most diverse, with Sites 2, 4, 1 and 5 following in order of decreasing diversity. The two evenness indices ranked Sites 1 and 5 as fourth and fifth (least even) respectively, but gave conflicting ranks for the other three sites. Measures such as these, which try to take both the number and abundance of species into account, are prone to such inconsistencies (Greig-Smith, 1983).

Of the 137 tree species > 70cm dbh encountered, 71 were present in one site only, and 29, 13, 9 and 15 were present in two, three, four and five sites respectively. Table 2.7 lists the percentage overlap of species between each of the sites, showing a similar pattern to that observed for small transects, with Sites 1 and 5, and Sites 2, 3 and 4 having most species in common. Table 2.8 gives the Czekanowski coefficient of similarity for the five sites. Overlap rankings were similar tu those far smaller transects, with Sites 1 & 5 again most similar although Sites 1 and 4 were most dissimilar.

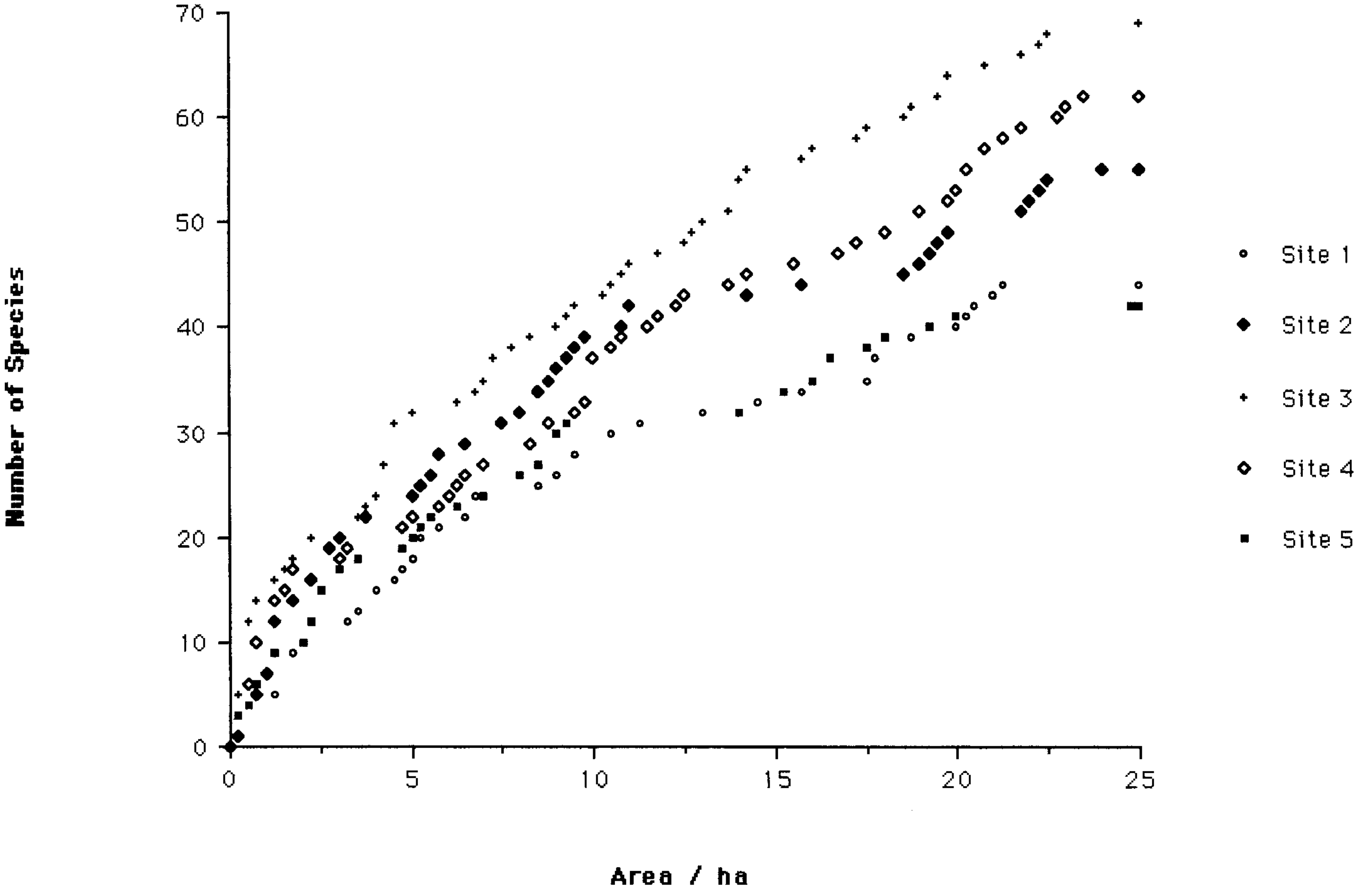


Figure 2.5: Species-area plot for trees >70 cm dbh.

Table 2.7: % species overlap between sites for species >70 cm dbh.

	Site 1	Site 2	Site 3	Site 4	Site 5
Site 1	---	43	49	51	60
Site 2	36	---	65	51	43
Site 3	32	51	---	51	36
Site 4	39	45	58	---	39
Site 5	67	52	60	57	---

Table 2.8: Czekanowski coefficient for trees > 70cm dbh.

	Site 1	Site 2	Site 3	Site 4	Site 5
Site 1	-	0.60	0.47	0.44	0.75
Site 2			0.69	0.67	0.46
Site 3				0.66	0.51
Site 4					0.45

Forest Structure

Differences in the number of individuals per unit area in the five sites have already been illustrated, and these indicated that there were distinct differences in forest structure between the sites, singling out Site 1 as being particulary different from the others. Table 2.9 gives the percentage canopy cover recorded along the five transects. Cite 1 differed markedly from the other sites, with low canopy cover at <10m and 10-20m, high cover >20m and a low overall value. Values for the other four sites were similar, except those for Site 2 at 10-20m and >20m, which were slightly below the other three sites.

Table 2.9: % canopy cover at different heights

Study Site	**Canopy Cover (%)** < 10 m	 10 - 20 m	 > 20 m	 Overall
1	29.3	48.7	68.2	84.0
2	64.3	69.3	56.9	93.3
3	63.6	77.6	.65.5	95.0
4	61.4	71.8	63.5	93.7
5	61.7	73.8	63.4	94.3

Figure 2.6 shows the proportion of trees >10cm dbh in each site in diameter categories increasing in steps of 10cm The distribution of trees between diameter classes was strongly skewed towards small trees, with trees <20cm dbh making up **47-53g** of the samples, but there were no obvious differences between the sites, except a slightly lower proportion of individuals in to 10-20cm glass in Site 4.

Figure 2.7 shows the distribution of tree heights for the five sites, which was negatively skewed. Average heights were 17m, 15m, 13m, 15m and 15m for Sites 1-5 respectively, ranging from 3-57m. There were no obvious differences between sites. Figure 2.8 shows the distribution of heights of trees >*70*cm dbh. Average heights of large trees were 34m, 36m, 34m, 33m and 36m for Sites 1-5 respectively. Trees 30-45m represented 57-81% of this sample and constituted the upper canopy (cf., Richards, 1952),and scattered emergent individuals 45-60m in height rose above this. Site 1 had a greater proportion of trees in the **30-**39m classes, with few emergent individuals above 44m compared to the other sites

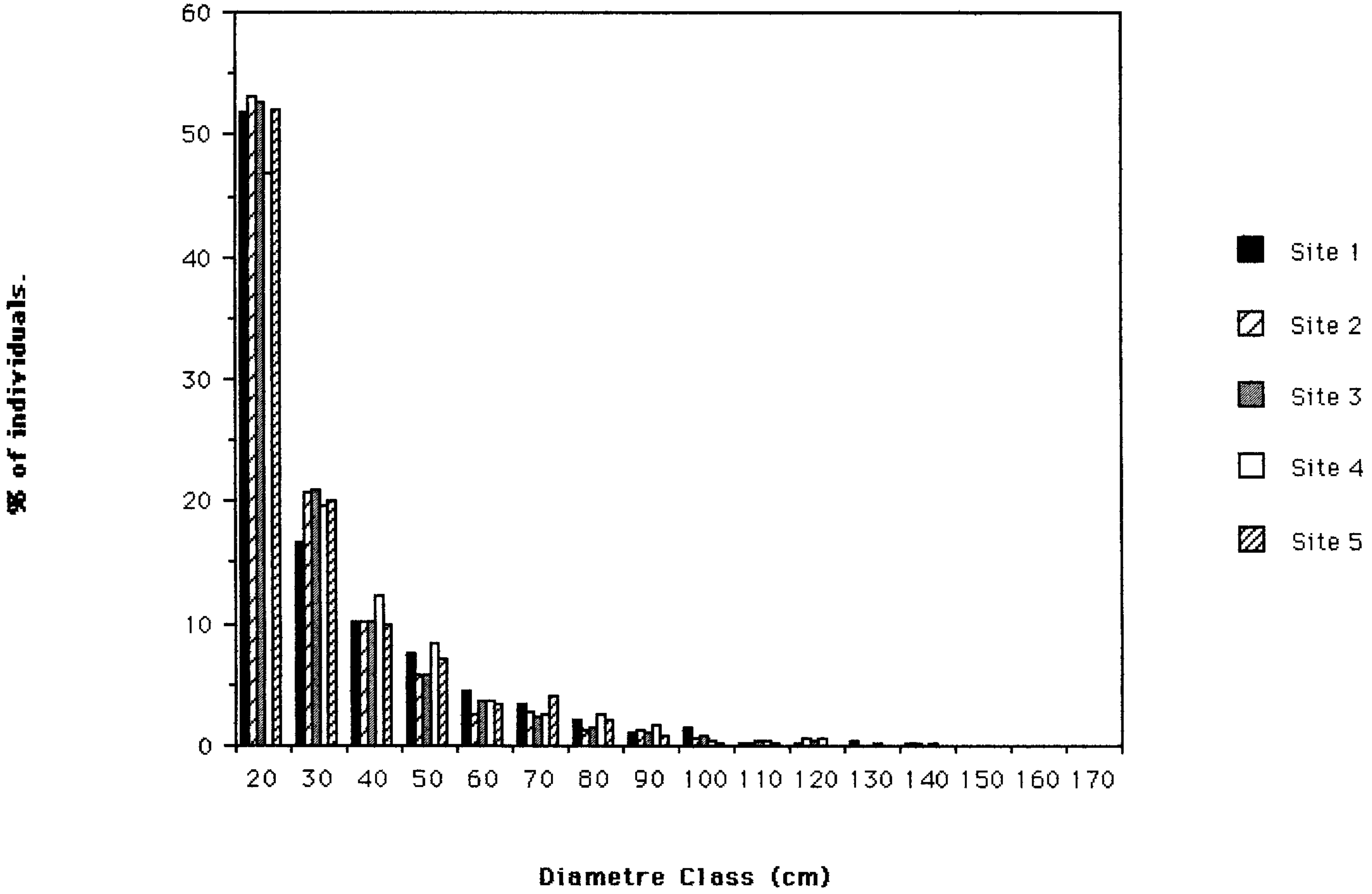


Figure 2.6: Diameter classes for plants >10 cm dbh.

Figure 2.7: Estimated heights for plants >10 cm dbh (excluding lianes).

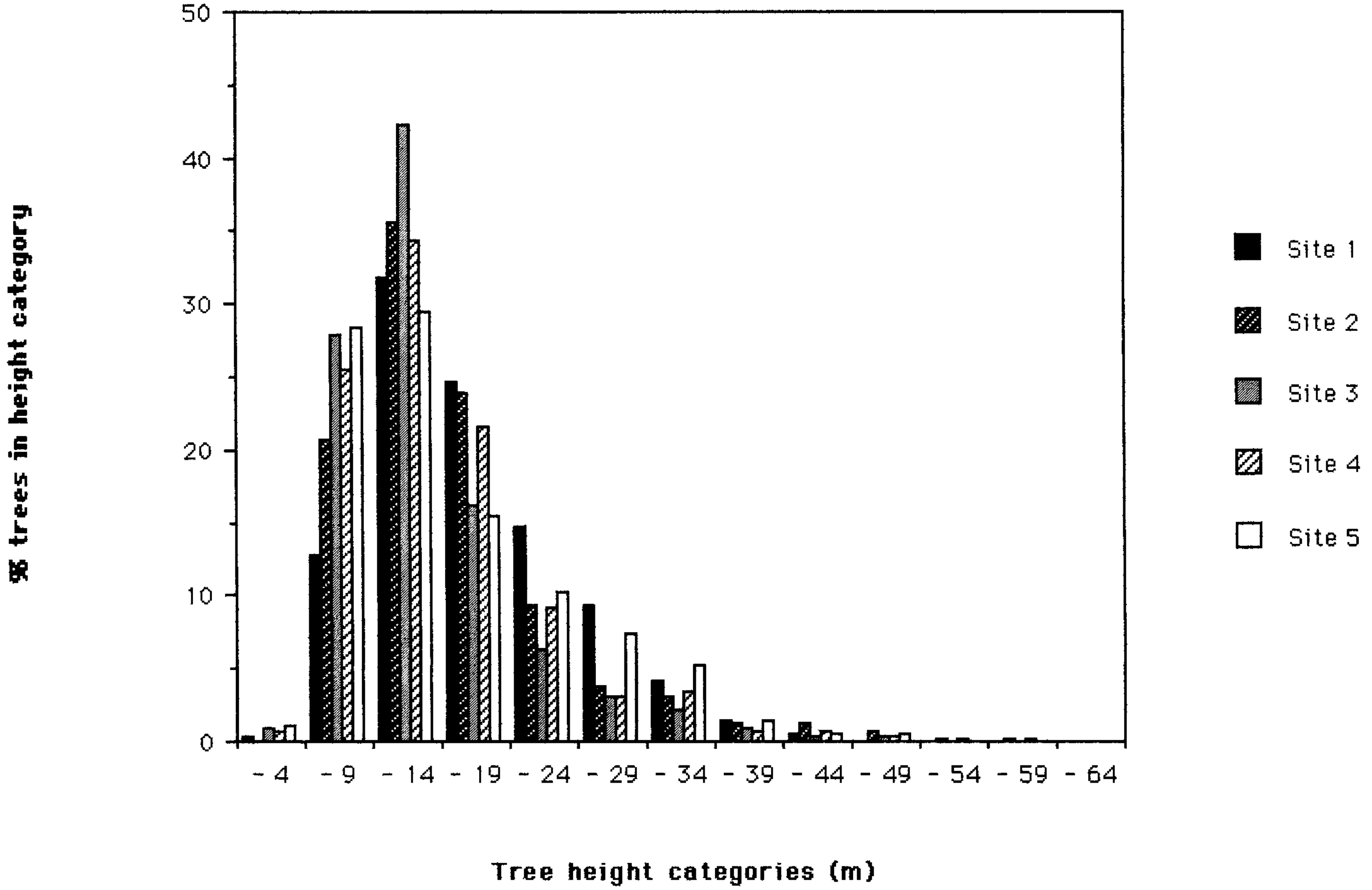


Figure 2.8: Estimated heights for trees >70 cm dbh.

