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STRUCTURAL AND BIOGEOGRAPHICAL PATTERNS OF VEGETATION IN EQUATORIAL SUDAN
I. TERRESTRIAL COMMUNITIES

A. Guillet[1] and E. J. Moll[2]

1 FitzPatrick Institute, University of Cape Town; and Faculty of General Agriculture, University College Dublin, Belfield, Dublin 4, Ireland
2 Department of Botany, University of Cape Town, Republic of South Africa

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Abstract. The floristic and structural intricacies of a catenary-mosaic vegetation complex in the south-west of the Sudan are investigated numerically. The vegetation of the area is not characterized simply by that of individual species, vegetation types or growth forms, but rather by different combinations of these. Even virtually ubiquitous and/or well distributed species change in dominance, growth form and associates through the study area. This complex of vegetation features is repetitive and helps to identify community types. Their distribution patterns divide the study area into major phytogeographical zones and elucidate environmental gradients. In turn, these last are primarily determined by soil type and topography (texture, depth, drainage) rather than merely climate. A northeasterly trend can be recognised from the more mesic - eluvial/colluvial soil associated - equatorial forest edges to drier - illuvial soil associated - lowland open grasslands. Perhaps, two vegetation types (Closed Woodland and Thicket) tend to dilute towards the north, however, no apparent subtraction effect with increasing latitude has been detected for major/dominant species. Conversely, although the woodland dominates overall, the bush to tree cover ratio increases in a northerly direction. In the north, the successional stages of major communities reflect 'fire pro-climax' equilibria. Only isolated relict southern mesic species survive in localised, *e.g.* riverine, strips. Otherwise these communities derive from persistent remnants of local associations primarily made of xeric species coping with fire and/or other man induced transformations. In the south, community successional position is more often mediated by the establishment of pioneer northern species.

Introduction

The typical vegetation of the equatorial Sudan is generally ascribed to the savanna-woodland mosaic complex (Harrison and Jackson 1958). In this region the vegetation and soils form catenary patterns reflecting the repetitive local patterns of topography. Morison et al. (1948) describe the structural and floristic complexity of this vegetation in relation to localised variation of the biotic (*e.g.*, termitaria) and abiotic (*e.g.*, topography, soil type, climate) environment. However, no previous study has attempted a structural classification on a numerical basis of the catenary-mosaic vegetation complex and its relationships with the environment. This study attempts to quantify structural features of the equatorial vegetation and relate them to the local environment.

Although the climate and geomorphology change little and gradually within the region, the complexities of the vegetation mosaic disguise some well-defined biotic zonations. For example the pattern of distribution of larger mammalian herbivores shows definite trends (Mackenzie 1954, A. Guillet unpubl.). Therefore this study also attempts a more detailed analysis of White's (1983) broad scale biogeographical zones.

Smith (1949) finds that there are apparent anomalies in vegetation distribution across wide spans of given climatic factors (*e.g.*, rainfall), in the Sudan's tropics. In this region, for example, northern dry area species persist in the relatively more mesic south. The same author also suggests that this trend is not explained by plant 'versatility', but by a combination of factors controlling soil moisture (rainfall and soil texture). Therefore the present finer-grained biogeographical investigations within the relatively minor equatorial climatic span could also provide a test of Smith's (1949) hypothesis, and identify zonal boundaries reflecting major ecological factors behind vegetation distribution in the southern Sudan.

Although the overall equilibrium of the natural vegetation in the southern Sudan, as we presently know it, reflects a long-term contribution of human influence (*e.g.*, Chipp 1930, Tothill 1948, White 1983), the 'natural' vegetation of the equatorial areas is relatively well conserved because it falls within the spread range of the tse-tse fly (Bloss 1945) which limited the distribution of cattle from the north (Tothill 1948). Moreover, political turmoil spanning more than a decade has resulted in the deterioration of the existing poor road system in the region and contributed to its inaccessibility. This particularly applies to the area set aside for this study, which encompasses the Southern National Park, a territory selected for its potential as a nature reserve and relatively low competition with human utilisation.

The primary objectives of this study are to identify major terrestrial vegetation communities (excluding those of rocky outcrops) and describe their physiognomic characteristics; to analyse these communities in the context of comparable studies elsewhere in Africa and of their general distribution in the equatorial Sudan; and to discuss riverine communities only in comparison with other vegetation types.

Study area

The study area lies primarily in the West-Equatoria Province (Southern Sudan) with, in the north, small parts falling within the Bahr al Ghazal and Lakes Provinces (Fig. 1a). This area comprises part of the 'Main Tributary-River Region' (Morison *et al.* 1948) *i.e.* in the western catchment of the upper Bahr al Jebel (White Nile) system, between the 'Watershed Region' in the south west and the 'Flood-Plain Region' in the northeast (ibid.).

The general topography is characterized by a gently undulating peneplain dissected by shallow river valleys; the ironstone plateau slopes gradually from ca. 800 m a.s.l. on the Nile-Congo watershed to ca. 400 m a.s.l. in the flood-plain region. Only local rock outcrops of the Basement Complex and major river beds disrupt this gentle topography.

Hydrographically the area falls within the southern section of the catchment of the Bahr al Ghazal and includes its northward-flowing major tributaries. In the south these are fed by a multitude of small perennial streams, which expand northwards into wider valleys and eventually merge with the flood plains between the Bahr al Ghazal and Bahr al Jebel systems (Hurst and Phillips 1931).

Climatically the area is characterized by a marked contrast between the pronounced desiccating effect of the dry season alternating with the heavy rains of the wet season; mean annual rainfall is 1100 to 1500 mm, and mean annual temperature ranges from a minimum of 27 °C to a maximum of 34 °C (Thompson 1965, Mahdi Amin el-Tom 1975). Phytogeographically this zone is part of the 'Sudanian Region' (White 1983) and is mapped by him as a band of the 'sudanian woodland with abundant Isoberlinia' enclosed between the