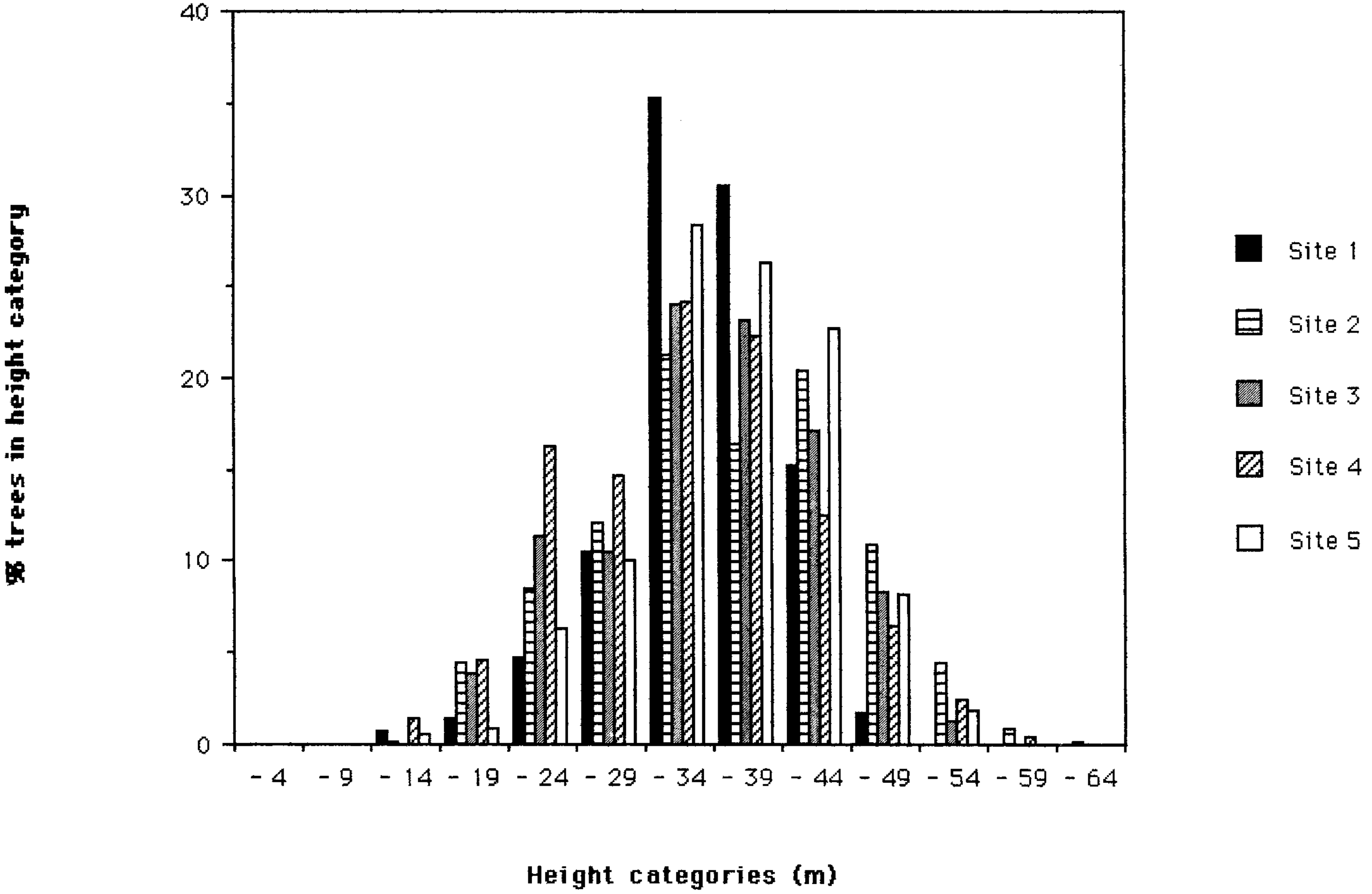


Table 2.10 gives densities for herbaceous species enumerated along the five transects. ***Halopegia azurea*** and *Marantochloa* spp. (not ***M filipes)*** were found in marshes and along water courses, whilst the remaining species occurred on dry land. Marshes contained either *Marantochloa* **spp.** or *Halopegia* ***azurea,*** but not both. *Haumania* ***liebrechtsiana*** and *Megaphrynium* spp. were numerically the most common species, and were more abundant in Sites 1 and 5 than the other sites. Most taxa proved to be more abundant in Sites 1 and/or 5, with the exception of *Halopegia azurea,* which was present in large numbers in marshy areas in Site 4, and *Marantochfilipes* and ***Costus*** spp. which were not common in any of the sites. The common *Aframomum* **sp.** in Cites 1 & 5 is probably an undescribed species (J. M. Lock, personal communication), and did not occur in Sites 2, 3 or 4.

In parts of Sites 1 & 5 herbaceous vegetation formed dense thickets which carpeted the ground and rose to 5m or more in tangled climbing towers. In these areas tree density and canopy cover were low, and the forest had a characteristic open appearance (Plate 2.3). In Sites 2, 3 & **4** ground vegetation was sparse, and is described by Reitsma (1988)

Table 2.10: Stem densities for Marantaceae and Zingiberaceae.

Family / Species	**Stem density (stems / hectare)**				
	Site 1	Site 2	Site 3	Site 4	Site 5
MARANTACEAE					
Ataenidia spp.	20	0	4	38	758
Halopegia azurea	174	24	32	974	0
Haumania liebrechtsiana	3606	1480	1050	724	2492
Hypselodelphys spp.	740	68	44	56	94.
Marantochloa filipes	116	76	62	120	150
Marantochloa spp.	932	0	0	0	122
Megaphrynium spp.	4186	380	136	0	1892
ZINGIBERACEAE					
Aframomum spp.	854	346	24	78	56
Costus spp.	28	52	2	0	0
Renealmia spp.	82	20	24	72	326

Effects of disturbance

Sites 1,2 and 4 had been logged at different times before the study commenced, whilst Site 3 was logged after vegetation enumeration had been completed. Logging in Site 3 reduced overall canopy cover to 89.9% (a reduction of 5.1%), and the reductions in cover at <10m, 10-20m and >20m were 5.0%, 6.2% and 6.7% respectively. Site 2, and Site 4 to some extent, had slightly lower canopy cover at 10-20m and >20m, compared to Site 3 (before logging), which may reflect previous logging damage. The number of major roads, detectable skidder trails and cut stumps suggested that logging intensity was similar in the three sites exploited previously, and in Site 3 after it had been logged. Chapter 4 describes changes caused by logging in Site 3 in detail.

Several species of tree were characteristic of areas that had been damaged by logging: *Xylopia aethiopica*, *Maprounea membrenacea* and *Discoglypremna caloneura* occurred at increased densities in Sites 1 and 4 close to logging damage, *Nauclea didderichi* was common along old logging roads in Site 4, and *Macaranga* spp. occurred in Sites 2 and 4, *Macaranga monandra* forming almost pure stands in places along logging roads in Site 2. Other species observed in areas damaged by logging, but not recorded in increased numbers on transects, included *Anthocleista* spp., *Pauridiantha* spp., *Psorospermum* spp. and *Porterandia cladantha*.

Vegetation and topsoil were cleared in a strip 10-20m wide on either side of major logging roads. Once these roads were abandoned the strip was colonised by a mixture of species including the trees mentioned above, as well as many herbs and lianes (e.g., *Haumania liebrechtsiana*, *Aframomum* spp., *Renealmia* spp., *Costus* spp., *Hypoestes verticillaris*, *Cissus* spp., *Combretum* spp., *Hippocratea* spp.), in addition to some grasses and ferns, more characteristic of savanna vegetation.

Vegetation categories.

During the course of the study it became apparent that there were distinct differences in forest structure and composition both between and within sites, as illustrated by the results noted above. With experience it became possible to subjectively assign plots to vegetation categories, on the basis of structure and composition. Initially classification was rudimentary, distinguishing between Sites 1 & 5, and Sites 2, 3 & 4, principally on the basis of the density of Marantaceae, the most obvious difference to an inexperienced observer. With practice a more detailed picture was obtained by incorporating species composition into the judgment.

Once enumerations on the transects had been completed the data was inspected by dividing it into 50m plots, with a view to fine tuning vegetation categories identified in the field. For each 50m plot, location, topography and species composition were evaluated, and plots considered similar were lumped together. Species generally found in association were identified, and plots were assigned to one or more of a set of 20 vegetation categories. Come of these vegetation categories were determined by physical factors (e.g., proximity to permanent water) which were easily identified, but often only affected a section of any 50m plot. Other vegetation categories occurred in areas that did not seem to differ physically, and for these it was sometimes difficult to distinguish exactly which category a given plot belonged to. Come categories were related, and probably represented different stages of a succession (see below). The categories were as follows:

1) Savanna, dominated by grasses, with shrubs patchily distributed in some areas (as described above). This vegetation type occurs in the north and east of the reserve. Much is presently maintained by regular burning of the savanna, but isolated patches occur where colonisation by forest species seems to be underway. Large continuous areas of savanna are restricted to low altitude areas, whilst small isolated patches occur either around these zones, or on hill tops with altitude of about 250-450m.

1a) Fern savannas, dominated by *Gleichenia linearis,* which generally occur on steep hillsides. ***Gleichenia linearis*** colonises bare earth besides roads and landslides elsewhere in Gabon. In Lope it colonises roadsides, and landslides may also be a factor in Lope, as most existing fern savannas were on steep slopes.

2) Forest which occurs adjacent to savannas, dominated by Aucoumea ***klaineana*** and Lophira ***alata,*** both of which are able to establish in savanna

conditions. Colonising individuals are generally small (compared to those of the same species in the forest), twisted and often branch low. Ground vegetation is dominated by grasses.

3) Forest dominated by *Aucoumea klaineana* and *Lophira alata*, but with other characteristic species (e.g., *Klainedoxa gabonensis*). Many individuals are crooked or branch low and most are smaller than is usual for their species. Ground vegetation is sparse, but some herbs may become established, notably *Aframomum longipetiolatum* and *Megaphrynium* spp.

4) Marantaceae forest, which is more diverse and structurally complex. *Lophira alata* becomes less common, and *Aucoumea klaineana* and *Cola lizae* dominate. Trees are better formed, canopy cover is increased and ground vegetation is more diverse, and is characterised by *Haumania liebrechtsiana*, *Aframomum* sp. ?nov and *Megaphrynium* spp. (Plate 2.3)

5) Marantaceae forest, again dominated by *Aucoumea klaineana* and *Cola lizae*, but a greater number of other species are present, adding to the structural complexity and species diversity of the forest. Herbaceous vegetation is abundant, especially *Haumania liebrechtsiana*, *Aframomum* sp. ?nov, *Hypselodelphys* spp. and *Megaphrynium* spp.. *Haumania liebrechtsiana* in particular is abundant, covering the ground to a height of up to about two metres, and forming dense tangles and vine towers on some trees, which reach a height of 5m or more.

6) Mixed forest, more diverse, with decreased relative importance of *Aucoumea klaineana* and *Cola lizae*, and characteristic species including *Santiria trimera* and *Scytopetalum* sp.. Stocking density of trees is higher than for (5), and canopy cover is increased resulting in decreased densities of Marantaceae and Zingiberaceae.

7) Bare rocks which occur both out in the savanna and within the forest.

8) Forest dominated by small trees, rarely exceeding 40cm dbh, including *Diospyros* spp., *Dichapetalum* sp., *Lecaniodiscus cupanioides* and, in some areas,

Cassipourea congoensis. This vegetation is associated with rock outcrops, and probably represents a colonisation process which proceeds as organic matter accumulates, especially in crevices (Plate 2.41.

9) Forest characterised by *Hylodendron gabunense* and *Scottellia coriacea* in addition to those seen in (8) which occurs on deeper soil from which some large rocks emerge.

10) More diverse forest with *Hylodendron gabunense, Heisteria parvifolia, Trichilia* cf, *prieureana* and ***ganophyllum giganteum***, again close to rocky outcrops or perhaps on thin soil.

11) Swampy areas introducing added variation to vegetation samples by supporting hydrophilic species (e.g., *Mitragyna ciliata)* as well as characteristic Marantaceae (e.g., ***Marantochloa*** spp., ***Halopegia*** *azurea* 1.

12) Seasonal water courses and dry gulleys, which channel rainfall down slopes increasing water availability, have characteristic species (e.g., *Antidesma laciniatum*, Hexalobus *crispiflorus* *Thomandersia hensii* 1.

13) Riverine vegetation, which occurs where streams and rivers provide a habitat with increased water availability in which some tree species (e.g., *Pseudospondias microcarpa, Myrianthus arboreus, Marquesia* ***excelsa*** 1 **and** Marantaceae (e.g., *Trachyphrynium brownii)* occur principally, or exclusively.

14) Disturbed vegetation with increased abundance of some secondary species (e.g., *Maprounea* ***membrenacea,*** *Xylopia aethiopica),* and sometimes increased density of herbaceous vegetation. It occurs naturally **(e.g.,** light gaps due to tree-fall), but most disturbance detected in botanical plots had resulted from past logging activities.

15) Areas at elevations above about 400-450m where certain species are found exclusively, or are more common (e.g., Treculia ***obovoidea,*** *Symphonia globulifera).* Opportunistic collections in areas higher than occurred on transects (up to 678m) revealed many species not found elsewhere, including one species,

Ocotea gabonensis, characteristic of montane floras at about 1,000m (Maley *et al*, 1990), which was found on a peak at about 650m, close to the end of the transect in Site 4 (Appendix 2.2).

16) Forest resembling (6) but with many additional species, often species associated with more ancient (mature) forest (e.g., *Coula edulis, Sindoropsis le-testui, Desbordesia glaucescens)* (cf. de Saint Aubin, 1963). Densities of Marantaceae and Zingiberaceae are further decreased (Plate 2.4).

17) '*Sacoglottis* forest' characterised by a forest type resembling (16) but where *Sacoglottis gabonensis* is one of the dominant upper canopy trees.

18) '***Paraberlinia*** forest' characterised by a forest type resembling (16) but where ***Paraberlinia* bifoliolata** was recorded.

19) '*Conceveiba* forest' at SOFORGA, resembling (16) but containing large numbers of the understorey tree *Conceveiba africana*

20) Vegetation characterised by increased abundance of trees of the Caesalpiniaceae, Olacaceae and Myristicaceae and sparse understorey vegetation. Many species represented here are characteristic of mature rain forest (e.g., ***Gilbertiodendron*** spp., *Strombosiopsis* sp. ?nov) (cf. de Saint Aubin, 1963).

Figure 2.9 shows the number of plots falling into each vegetation category in each site [when a plot was considered to be intermediate between two or more categories the appropriate fraction was assigned to each). Sites 1 & 5 were dominated by vegetation categories 3 - 5, and Sites 2, 3 & 4 by categories 16 - 20.

Plate 2.3.

'Marantaceae forest' - note the general open appearence, and the lack of canopy cover in the middle storey.

An elephant charges through a thicket of *Haumania liebrechtsiana* - there are four more elephants withion 20m of the camera, concealed by the dense herbaceous vegetation.

Plate 2.4.

Forest on rocky ground, dominated by *Diospyros* spp. Note the small size of trees and almost complete absence of ground cover. Soil depth is about 10cm.

Forest type (16) - note the increased numbers of trees in the middle-story compared to Plate 2.3, and the sparse ground cover.

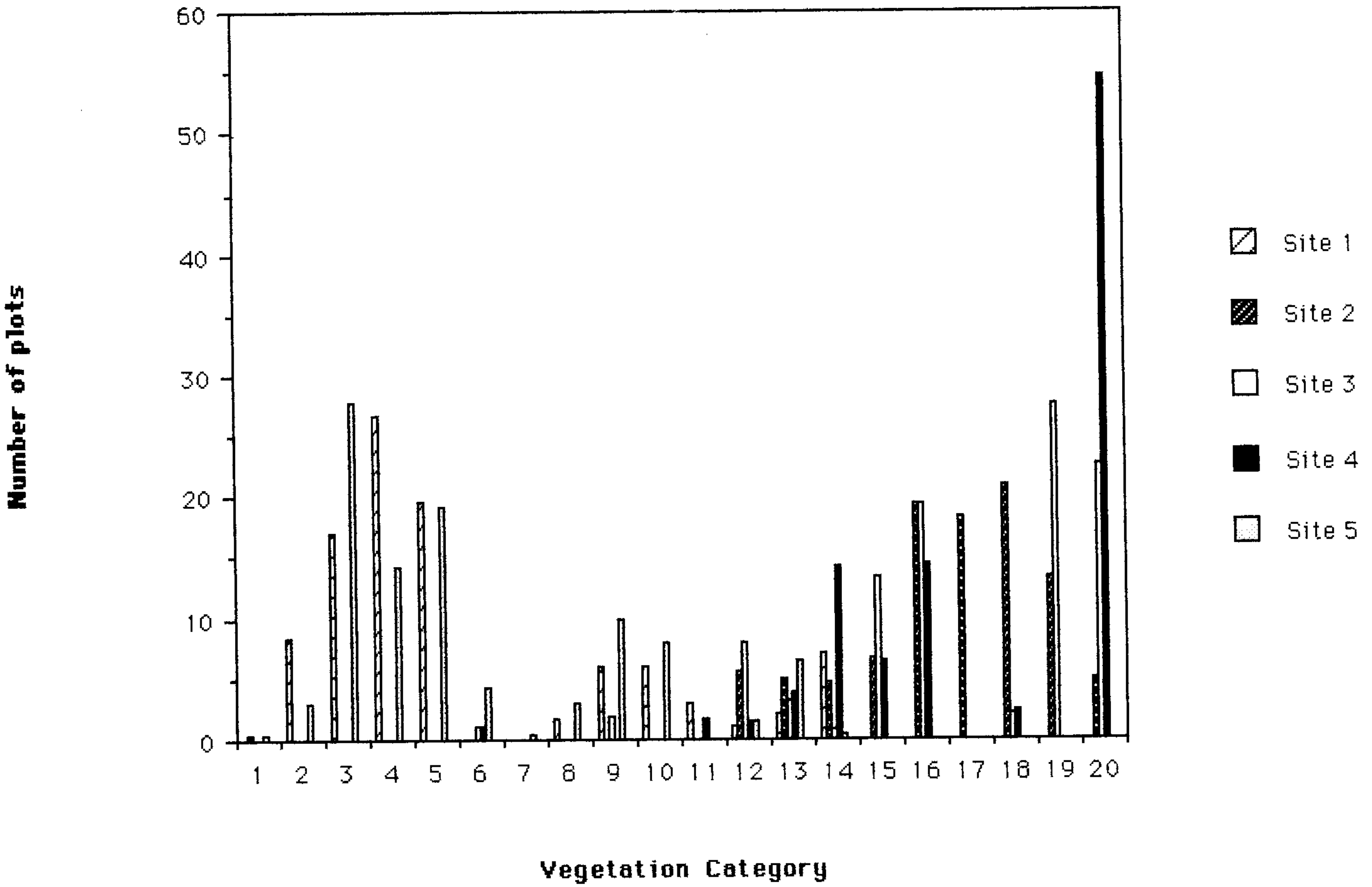


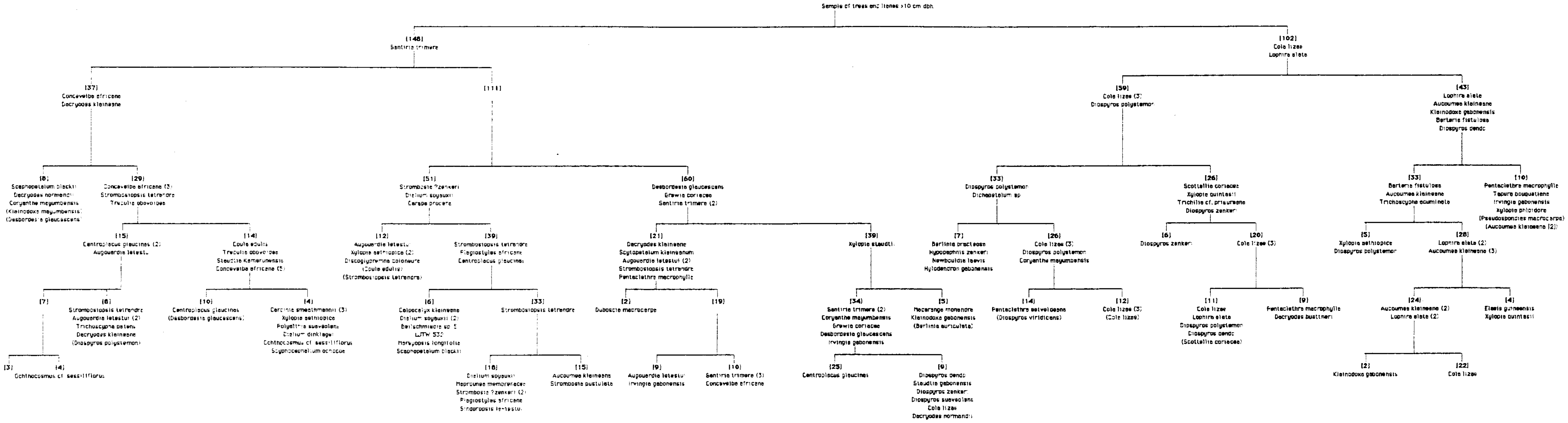
Figure 2.9: Distribution of 50m segments of the five transects into vegetation categories.

Multivariate analyses

Figures 2.10 and 2.11 summarise data from TWINSPAN analyses of trees >10 cm dbh and >70 cm dbh respectively (after trial runs, only species which occurred in at least three 100m plots were included). For plants >10 cm dbh the first division gave an almost perfect separation of plots in Sites 1 & 5, from those in Sites 2, 3 & 4, on the basis of the presence of Cola lizae and *Lophira alata* in the former, and *Santiria* trimera in the latter grouping. This division can be recognised in the field, and separates forest with dense Marantaceae and Zingiberaceae from forest with sparse undergrowth (i.e., it separated forest from categories [2]-[6] above, from those in [16]-[20]). Plots in Sites 1 and 5 were spread almost equally over the second division, which distinguished between *Cola lizae* (at densities of at least four individuals per plot) and *Diospyros polystemon* ([4]-[6] above), and plots with ***Lophira alata, Aucoumea klaineana Klainedoxa*** *gabonensis,* ***Barteria*** *fistulosa* and Diospyros ***dendo*** ([2] & [31 above, with the influence of rocky areas complicating the division). Again, this division is easily recognised in the field, as were many of the successive divisions on this side of the classification. Plots in Sites 2, 3 & 4 tended to be separated from one another on the other side of the classification, initially on the basis of *Conceveiba* ***africana*** and ***Dacryodes klaineana*** ([19] above) and again, many of the divisions could be identified in the field, and fitted into one or more of the above vegetation categories. However, effects of disturbance and water, which were generally localised within a portion of any 100m section, tended not to influence divisions in any consistent manner.

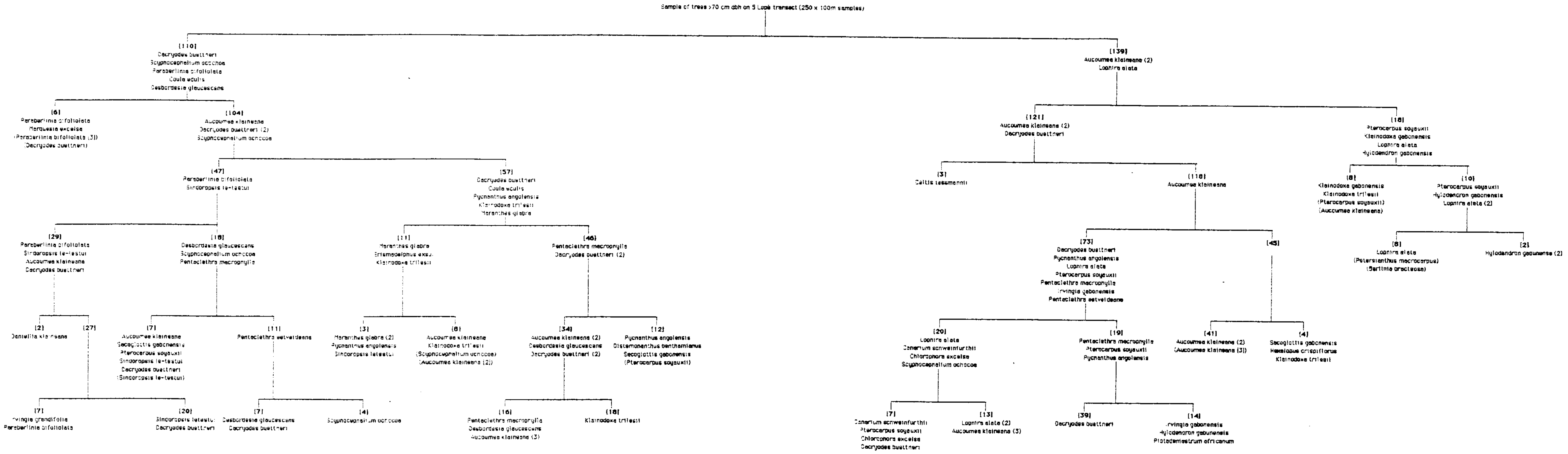
Data for trees >70 cm dbh were divided in a similar fashion to that >10 cm dbh, although the division between sites was less clear-cut. All but one of the plots in Site 1, and the majority in Cite 5, were in the category characterised by *Aucoumea klaineana* and *Lophira* ***alata*** (again separating [2]-[6] from [16]-[20]). This division is one that can easily be made in the field, but the ecological significance of most of the further divisions was less clear. When the two data sets were combined the divisions were little altered from those obtained considering only trees >10 cm dbh, and few of the large trees were classed as indicators. Adding herbs to the analysis for trees >10 cm dbh had little effect on the final classification, but many of the herbs were chosen as indicators in the early divisions.

Figure 2.10 TWINSPAN vegetation categories for plants >10 cm dbh



Emboldened figures in [ ] show the number of 100m plots that were classified in that vegetation category. Figures in ( ) indicate the pseudospecies level at which a species is an indicator.

Figure 2.11: TWINSPAN vegetation categories for plants >70 cm dbh.



Emboldened figures in [ ] show the number of 100m plots that were classified in that vegetation category. Figures in ( ) indicate the pseudospecies level at which a species is an indicator.

Figure 2.12 shows the CANOCO output for axes 1 and 2, for trees >10cm dbh which occurred in at least three 100m samples. The symbols used correspond to different groups from the equivalent TWINSPAN analysis, and tend to occur in clumps, demonstrating that the two analyses detected similar patterns. An environment ‘biplot’ is overlayed onto the species distribution. Moving away from the origin, these axes represent increasing correlation between the species in that part of the ordination and the environmental variable. Species in the botton right of the plot are positively associated with rock outcrops. Those in the top left with high canopy cover at <10m and 10-20m, and so on.

Figure 2.13 is a plot of the same output showing species names. Although this figure is cluttered, those species of most interest are the outliers, which can be distinguished. Many of the species cited as being characteristic of vegetation categories which are visible in the field, appear on the edge of the ordination. Throughout the CANOCO analyses, certain species groups tended to be clustered together as outliers. This was most consistent for a group including *Cassipourea* ***congoensis, Lecaniodiscus cupanioides*** *Dichapetalum* sp, and several Diospyros spp., amongst others (groups [8]-[10] above). These species ‘were known to be characteristic of areas where rock outcrops occurred, so an ecological interpretation of this part of the analysis seemed safe, and was confirmed by the environment biplot. Species considered characteristic of areas further from the outcrop itself were located progressively closer to the centre of the ordination. Savanna colonisers, and species characteristic of categories [3] and [4] tended to be in the top right of the plot. This is confusing, as the environmental biplot indicates that species characteristic of areas close to the savanna edge should occur to the left of the ordination. However, proximity to the savanna edge was complicated by location with respect to geomorphological sub-regions (see below). The centre of the plot is difficult to interpret, although most species generally found at higher altitudes are towards the far left of the ordination. These groups were consistently on the periphery of other CANOCO plots, and some of the ordinations also picked out a mixed group of species characteristic of disturbance and water. Figure 2.14 is a plot of the output for 100m samples (as opposed to species) from the same analysis. It shows a clear division between Sites 1 & 5, and Sites 2, 3 & 4, as was indicated by the descriptive data presented above, but within these two groups there was considerable overlap.

Figure 2.12: CANOCO plot for plants >10 cm dbh (for species occurring in at least 3 x 100m samples, showing environment biplot, and TWINSPAN categories).

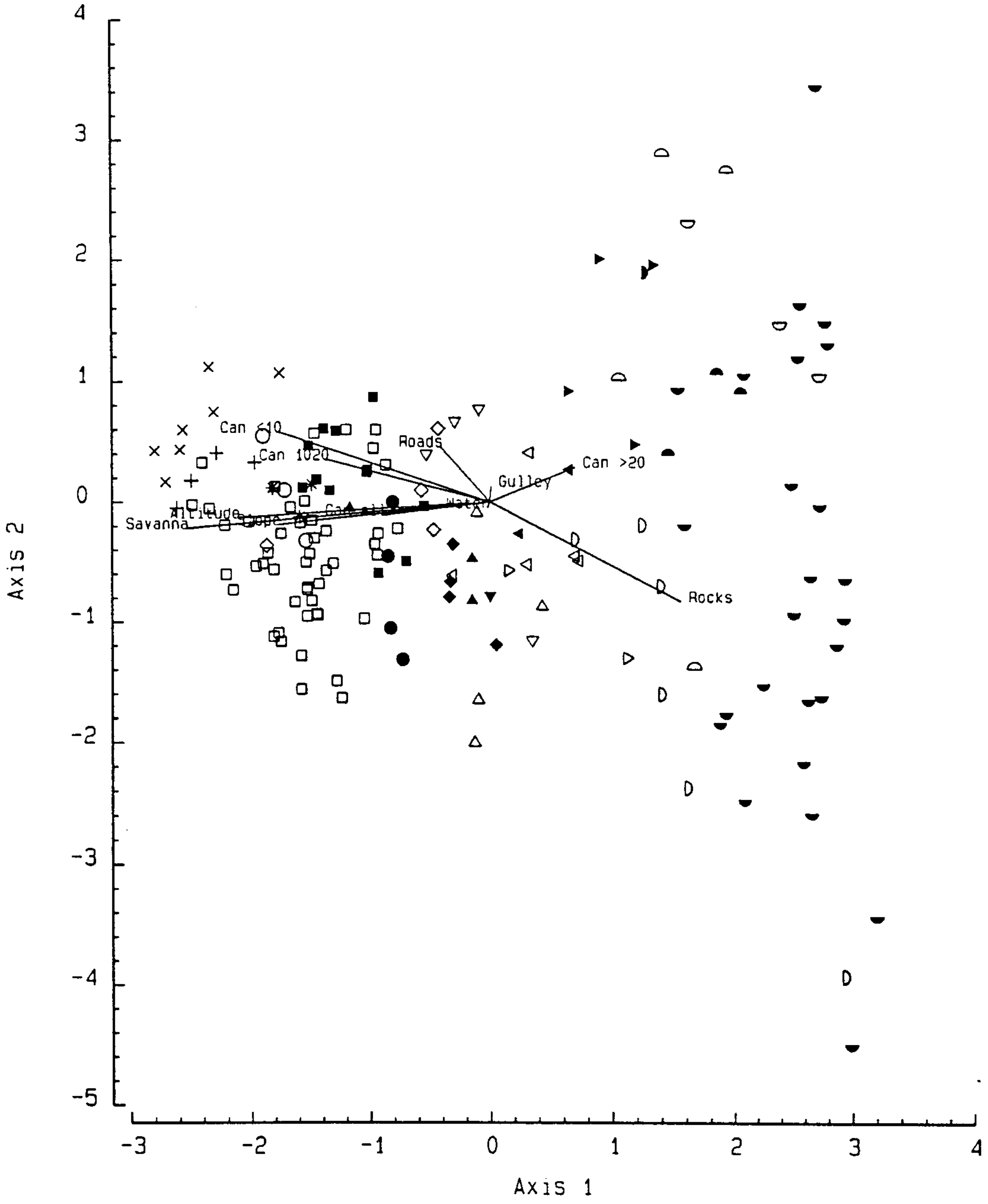


Figure 2.13: CANOCO plot for plants >10 cm dbh (species in at least 3 x 100m samples only, see Appendix 2.1 for full species names).

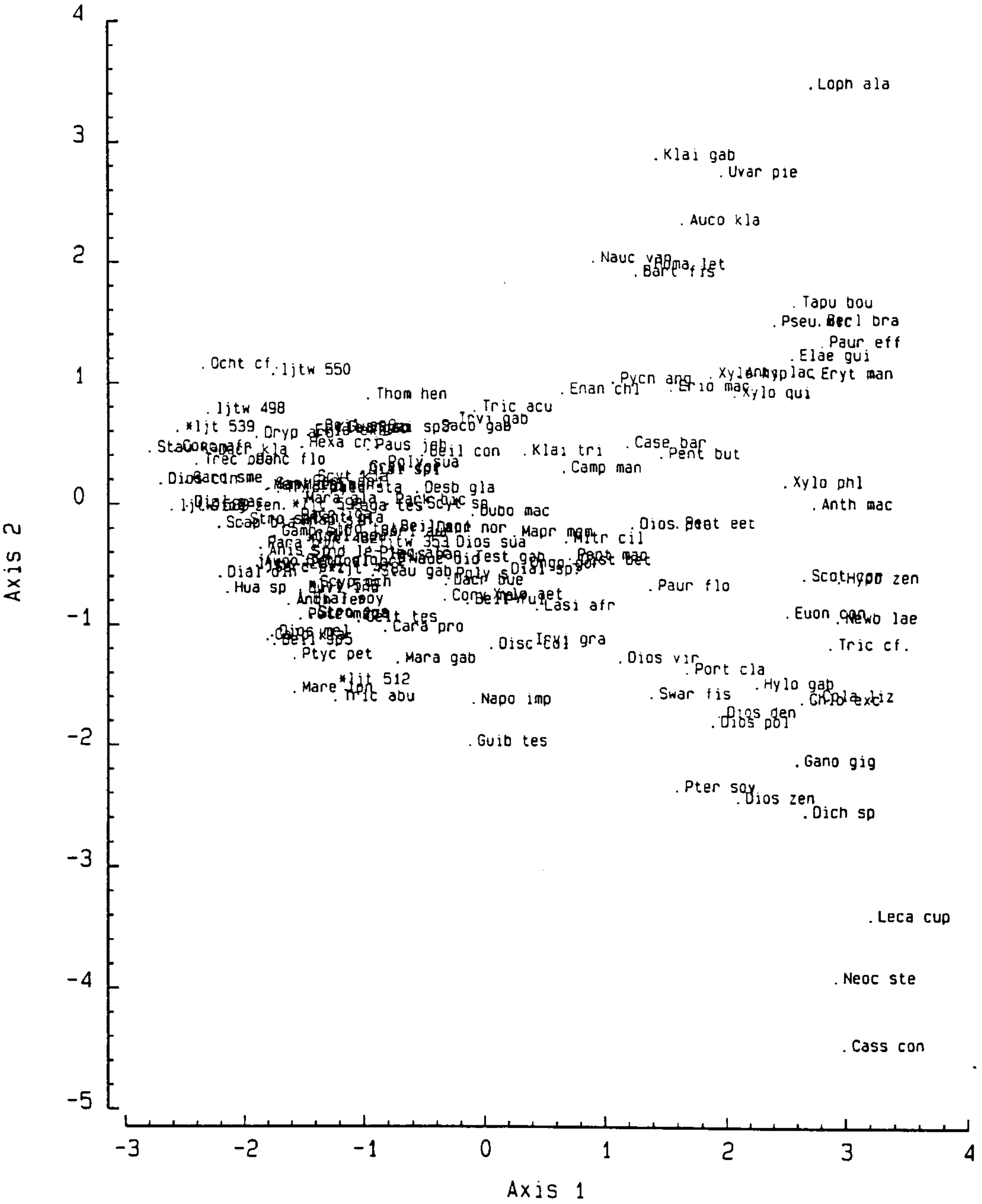
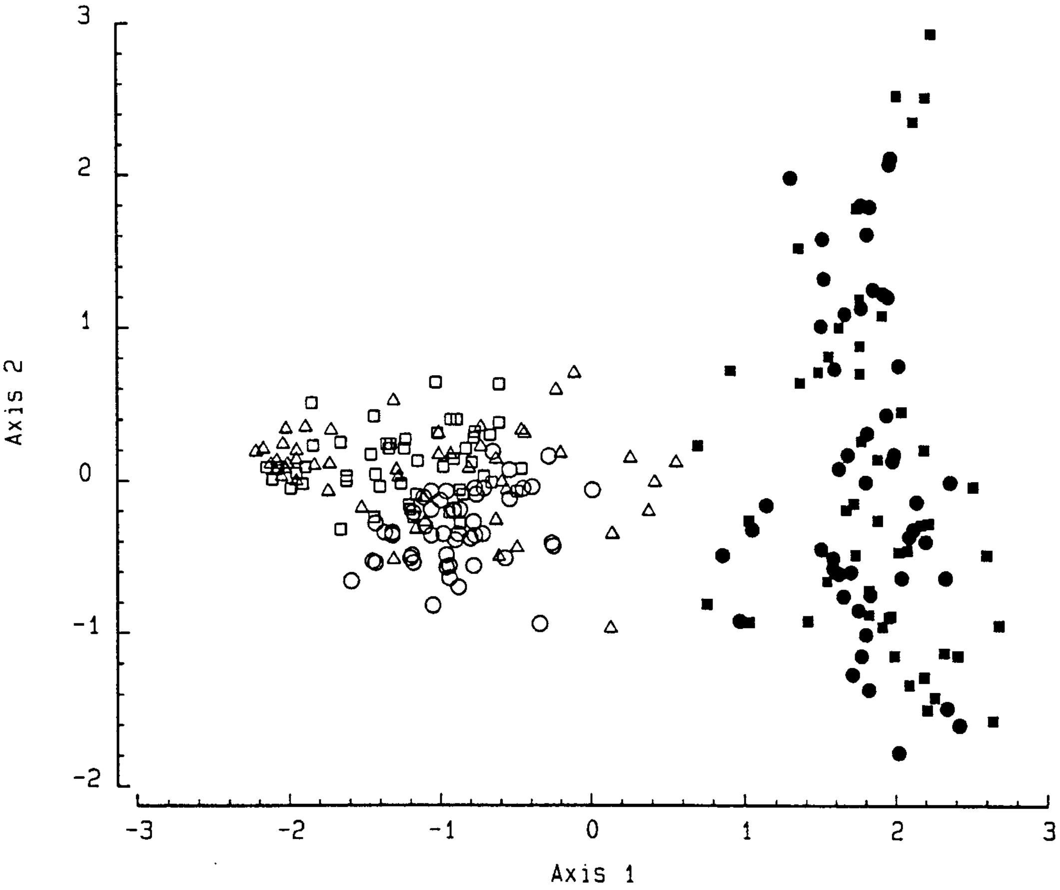


Figure 2.14: CANOCO plot for 100m samples of trees >10 cm dbh (species in at least 3 x 100m samples only).



■ Site 1; □ Site 2; △ Site 3; ○ Site 4; ● Site 5

Discussion.

Comparison with other ***areas***

There was considerable variation between, and indeed within sites, in terms of forest composition and structure. Sites 1 & 5 could be distinguished from the other three sites in terms of tree species composition and density of herbs. Site 1 stood out from all other sites as having a different structure in terms of stocking density of trees and canopy cover. Sections where herbaceous vegetation was particularly dense in Site 5 were comparable, although overall this site resembled the other three. Letouzey (1968) described similar forest in Cameroun as "forêts clairsemées a strate inférieure de Marantacées" and comparable formations occur in Congo (de Foresta, 1990) and Central African Republic (D.Harris, personal communication). In Lopé, as in Cameroun and Congo, these forests are closely associated with patches of savanna (de Foresta, 1990; Letouzey, 1968) and are thought to reflect fairly recent colonisation of savanna by forest vegetation (de Foresta, 1990).

Williamson (1988) recorded 138 species of at least 32 families in a 4-ha sample of trees >10 cm dbh enumerated along transects and trails in 'Marantaceae forest' closer to the savanna edge at SEGC. She found 54 species in a 1-ha sample along a line transect, which is comparable to Sites 1 and 5, as would be expected. Reitsma (1988) enumerated four square 1-ha plots in different areas of Gabon, and recorded 69 - 131 species present of dbh >10cm. The lowest figure was for a plot at SOFORGA, located (by chance) about 100m from the transect in Site 2, and the highest was for forest in the 'Monts de Crystal', which is thought to have been a Pleistocene forest refuge (Bourlière, 1973). Reitsma suggested that species diversity was lowest in his Lope plot because the region has lower rainfall and poorer soil quality compared to his other study sites. The higher number of species in Sites 2, 3 & 4 compared to Reitsma's Lope plot could partly be because a line transect, rather than a square plot, was used to sample vegetation (Reitsma, 1988). However, Reitsma's plot cannot be considered representative of vegetation in Lope as a whole (see below).

Unlike other parts of Gabon, Burseraceae (not Caesalpiniaceae) was the dominant family in Lope (cf. Reitsma, 1988). Tree species diversity was comparable to other areas in Gabon (e.g., Aubréville, 1967b; Hladik, 1978, 1982, 1986), and was higher than for rain forest in other parts of Africa (e.g., Gartlan *et* al., 1986; Hopkins, 1974; Jones, 1954,1955; Newbery ***et* al.,** 1986; Richards, 1952; Struhsaker, 1975).

Studies in the Neotropics and southeast Asia have often revealed higher tree species diversity: Nicholson (1 965) found 198 tree species >10 cm dbh in a 0.5 ha sample in Borneo; Gentry (1987) found about 300 species in a sample of 600 individuals >10 cm dbh (for a review, see Reitsma 1988). However, there is a great deal of variation between sites and Hladik (1986) found that species diversity in Gabon was comparable with many Neotropical sites. Newbery ***at al.*** , (1 992) warned that comparisons between sites should only be made with caution, especially when considering studies in small areas, when criteria for site choice are not made clear. Reitsma (1988) also enumerated sub-plots of vegetation in all size categories, and found the second mast species-rich plot recorded anywhere in the World, in his Monts de Cristales study area. For trees >70 cm dbh species diversity compared favourably with 74-90 species >60 cm dbh / 40 ha found in large-scale inventories in North-East Gabon (Hladik, 1986).

Basal area in this study was 29.6 - 40.0 m^2 ha-1 for trees >10 cm dbh, which is comparable to, or higher than other African forests, but is lower than that recorded for some Neotropical and southeast Asian forests, although again there is a great deal of variation between sites within geographical regions (Reitsma, 1988). Reitsma (1988) noted that Gabonese forests tend to have relatively high basal areas, especially in high diameter classes. Rollet (1974) gave a pan-tropical average basal area of 7 m2 ha-1 for trees >60 cm dbh, so the figure of 12.1m2 ha-1 for trees >70 cm dbh for this study is above average. There were 304 - 468 trees >10 cm dbh ha-', which is lower than in many other sites in Gabon (Aubréville, 1967b; Hladik, 1978; Reitsma, 1988). Figures for Neotropical forests are 167 - 1947 individuals > 10 cm dbh (Gentry, 1982) and Proctor *et* ***al.*** (1983) recorded *o* mean density of 678 trees >10cm dbh ha-1 in Malaysia. Therefore, tree density should be taken into account when comparing species densities between areas (Reitsma, 1988).

Overall canopy cover in undisturbed forest, in Sites 3 (before logging) and 5, was 94-95%. There are few comparable data, but Skorupa (1986) gave figures of 87% and 72% cover above 9m and **15m** respectively for undisturbed forest in Kibale, Uganda.

Plate 2.5.

In Lopé dry season savanna fires are lit in the evening, so that cool conditions prevent them getting out of control.

Annual fires maintain a sharp boundary between the forest and savanna.

Forest history in Lopé.

Composition and structure of the forest differed in response to several environmental factors: proximity to savanna; drainage (distance to standing water or a stream); altitude; proximity to rocky outcrops; and past disturbance, due either to natural tree-fall, or logging. Savanna vegetation in much of Lopé is maintained by regular fires (Plate 2.51, which result in sharp boundaries between forest and savanna, and prevent colonisation by forest plant species. However, in some more isolated areas fires are rare, and forest vegetation seems to be colonising the savanna (Plate 2.2). Around SEGC the principal colonising tree species are Aucoumea klaineana and ***Lophira** alata* but in parts of SOFDRGA, *Sacoglottis gabonensis* colonises in pure stands.

It is generally accepted that there is a long history of expansion and contraction of forest and savanna zones in Africa, in response to climatic fluctuation between glacial maxima (see Hamilton 1982; Livingstone, 1975; Maley 1991). There is good evidence for East Africa that during the last glacial maximum, aridity increased and resulted in reduction in forest cover in favour of more open habitats, whilst lower temperatures depressed the lowland-montane vegetation boundary, allowing montane species to survive at altitudes approximately 900m below their current limits (e.g., Hamilton, 1988). Maley (1990a, 1991) reviewed data for Central Africa and concluded that from the Present to about 30,000 6P the principal climatic phases were similar to those in East Africa.

Gabon was the centre of a forest refuge during arid climatic phases (Hamilton, 1976, 1982; Kingdon, 1980; Maley 1987). Gradients of decreasing biotic diversity can be identified moving away from such refugia in various parts of Africa (Hamilton, 1976, 1982; Kingdon, 1990). *As* noted above, there has been some debate about the origins of savannas which occur within the forest zone of west and central Africa, but the consensus is that some at least are of paleoclimatic origin. They appeared during an arid climatic phase, and have not yet been recolonised by forest, although the prevailing climate could support forest vegetation (Aubreville, 1967; de Foresta, 1990; Maley, 1990b; Nicolas, 1977; Schwartz *et **al,*** 1990).

Maley *et **al.*** (1990) found patches of forest in isolated pockets of savanna in the Massif du Chaillu, Congo, where remnant populations of montane flora survive at about 650m, including *Podocarpus* ***latifolius,*** a tree which does not generally occur below 1,500m, and *Ocotea gabonensis,* generally found at about 1,000m. They interpreted this as evidence that montane vegetation was able to become established at this altitude during periods of depressed temperature. De Foresta (1990) cited botanical evidence that forest colonises savanna in the Mayombe, Congo, where "foret clairsemée **à** Marantaceae" {clear forest with Marantaceae) forms behind an advancing forest front. Similar formations have been documented in Cameroun (Letouzey, 1968, p. 224) in association with savannas, and descriptions, photos and botanical data leave no doubt that these forests correspond to vegetation in Sites 1 & 5.

Considering climatic information and the present distribution of savanna and forest the following scenario, much along the lines of that presented by Aubreville (1968), seems likely in Lope:

Due to its location in respect to the surrounding mountain ranges, Lope experiences a rain shadow effect which reduces rainfall (Nicolas, 1977). In addition, there is a narrow corridor of low rainfall along the Ogooué river (Nicolas, 1977). Therefore, Lope would be more adversely affected than other areas of Gabon by water stress in arid periods, especially in areas either side of the Ogooué Forest vegetation would have receded away (north and south) from the area of water stress and would have been replaced by savanna. Decreased temperatures would have enabled montane forest to become established on higher hilltops. The presence of ***Ocoteagabonensis*** at 650m, suggests that relict populations of montane flora may exist in Lope, as found in Congo (cf. Maley *et* al., 1990). Once the climate became warmer and wetter, forest vegetation would have been able to re-establish in savanna. Forest would have expanded from refugia thought to have existed to the northeast and southeast (Maley, 1987), and from montane forest on hilltops. A succession would have occurred away from the savanna edge, where forest would have been dominated **by** colonising species, back towards the refugia, where species characteristic of mature forest would have been more common.

Modern savanna distribution in Lopé supports this scenario. The extensive **low** lying areas in geological Sub-Region 4, close to the Ogooué, would have become savanna, and would have been the last to be re-colonised by a forest front advancing from north and south. Hilltops covered by savanna would be the last areas to be re-colonised, so would persist as isolated patches after other areas had been colonised. These would have been the last areas to have been cleared of forest by humans, were the savannas anthropic in origin. Hilltops above a certain threshold altitude, which had supported montane forest, would maintain a forest cover, and perhaps still have remnant populations of montane flora today.

Neither TWINSPAN nor CANOCO is a rigid statistical technique. Data input into both can be manipulated to (subjectively) 'improve' the ecological significance of the outputs, or alternatively, to massage results to better conform to a hypothesis. They should be used to develop, rather than test hypotheses concerning vegetation pattern and process (C. Legg, personal communication).

The classifications presented in Figures *2.9* - 2.14 are consistent with the vegetation categories listed above as being visible in the field. Separation of sites between vegetation categories recognised in the field (Figure 2.9) was similar to that in the CANOCO ordination {Figure 2.14). Figure 2.15 presents a schematic diagram of the succession from savanna to mature forest, using the vegetation categories to represent stages in the succession. This was developed in Lope and was refined after data analysis, and has since been checked by workers in the field, who have found it of use (C. E. *G.* Tutin & R. Ham, personal cornmunication).

Figure 2.16 shows the CANOCO output for trees >10cm dbh (as 2.12 & 2.13). Species named are those considered to be indicators for the vegetation categories presented above. Indicator species tend to be grouped together, and are arranged in a clear pattern. Figure 2.17 is the same CANOCO plot, with indicator species of each category given different symbols. Indicator species are aligned on two axes, in the order predicted by Figure 2.15, as shown on the overlay plot, providing independent support for the validity of the succession model.

Following this scheme, colonisation of savanna would proceed as follows:

Lophira alata and *Aucoumeaklaineana* have wind dispersed seeds, which are able to establish in savanna conditions. They form an early colonising forest providing shade, which moderates the extremes of temperature and humidity experienced in open savanna. Early colonising individuals have low, round canopies and branch low down, but successive generations of seedling grow taller and branch higher to escape from the shadow of their predecessors. As more individuals become established canopy cover increases, and there is a corresponding increase in relative humidity and rates of organic deposition, whilst

Figure 2.15: Model for succession from savanna to mature forest in Lopé (Unbroken arrows indicate direction of successions. Broken arrows indicate that the vegetation type in question can occur at any point in the succession).

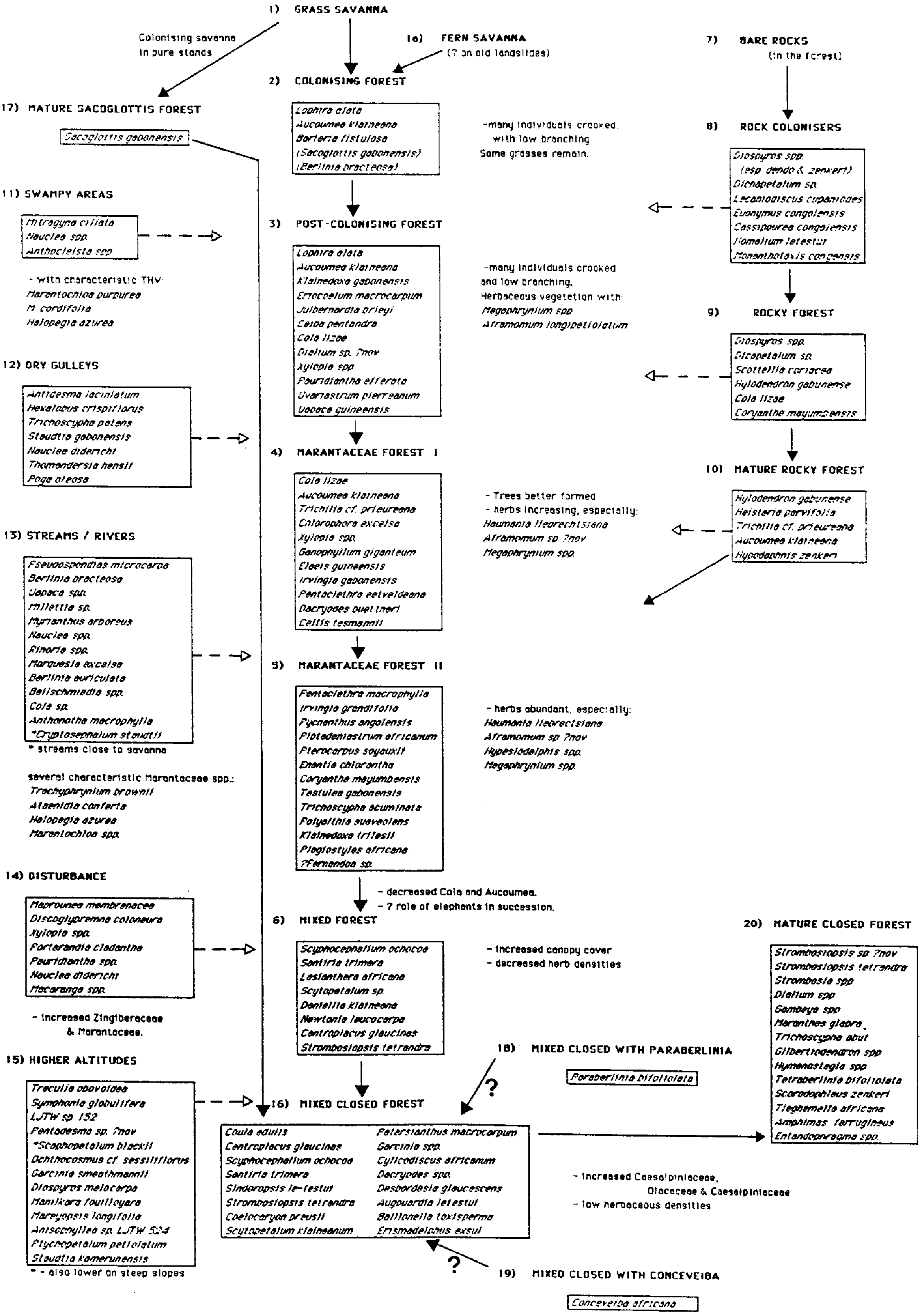
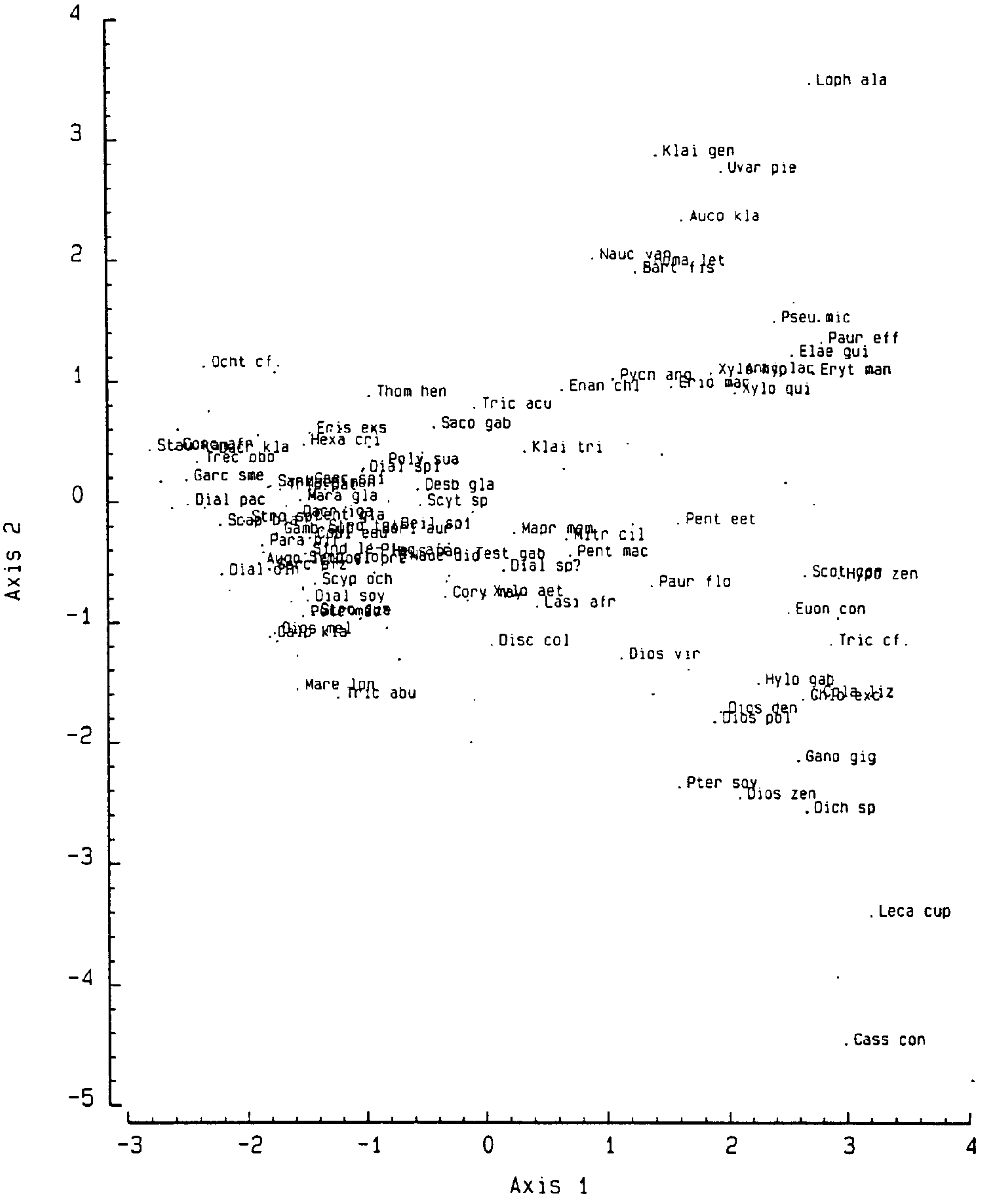
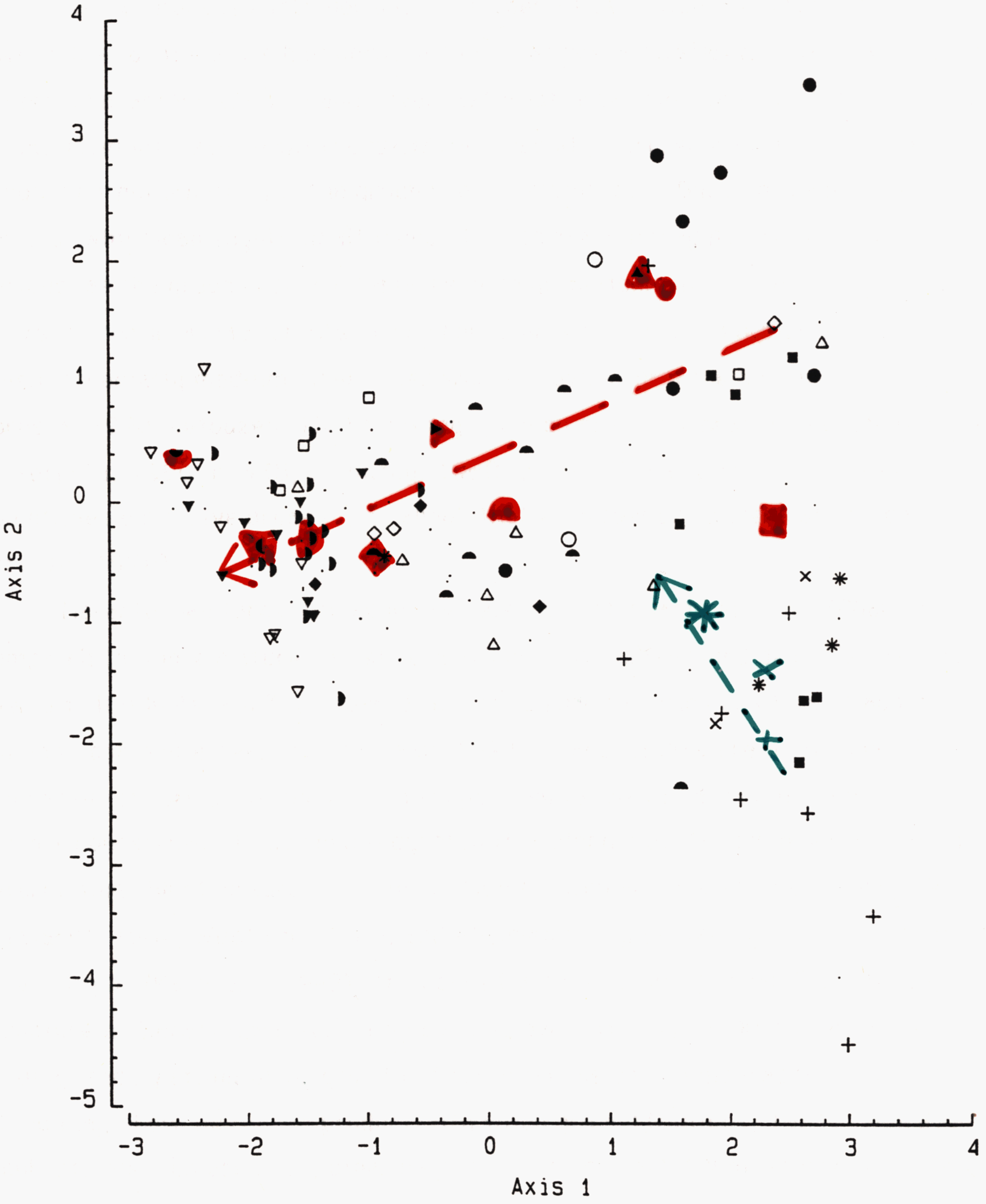


Figure 2.16: CANOCO plot for plants >10 cm dbh (species in at least 3 x 100m samples, species labelled are those considered to be indicators of vegetation types in Figure 2.15).



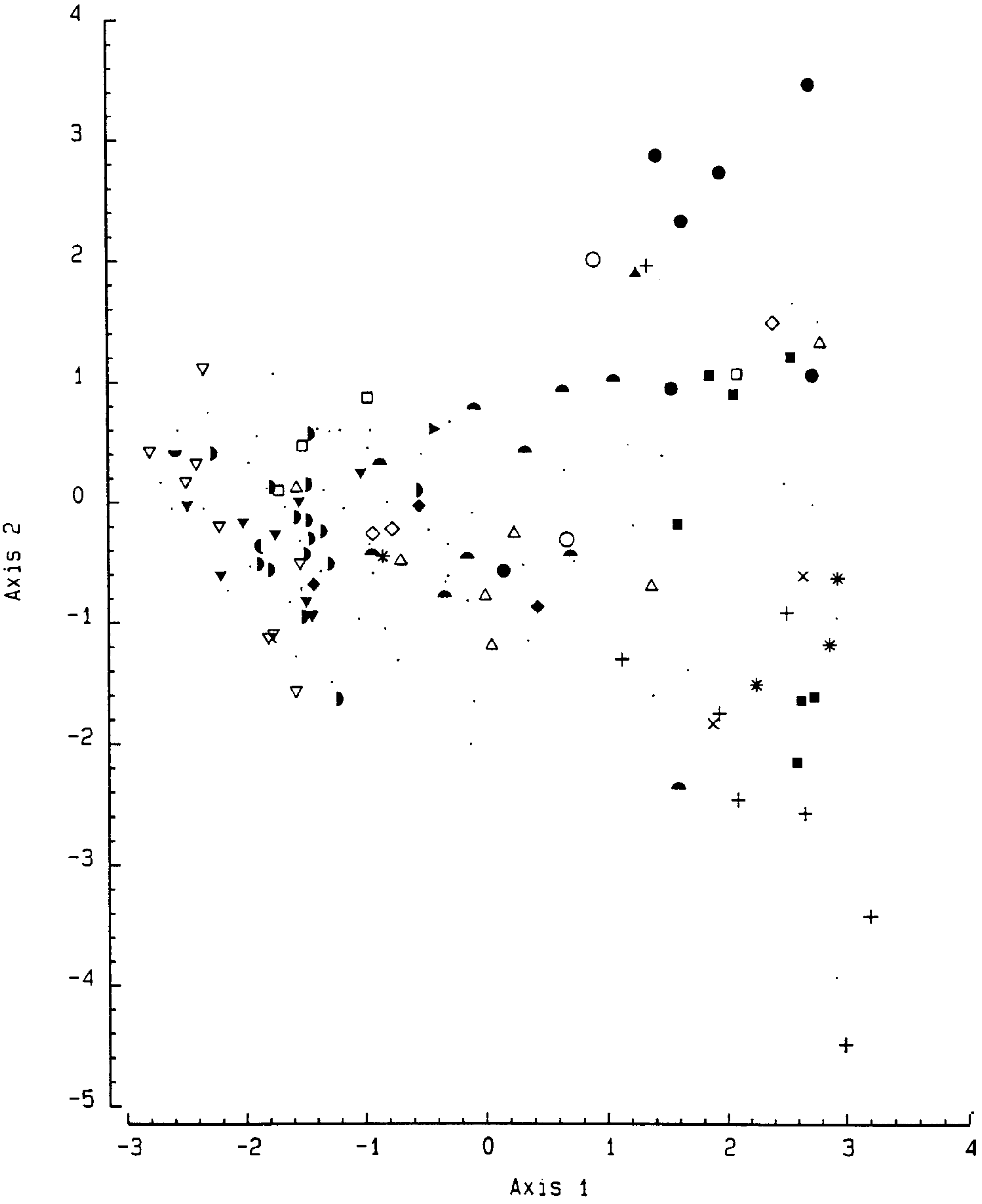
· = species not considered to be indicators.

Figure 2.17: CANOCO plot for plants >10 cm dbh (species present in 3 x 100m samples, species considered characteristic of different vegetation types have different symbols. Overlay plot shows the centre of each group of species, and arrows indicate the direction of the succession model).



Key to symbols: vegetation category 2 = ▲ ; 3 = ● ; 4 = ■ ; 5 = ◓ ; 6 = ◆ 8 = + ; 9 = × ; 10 = ✱ ; 11 = ○ ; 12 = □ ; 13 = ◇ ; 14 = △ ; 15 = ▽ ; 16 = ◗ ; 17 = ▶ ; 18 = ◖ ; 19 = ◒ ; 20 = ◗ (see Figure 2.15 for explanation of categories).

Figure 2.17: CANOCO plot for plants >10 cm dbh (species present in 3 x 100m samples, species considered characteristic of different vegetation types have different symbols. Overlay plot shows the centre of each group of species, and arrows indicate the direction of the succession model).



Key to symbols: vegetation category 2 = ▲ ; 3 = ● ; 4 = ■ ; 5 = ◓ ; 6 = ◆ 8 = + ; 9 = × ;
10 = ✱ ; 11 = ○ ; 12 = □ ; 13 = ◇ ; 14 = △ ; 15 = ▽ ; 16 = ◗ ; 17 = ▶ ; 18 = ◖ ; 19 = ▼ ;
20 = ◗ (see Figure 2.15 for explanation of categories).

soil temperatures come to resemble those found within the forest. Soil quality improves, and new species are able to become established forming a post-colonising formation. Increased shade reduces the competitiveness of grasses and new species of herbs and shrubs appear.

As the process continues and more species establish, conditions become favourable for the growth of herbs such as ***Haumania** liebrechtsiana:* Marantaceae forest, characteristic of many savanna/forest areas (de Foresta, 1990; Letouzey, 1968) develops. ***Haumania*** liebrechtsiana densities increase until it forms a tangled carpet smothenng the ground and climbing up to 5m or more in dense vine towers, which can engulf small trees. This formation may persist for long periods, as the ground cover interferes with establishment of the next generations of trees. Marantaceae forests have characteristic low stocking densities of trees, especially medium sized trees whose crowns form the middle canopy (de Foresta, 1990; Letouzey, 1968), giving them an open appearance (see photos in: de Foresta, 1990, p. 335; Letouzey, 1968, p. 225; Plate 2.3) and there are sometimes extensive areas (up to about 1ha) with few or no trees at all (de Foresta, 1990).

Marantaceae forests in Lope have elevated elephant densities [Chapter *5)* compared to more mature forest formations, with year-round densities averaging over 2 individuals km-^{2}, compared to more characteristic densities of about 0.3 km-^{2} in Lop6 and elsewhere (e.g., Fay, 1991). Marantaceae are an important component of forest elephant diet in Lop6 (Chapter *5)* which may explain the elevated densities. It has been suggested that elephants play an important role in determining the structure and composition of African forests (e.g., Jones, 1954; Kortlandt, 1984; Western, 1989), and elephants may prevent forest regeneration after logging (Kasenene, 1992). It is possible that elephants contribute to the structure of Marantaceae forest by pushing over trees up to 40cm dbh during feeding, and by stimulating growth of Marantaceae and Zingiberaceae, some of which may show increased productivity when grazed (Bullock, 1981). However; elephants also, on occasion, clear patches of up to about 100m2 in Marantaceae thickets, within which tree seedlings may be better able to become established, so their role in the succession is not necessarily a negative one.

There is a gradual build-up of canopy cover in Marantaceae forest, which would result in a decrease in herb densities, and new tree species invade which are characteristic of mixed forest. **As** these become established the succession proceeds towards the most mature phase recorded in this study, characterised by increased dominance of the Caesalpiniaceae, Olacaceae and Myristicaceae. There are two anomalies in the latter stages of the proposed succession:

First is the occurrence of forest resembling mixed closed forest (16) but with Paraberlinia bifoliolata as one of the common upper storey trees. It is not clear whether *Paraberlinia bifoliolata is* an early member of mixed closed forest which tends to disappear in later stages, but its absence from plots classified as mature closed forest suggests this is the case. Caesalpiniaceae often have patchy distribution, occurring in scattered dense pockets (C. Wilks, personal communication) so their distribution patterns may be difficult to interpret.

Second is mixed closed forest with **Conceveiba** as a common middle canopy tree. *Conceveiba* africana is the commonest tree in Cites 2 & 3, attaining densities comparable to **Cola lizae** in Cites 1 & 5. It is most dense in lower altitude areas, and may reflect more recent colonisation of these areas than the adjacent mountains, which may have been high enough to have supported montane forest. However, dominance of single species of Euphorbiaceae in the understorey of mature rain forests has been reported elsewhere, and has yet to be explained (Newbery *et* **al.,** 1992).

The above scheme covers the main succession from savanna to forest, but in parts of SOFORGA, north of Sites 2 & *3, Sacoglottis gabonensis* colonises savanna in pure stands. As for *Lophira* **alata** and *Aucoumea klaineana,* colonising individuals generally branch low and have rounded canopies. ***Sacoglottis gabonensis*** is common in the coastal sedimentary basin of west and central Africa (Letouzey, 1968; de Saint Aubin, 1968) but was only recently found in Lope (Reitsma, 1988; Williamson, 1988), about 120km east of the sedimentary basin. It has also been reported in the Chaillu mountain region (Gloriod, 1974) and is known to colonise savannas and old plantations elsewhere in Gabon (Aubréville, 1967b). In Site 2 some plots contained large individuals of **Sacoglottis gabonensis,** which dominated the canopy in places, but there was no regeneration under the closed canopy, suggesting that it was a relict population of mature and senescing individuals, left over from a savanna colonisation in the past.

A second succession *was* observed *in* areas where the topsoil was thin and rock outcrops occurred. The starting point is a situation where bare rock is present within the forest. This may be a result of severe erosion characteristic of savanna (cf. Maley *et al., 1990),* which removed topsoil when forest cover *was* lost, revealing the substrate; or to changes in the course of forest streams that have exposed rocks. Organic material accumulates in rock crevices enabling plants to become established. Organic matter is deposited upon the rocks and a shallow topsoil is formed, on which a characteristic community of trees (e.g., *Diospyros dendo*, *Dichapetalum* sp., *Cassipourea congolensis*) become established. With time, soil becomes deeper (or, close to the outcrop, soil removal was less complete) and different species appear, until mature rocky forest becomes indistinguishable from the dominant forest type in the area. In this study rocky areas rarely occupied an entire plot, although these forest types were found to cover areas of a hectare or more off transects.

In addition to their position in the succession from savanna or bare rock to mature forest, the composition of plots was influenced by several other factors, as shown in Figure 2.15. Water availability had a significant effect on botanical composition, and some tree and herb species were associated with swamps, perennial rivers and streams, or seasonal streams and dry gulleys which became water courses during rainfall. Some species characteristic of rocky areas also occurred secondarily close to streams, presumably because rocks are exposed by the water and deviations in the water course can then leave these dry. Altitude was also important, with some species restricted to higher areas, perhaps because they required cooler conditions, or benefited from frequent mists, which caused increased relative humidity and hence water availability. Finally, many plots had been subject to disturbance, mostly due to logging activity at some stage in the past, and several species were good indicators of this.

Fires have influenced rain forest vegetation in many regions (e.g., Beaman *et al.*, 1983; Hawthorne, in press(a); Sanford *et al.*, 1985). Hawthorne (in press[a]) demonstrated that fire has a profound influence on the structure and composition of vegetation over most of Ghana, West Africa, maintaining savanna areas that would otherwise be recolonised by forest, and altering forest vegetation throughout the dry semideciduous zone (cf. Hall & Swaine, 1981). Fires were more common in logged forest and fire was considered to be the greatest threat to the long term productivity, genetic wealth and general health of about half of the remaining forest in Ghana (see also Uhl & Buschbacher, 1985). A type of 'Marantaceae forest' develops in areas that have been affected by fire, with the same general appearance as that at Lopé (M. D. Swaine, personal communication). The possibility that fire has played a part in the development of

Marantaceae forest in Lope cannot be ruled out, although there are no records of forest fires in the area. In forest affected by fire in Ghana, there was a decrease in the proportion of trees in smaller girth classes (Hawthorne, in press[a]), and the bases of larger trees often have scars reflecting the passage of flames at some time in the past (M. D. Swaine, personal communication). None of these indicators were observed in Lopé, suggesting that the forest has not burnt in the recent past.

Timber extraction in Gabon is low intensity and a typical logging operation results in the loss of 5-10% of canopy cover. Within the forest, gaps are created when large trees are felled, and access roads are constructed to extract cut timber. These roads are generally about 5-10m wide, with a band of 10-25m on either side deforested to allow sunshine to dry out the road surface during the wet season. By removing forest cover the loggers mimic climatic changes, especially along roads where large clearings are created for log parks (areas where logs are loaded onto lorries), and where erosion similar to that seen in some savanna areas is possible (see Plate 4.2 - p. 134). This can result in invasion by savanna species (e.g., many species of grass) and effectively set the succession back to stage one in small isolated patches. Where road construction results in extensive patches of bare soil on slopes, or in landslides, Gleichenia *linearis* often colonises, forming areas of 'fern savanna'. *Sacoglottis gabonensis* seeds were observed germinating along an abandoned logging road that crossed Site 2, but seedlings were not found in the forest under closed canopy conditions.

Hence, the composition of any plot from the botanical sample could be explained by its place in the succession from savanna to open mature forest, and/or the succession from bare rock, as well as reflecting the influence of any other factors outside of these successions (11-15). Conversely, knowing its composition, it is possible to predict a plot's position in relation to the savanna, rocky outcrops, water, high altitude and past disturbance. The majority of plots fall within the main succession from savanna to open mature forest, but there are marked differences in the proportion of each category between the sites. In Sites 1 and 5 early successional stages dominate, whilst in the other sites later stages dominate. Site 4 has the greatest proportion of open mature forest. This scenario would account for the differences in the botanical structure and composition of the five sites, and therefore, the sites provide support for the theory that the Lopé savannas were indeed formed naturally, and that they would probably disappear in the course of time, if not maintained by humans.

How old are the savannas ? Maley et *al.* (1990) and Schwartz (1992), traced the origins of comparable savannas in Congo to at least 3,000 BP, when an arid period affected the region, but were unable to confirm that it was this and not a previous more severe arid period that was responsible. Datation of clay Sediments from an ancient extension of the Ogooué river in the north of the Lope Reserve, together with an analysis of a pollen core, dates vegetation dominated by grasses back to 1610 ±50 years BP, and savannas probably date back to at least 2500-2000 years BP (J. Maley, personal communication). One scenario for the history of vegetation in the Lope area (J. Maley, personal communication) would be: After the last major dry climatic phase around 18,000 years BP (e.g., Hamilton, 1982; Maley, 1991), when much or all of the area might have been savanna, forest vegetation would have started to re-colonise around 12-13,000 years BP, Maximum extension of the forest occurred in the middle Holocene *(7-*4,000 BP), at which point the Lope savannas would probably have been much reduced, or almost entirely re-colonised. Savannas probably then re-opened between 3-4,000 BP, expanding during a marked arid phase between 2500 - 2000 BP (Maley, 1992), when they were probably more extensive than today. The return of more humid conditions between 1900 - 1400 BP (Maley, 1992) would have initiated a new phase of forest re-colonisation, which may be what we see underway today in Lopé, in places where fire does not interfere with the succession.

An advancing forest front colonising savanna Cor a retreating forest front) would be a rapidly changing environment where species able to adapt would be likely to flourish. In such a situation rapid speciation might occur (e.g., Gentry, 1989) and the distribution and abundance of Cola *lizae* provides some evidence to suggest that this has been the case in Lope. In addition to Cola lizae, *Aframomum* sp. ?nov, the dominant Zingiberaceae in the Lope Marantaceae forest, which has a similarly restricted range, may be a new species (J. M. Lock, personal communication), as is the case for the *Dialium* species found most commonly close to the savanna edge IF. J. Breteler, personal communication). These three common species, with restricted range, which occur in the Marantaceae forests fringing the present forest-savanna boundary, are perhaps the strongest evidence for suggesting that environmental flux has played a vital role in determining the present structure and composition of vegetation in the Lope Reserve.

Appendix 2.1: Plant species >10 and >70 cm dbh on transects.

FAMILY / SPECIES	**Number of Individuals**									
	Site 1		**Site 2**		**Site 3**		**Site 4**		**Site 5**	
	>10	>70	>10	>70	>10	>70	>10	>70	>10	>70
ACANTHACEAE										
Thomandersia hensii			3		14					
ANACARDIACEAE										
Antrocaryon klaineanum							1	1		
Pseudospondias microcarpa	1					1			2	1
Sorindeia cf. *juglandifolia*	2									
Sorindeia sp. LJTW 555					1					
? *Sorindeia* sp. LJTW 410									2	
Trichoschypha abut					1		5			
Trichoschypha acuminata	11		32		12		3		12	
Trichoschypha arborea				1						
Trichoschypha patens			11		5					
ANNONACEAE										
Enantia chlorantha	4		9		12		5		21	
Hexalobus crispiflorus			3	10		1				
Polyalthia suaveolens gabonica	2		14		6		12		6	
Polyalthia s. suaveolens					5					
Uavaria sp. LJTW 553					1					
Uvariastrum pierreanum	5		3						8	
Xylopia aethiopica	21		1		3		36		3	
Xylopia hypolampra	16		2		2		1		6	1
Xylopia phloidora	3								8	
Xylopia quintasii	38		6		19		5		95	
Xylopia staudtii			14		4		2			
? *Xylopia* sp. LJTW 438							1			
? *Xylopia* sp. LJTW 609										
LJTW 413									1	
LJTW 499			1							
APOCYNACEAE										
LJTW 500			2							
LJTW 556					1					
*LJTW 583			1							
BIGNONIACEAE										
Newbouldia laevis	5								1	
BOMBACACEAE										
Ceiba pentandra		1							2	2
? *Rhodognaphalon* sp. LJTW 188			1			1				

Appendix 2.1: Plant species >10 and >70 cm dbh on transects / continued.

FAMILY / SPECIES	**Number of Individuals**									
	Site 1		**Site 2**		**Site 3**		**Site 4**		**Site 5**	
	>10	>70	>10	>70	>10	>70	>10	>70	>10	>70
BURSERACEAE										
Aucoumea klaineana	61	119	14	86	21	94	16	78	96	166
Canarium schweinfurthii		2		3		2		5		3
Dacryodes buettneri	8	16	29	52	9	47	29	68	18	20
Dacryodes edulis							1			
Dacryodes igaganga			4		8	4				
Dacryodes klaineana			40		38					
Dacryodes normandii	3		13	1	8	1	5		6	
Dacryodes sp. LJTW 591					1					
Santiria trimera			143		121		54		1	
CAESALPINIACEAE										
Afzelia sp. LJTW 450								1		
Amphimas ferrugineus						1	2	2		
Anthonotha ferruginea					2		3			
Anthonotha macrophylla	6						1		2	
Augouardia letestui			34		20	1	40			
Berlinia auriculata					1		3			
Berlinia bracteosa	8	2							1	2
? *Brachystegia mildbraedii*				1		1				
Calpocalyx klaina			2				16			
Daniellia klaineana			2	2	1	4		1		1
Detarium macrocarpum		2								3
Dialium dinklagei			1	1	2		4			
Dialium eurysephalum					2					
Dialium pachyphyllum				1	4	4	2			
Dialium soxauxii			7		4		29	1		
Dialium sp. ?nov	6	1	6		5	2	4	4	8	
Dialium sp. LJTW 115					2					
Dialium sp. LJTW 390								2		
Dialium sp. LJTW 586			4							
Dialium sp. LJTW 601								2		
Distemonanthus bethamianus	2	5	1	1		1	1	1		1
Eurypetalum batesii							1			
Gilbertiodendron sp. LJTW 336					1	1				
Guibortia demeusii					1		1	1		
Guibortia ehie							1			
Guibortia tessmannii						4	2	2	1	1
Hylodendron gabunense	6	12			4	2			9	2
Hymenostegia sp.			2		1	1				
Hymenostegia sp. LJTW 130							6			

Appendix 2.1: Plant species >10 and >70 cm dbh on transects / continued.

FAMILY / SPECIES	**Number of Individuals**									
	Site 1		**Site 2**		**Site 3**		**Site 4**		**Site 5**	
	>10	>70	>10	>70	>10	>70	>10	>70	>10	>70
CAESALPINIACEAE / continued.										
Julbernardia brieyi		1					2	1	1	2
Neochevalieradendron stephanii	6						1			
Paraberlinia bifoliolata			9	39	2	11		6		
Scorodophloeus zenkeri			3				1	2		
Sindoropsis le-testui			3	19	3	10	11	17		
Swartzia fistuloides	2	4		1	1	3				1
LJTW 395								1		
LJTW 466								1		
LJTW 474										
LJTW 572			1							
*LJTW 596						1				
LJTW 602								1		
CELASTACEAE										
Euonymus congolensis	3								3	
CHRYSOBALANACEAE										
Maranthes aubrevillei						1	1	1		
Maranthes gabunensis	2	1	1		4		5			
Maranthes glabra					4	9	3	17		
Parinari excelsa								2		
Parinari hypochrysea					1	3				
LJTW 533							1			
COMBRETACEAE										
* *Combretum* sp. LJTW 531					1		1			
CONNERACEAE										
*LJTW 470			1							
*LJTW 539					4					
DICHAPETALACEAE										
* *Dichapetalum angolense*					1					
Dichapetalum sp. LJTW 287	9				1				7	
Tapura bouquetiana									17	
DIPTEROCARPIACEAE										
Marquesia excelsa			3	6						
EBENACEAE										
Diospyros cinnabarina			5		2		1			

Appendix 2.1: Plant species >10 and >70 cm dbh on transects / continued.

FAMILY / SPECIES	**Number of Individuals**									
	Site 1		**Site 2**		**Site 3**		**Site 4**		**Site 5**	
	>10	>70	>10	>70	>10	>70	>10	>70	>10	>70
EBENACEAE / continued.										
Diospyros dendo	29		1		14		6		28	
Diospyros kamerunensis									1	
Diospyros mannii	2								7	
Diospyros melocarpa							6			
Diospyros piscatoria	1				2		2		7	
Diospyros polystemon	38		6		8		4		26	1
Diospyros suaveolens			7		19		1			
Diospyros viridicans	2				1		1		1	
Diospyros zenkeri					7		1		40	
Diospyros sp. LJTW 409									1	
ERYTHROXYLACEAE										
Erythroxylum mannii	1								2	
EUPHORBIACEAE										
Antidesma laciniatum	2				2				5	
Antidesma vogelianum							1			
? *Cleistanthus* sp. LJTW 546					1					
Conceveiba africana			102		210					
Crotonogyne argentea					2	5				
? *Dichostemma* sp. LJTW 288									1	
Discoglypremna caloneura	2	1					7			
Drypetes arborescens			5							
Duvigneaudia inopinata					1		7			
Grossera sp. LJTW 557					1					
Klaineanthus gaboniae			17		5				1	
Lingelsheimia sp. LJTW 127							1			
Macaranga barteri							6			
Macaranga monandra			15							
Maesobotrya cf. *pynaerti*							1			
Maprounea membranacea	17		3		1		25		8	
Mareya micrantha							3			
Mareyopsis longifolia							14			
Plagiostyles africana	3	1	12		12	1	18		3	
Sapium ellipticum	1	1								
Uapaca guineensis									1	3
Uapaca heudelotii		3		2				1	1	1
Uapaca aff. *togoensis*									1	
Uapaca sp. LJTW 612							1			
LJTW 243							2			
LJTW 255							1			

Appendix 2.1: Plant species >10 and >70 cm dbh on transects / continued.

FAMILY / SPECIES	**Number of Individuals**									
	Site 1		**Site 2**		**Site 3**		**Site 4**		**Site 5**	
	>10	>70	>10	>70	>10	>70	>10	>70	>10	>70
EUPHORBIACEAE / continued.										
LJTW 526							2			
LJTW 543					4					
LJTW 548					2					
LJTW 551					1					
LJTW 558					2					
LJTW 567									1	
FLACOURTIACEAE										
Caloncoba glauca									1	
Campostyles mannii							4		4	
Casearea barteri	5		1		1		2		1	
Homalium letestui					1				3	
Scottellia coriacea	8								23	2
Scottellia sp. LJTW 453					1					
GUTTIFERAE										
Garcinia afzelii			1		4		7			
Garcinia conrauana					4					
Garcinia smeathmannii			3		26					
Garcinia sp. LJTW 153			6		3					
Garcinia sp. LJTW 455			1							
Mammea africana				1						
Pentadesma butyracea	1		1			1			2	
Pentadesma sp. ?nov							1	1		
Symphonia globulifera			1		3		10			
HUACEAE										
Afrostylax lepidophyllus					1		2			
HUMIRIACEAE										
Sacoglottis gabonensis			6	32					2	
HYPERICACEAE										
Psorospermum tenuifolium	2									
Psorospermum sp. LJTW 431			2	1						
Psorospermum sp. LJTW 570									1	
ICACINACEAE										
Lasianthera africana							4		2	

Appendix 2.1: Plant species >10 and >70 cm dbh on transects / continued.

FAMILY / SPECIES	**Number of Individuals**									
	Site 1		**Site 2**		**Site 3**		**Site 4**		**Site 5**	
	>10	>70	>10	>70	>10	>70	>10	>70	>10	>70
IRVINGIACEAE										
Desbordesia glaucescens	3	2	22	13	15	13	12	9	5	3
Irvingia gabonensis	4	4	17	7	6	4	6	1	7	6
Irvingia grandifolia	1	3	3	3	2	1	1	1	2	2
Irvingia robor				1	1	1				
Klainedoxa gabonensis	9	8	6	3	5	14	2		20	9
Klainedoxa trilesii	1	1	5	9	1	12	3	5	7	2
IXONANTHACEAE										
Ochthocosmus cf. *sessiliflorus*			11		7					
LAURACEAE										
Beilschmeidia conjolana					3					
Beilschmiedia fulva	2				2		1			
Beilschmeidia sp. LJTW 37									2	
Beilschmeidia sp. LJTW 439			1		4		6			
Beilschmeidia sp. LJTW 537									1	
Beilschmiedia sp. LJTW 436			1							
Beilschmiedia sp. LJTW 530							6			
Beilschmiedia sp. LJTW 587			1							
Beilschmiedia sp. LJTW 588			4							
Beilschmiedia sp. LJTW 611				2						
Hypodaphnis zenkeri	18								10	
LECYTHIDACEAE										
Napoleona imperialis							3		2	
Petersianthus macrocarpus						1	4	3		
LOGANIACEAE										
Anthocleista sp. LJTW 373	2									
Anthocleista sp. LJTW 404					1					
LUXEMBURGIACEAE										
Testulea gabonensis	1	2				1	4	4	1	3
MELASTOMATACEAE										
Memecylon diluviorum			9		4					
MELIACEAE										
Carapa procera			5		3		15		5	
Entandophragma candolei								1		

Appendix 2.1: Plant species >10 and >70 cm dbh on transects / continued.

FAMILY / SPECIES	**Number of Individuals**									
	Site 1		**Site 2**		**Site 3**		**Site 4**		**Site 5**	
	>10	>70	>10	>70	>10	>70	>10	>70	>10	>70
MELIACEAE / continued.										
Entandophragma utile						1		1		
Guarea sp. LJTW 108			1		2	3				
Lovoa trichilioides				1	2	1				
Trichilia monadelpha									2	
Trichilia cf. *prieureana*	16		1						28	
Trichilia sp. LJTW 581			1							
MIMOSACEAE										
Cylicodiscus gabonensis						2	2	2		
Fillaeopsis discophora				1	1	6		1		
Newtonia leucocarpa			1	1				2		1
Parkia bicolor	1	1		1	3	2	2	1		2
Parkia filicoidea	1	1								1
Pentaclethra eetveldeana	14	4	1	4	4	2	6	3	18	3
Pentaclethra macrophylla	14	7	7	17	16	15	11	11	21	11
Piptadeniastrum africanum	1	9		3		2		4	1	6
? *Samanea leptophylla*							1	1		
Tetrapleura tetraptera	1	1							1	
MORACEAE										
Chlorophora excelsa	2	1						1	2	2
Ficus cf. *dicranostyla*		1								
Ficus recurvata										1
Treculia obovoidea					29		5			
MYRISTICACEAE										
Coelocaryon preussi					1	3	9			
Pycnanthus angolensis	4	8	2	11	1	14	3	7	3	14
Scyphocephalium ochocoa			3	31	10	31	23	43	1	3
Staudtia gabunensis			6	2	18	6	5			
Staudtia kamerunensis			1	1	21	3				
MYRTACEAE										
Syzigium sp. LJTW 31		1								
Syzigium sp. LJTW 468			1	1	4	1				
OCHNACEAE										
Lophira alata	62	21				1		2	75	24
Ouratea calophylla					1					

Appendix 2.1: Plant species >10 and >70 cm dbh on transects / continued.

FAMILY / SPECIES	**Number of Individuals**									
	Site 1		**Site 2**		**Site 3**		**Site 4**		**Site 5**	
	>10	>70	>10	>70	>10	>70	>10	>70	>10	>70
OLACACEAE										
Coula edulis			23	22	23	7	44	15		
Diogoa zenkeri			3		1					
Heisteria parvifolia	2	2	2	1	11		6	1	4	
Ongokea gore	2	4	2	3		2	2	3	1	3
Ptychopetalum petiolatum							4			
Strombosia pustulata			2				10			
Strombosia ? zenkeri			1		20		68			
Strombosia sp. LJTW 279					2					
Strombosiopsis sp. ?nov					7	9	2			
Strombosiopsis tetrandra			20		38		49		6	
PALMAE										
Elaeis guineensis	5								4	
PANDACEAE										
Centroplacus glaucinas			55		37		68		5	
Panda oleosa									1	
PAPILIONACEAE										
Milletia? saragana	1								1	
Milletia sp. LJTW 329									1	
Milletia sp. LJTW 565					1					
? *Milletia laurentii*								1		
? *Milletia* sp. LJTW 568									2	
* *Platysepalum* sp. LJTW 478									6	
Pterocarpus soyauxii	1	21		9	1	6		5	3	13
*LJTW 483			1				1			
*LJTW 484							1			
*LJTW 522								1		
*LJTW 538					2					
*LJTW 593					8					
PASSILFORACEAE										
Barteria fistulosa	12		1		5		9		14	
RHIZOPHORACEAE										
Anisophyllea sp. LJTW 524			2				2	1		
Anopyxis klaineana				3						
Cassipourea congoensis									9	
Poga oleosa						2		1		

Appendix 2.1: Plant species >10 and >70 cm dbh on transects / continued.

FAMILY / SPECIES	**Number of Individuals**									
	Site 1		**Site 2**		**Site 3**		**Site 4**		**Site 5**	
	>10	>70	>10	>70	>10	>70	>10	>70	>10	>70
RUBIACEAE										
Corynanthe mayumbensis	13		14		21		21		4	
Masularia acuminata					1					
Mitragyna ciliata	3	1					3	4	1	
Nauclea diderrichii	1	1	1				15	1		
Nauclea vanderguchtii			1	1	1			1	3	
Pauridiantha afferata	7								4	
Pauridiantha floribunda	5						3			
Pausinystalia johimbe	1		1		4					
Pavetta puberula									1	
? *Pavetta* sp. LJTW 536									2	
Porterandia cladantha	5		1		1				1	
Tricalysia sp. LJTW 559					1					
LJTW 140	2									
LJTW 387							1			
LJTW 514							1			
LJTW 528							1			
LJTW 540					1					
LJTW 550					5					
LJTW 566									1	
LJTW 571			2							
RUTACEAE										
Fagara tessmannii			1		1	1	1			
LJTW 353					1		2			
SAPINDACEAE										
Eriocoelum ?panisculatum	1									
Eriocoelum macrocarpum	4		1		3		7		23	
Eriocoelum sp. LJTW 132	1									
Eriocoelum sp. LJTW 187					1					
Eriocoelum sp. LJTW 304	1				1					
Eriocoelum sp. LJTW 544			1		1					
Ganophyllum giganteum	3	6							1	4
Lecaniodiscus cupanioides	4								1	
Pancovia floribunda			6		2					
LJTW 523				1				1		
SAPOTACEAE										
Baillonella toxisperma				1		3	1	1		1
Gambeya africana				3	1	5	1	2		
Gambeya subnuda			1		2	1	1			

Appendix 2.1: Plant species >10 and >70 cm dbh on transects / continued.

FAMILY / SPECIES	Number of Individuals									
	Site 1		Site 2		Site 3		Site 4		Site 5	
	>10	>70	>10	>70	>10	>70	>10	>70	>10	>70
SAPOTACEAE / continued.										
Letestua durissima		1								1
Manilkara fouilloyara							1	1		
Tieghemella africana						1				
LJTW 112			2							
LJTW 237		1								
LJTW 425					1		4			
LJTW 471				1						
LJTW 561					1					
LJTW 563						1				
LJTW 564						1				
LJTW 594					1					
SCYTOPETALACEAE										
Rhaptopetalum sindarense			1		4					
Scytopetalum klaineanum			11	2	4	1				
Scytopetalum sp. LJTW 227			8		10		6		6	
STERCULIACEAE										
Cola lizae	179	4			7				194	
Cola sp. LJTW 346					1		1			
Nesogordonia papaverifera				1						
Scaphopetalum blackii			12		11		4			
Sterculia tragacantha	1	1							1	
LJTW 496			1							
TILIACEAE										
Duboscia macrocarpa	1	1			4		3		1	
Grewia coriacea			20		10					
ULMACEAE										
Celtis tessmannii		4		2		1	5	7		
Celtis sp. LJTW 200					1					
Celtis sp. LJTW 444							1			
VERBENACEAE										
Vitex ? vivularis			1				1	1		
VIOLACEAE										
Rinoria sp.LJTW 457			1							
Rinoria sp. LJTW 380							3			
Rinoria sp. LJTW 440							1			

Appendix 2.1: Plant species >10 and >70 cm dbh on transects / continued.

FAMILY / SPECIES	**Number of Individuals**									
	Site 1		**Site 2**		**Site 3**		**Site 4**		**Site 5**	
	>10	>70	>10	>70	>10	>70	>10	>70	>10	>70
VIOLACEAE / continued.										
Rinorea sp. LJTW 491			1							
VITACEAE										
LJTW 482			2		1					
VOCHYSIACEAE										
Erismadelphus exsul			2	2	9	7	1	2		
FAMILY UNKNOWN										
LJTW 131							1			
LJTW 199					3					
LJTW 283					1					
LJTW 302	1									
LJTW 334					2					
LJTW 340	1	2							1	
LJTW 342		1								
LJTW 348					1					
LJTW 351					1	1				
LJTW 354					1					
LJTW 355					1					
LJTW 360					1					
LJTW 411									1	
LJTW 414									1	
LJTW 432				1						
LJTW 433										
LJTW 442							2			
LJTW 469			1							
LJTW 472				1						
LJTW 479										
LJTW 492			1							
LJTW 494				1						
LJTW 497			1							
LJTW 498			7							
LJTW 504										1
LJTW 506									1	
LJTW 507									1	1
LJTW 509								1		
*LJTW 512							4			
*LJTW 513							1			
*LJTW 515							1			

Appendix 2.1: Plant species >10 and >70 cm dbh on transects / continued.

FAMILY / SPECIES	**Number of Individuals**									
	Site 1		**Site 2**		**Site 3**		**Site 4**		**Site 5**	
	>10	>70	>10	>70	>10	>70	>10	>70	>10	>70
FAMILY UNKNOWN / continued.										
LJTW 527							1			
LJTW 532							9			
LJTW 541					1					
*LJTW 542					2					
LJTW 545					1					
LJTW 549					1					
LJTW 552					4					
LJTW 554					2					
LJTW 562						1				
LJTW 569									1	
LJTW 573			1							
LJTW 574			1							
LJTW 575			1							
LJTW 576			1							
LJTW 577			1							
LJTW 578			1							
LJTW 579			1							
LJTW 580			1							
*LJTW 584			1							
LJTW 589					3					
LJTW 590					1					
*LJTW 592					1					
*LJTW 595					1					
*LJTW 598							1			
*LJTW 600							1			
*LJTW 608	1									

* = liane

Appendix 2.2: Supplementary list of plant species collected.

FAMILY	**Species**	**Life-form**[1]	**Site**[2]
ACANTHACEAE			
	**Asystasia gangetica*	h	1
	Hypoestse verticillaris	h	1
	Justicia tenella	h	5
	Pseuderanthemum tunicatum	h	1,4
BIGNONIACEAE			
	Spathodea campanulata	t	1
CAESALPINIACEAE			
	Copaifera mildbraedii	t	4
	**Cassia mimosoides*	h	1
CELASTRACEAE			
	Salacia mayumbensis	l	4
CLUSIACEAE (GUTT)			
	Visimia guineensis	s	1
COMBRETACEAE			
	Combretum platypterum	l	1
COMMELINACEAE			
	Commelina capitata	h	1
COMPOSITAE			
	**Aspilia africana*	h	1
CONNERACEAE			
	Cnestis corniculata	l	1
	Cnestis ferruginea	t/l	1
	Jollydora duparquetiana	s	4
CONVOLVULACEAE			
	**Ipomoea blepharophylla*	h	1
CYPERACEAE			
	**Bulbostylis cf. densa*	se	1
	**Bulbostylis laniceps*	se	1
	**Fimbristylis cf. debilis*	se	1

Appendix 2.2: Supplementary list of plant species collected / continued.

FAMILY	**Species**	**Life-form**	**Site**[1]
CYPERACEAE / continued			
	* *Fimbristylis pilosa*	se	1
EUPHORBIACEAE			
	* *Euphorbia thymifolia*	h	1
	Manniophyton fulvum	l	1
	Monanthotaxis congoensis	t	1
	Uapaca vanhouttei	t	5
FABACEAE			
	Aganope impressa	l	4
FLACOURTIACEAE			
	* *Oncoba brachyanthera*	t	1
GENTIANACEAE			
	* *Neurotheca loeselioides*	h	1
GRAMINAE			
	* *Andropogon fastigiatus*	g	1
	* *Axonopus compressus*	g	1
	* *Brachiaria jubata*	g	1
	Centotheca lappacea	g	1
	* *Ctenium newtonii*	g	1
	* *Hyparrhenia diplandra*	g	1
	* *Hyparrhenia familiaris*	g	1
	Olyra latifolia	g	1
	Oplismenus hirtellus	g	1
	* *Panicum* cf. *walense*	g	1
	* *Panicum dregeanum*	g	1
	Paspalum paniculatum	g	1
	* *Pennisetum polystachyon*	g	1
	* *Perotis indica*	g	1
	* *Sporobolus pyramidalis*	g	1
	Streptogyna crinita	g	1

Appendix 2.2: Supplementary list of plant species collected / continued.

FAMILY	Species	Life-form	Site[1]
HIPPOCRATACEAE			
	Hippocratea myriantha	l	1
IXONANTHACEAE			
	Ochthocosmus congolensis	t	1
LAURACEAE			
	Ocotea gabonensis	t	4
LECYTHIDACEAE			
	Napoleona cf. *leonensis*	s/t	4
LOGANIACEAE			
	Strychnos malacoclados	l	5
MALPIGHIACEAE			
	Acridocarpus longifolius	s/t	4
MALVACEAE			
	Sida rhombifolia	h	1
MORACEAE			
	Dorstenia aff. *barteri*	h	3
	Ficus kimuenzensis	l	4
MYRTACEAE			
	Psidium guineense	s	1
OCHNACEAE			
	Ouratea cf. *myrioneura*	s	4
	Ouratea flava	l	?
OXALIDACEAE			
	* *Biophytum petersianum*	h	1
	Biophytum talbotii	h	1
PAPILIONACEAE			
	Dalhousiea africana	l	3
	* *Desmodium ramosissimum*	h	1
	* *Desmodium scorpiurus*	h	1
	* *Uraria picta*	h	1

Appendix 2.2: Supplementary list of plant species collected / continued.

FAMILY	Species	Life-form	Site[1]
PAPILIONACEAE / continued.			
	* *Zornia latifolia*	h	1
PTERIDOPHYTE			
	* *Pityrogramma calomelanos*	f	1
RUBIACEAE			
	Atractogyne gabonii	l	1,2,4
	Bertiera aethiopica	t	1
	Bertiera batesii	s	2,4
	* *Borreria latifolia*	h	1
	* *Borreria pusilla*	h	1
	Gaertnera paniculata	t	3
	Geophila afzelii	h	1
	Heinsia crinata	t	4
	Leptactina cf. *arnoldiana*	s/t	4
	* *Mitracarpus scaber*	h	1
	Mussaenda cf. *tenuiflora*	l	3
	* *Oldenlandia corymbosa*	h	1
	* *Oldenlandia lancifolia*	h	1
	Pauridiantha callicarpoides	t	2
	Pavetta hispida	s	4
	Pseudosabicea mildbraedii	h	4
	Tarenna lasiorachis	t	2
	* *Tephrosia purpurea*	h	1
	Tricalysia cf. *oligoneura*	s	1
	Tricalysia cf. *pallens*	s	5
	Trichostachys aurea	h	5
RUTACEAE			
	Vepris cf. *louisii*	t	5
SAPINDACEAE			
	Allophyllus ? ayemensis	s	2

Appendix 2.2: Supplementary list of plant species collected / continued.

FAMILY	**Species**	**Life-form**	**Site**[1]
SAPINDACEAE / continued.			
	Blighia welwitschii	t	1
SIMAROUBACEAE			
	Quassia africana	s	2,3
SOLANACEAE			
	* *Schwenckia americana*	h	1
THYMELACEAE			
	Dicranolepis buchholzii	s	4
TILIACEAE			
	Triumfetta cordifolia	s	1
VERBENACEAE			
	Vitex doniana	t	1,4
VIOLACEAE			
	* *Hybanthus enneaspermus*	h	1
VITACEAE			
	Cissus aff. *barteri*	l	4
	Cissus dinklagei	l	1
	Cissus ruginosicarpa	l	2

* = collected in savanna adjacent to Site 1.

[1] - t = tree; s = shrub; h = herb; l = liane; g = grass; f = fern; se = sedge.

[1] - site from which fertile collections were obtained - species are not necessarily restricted to this site.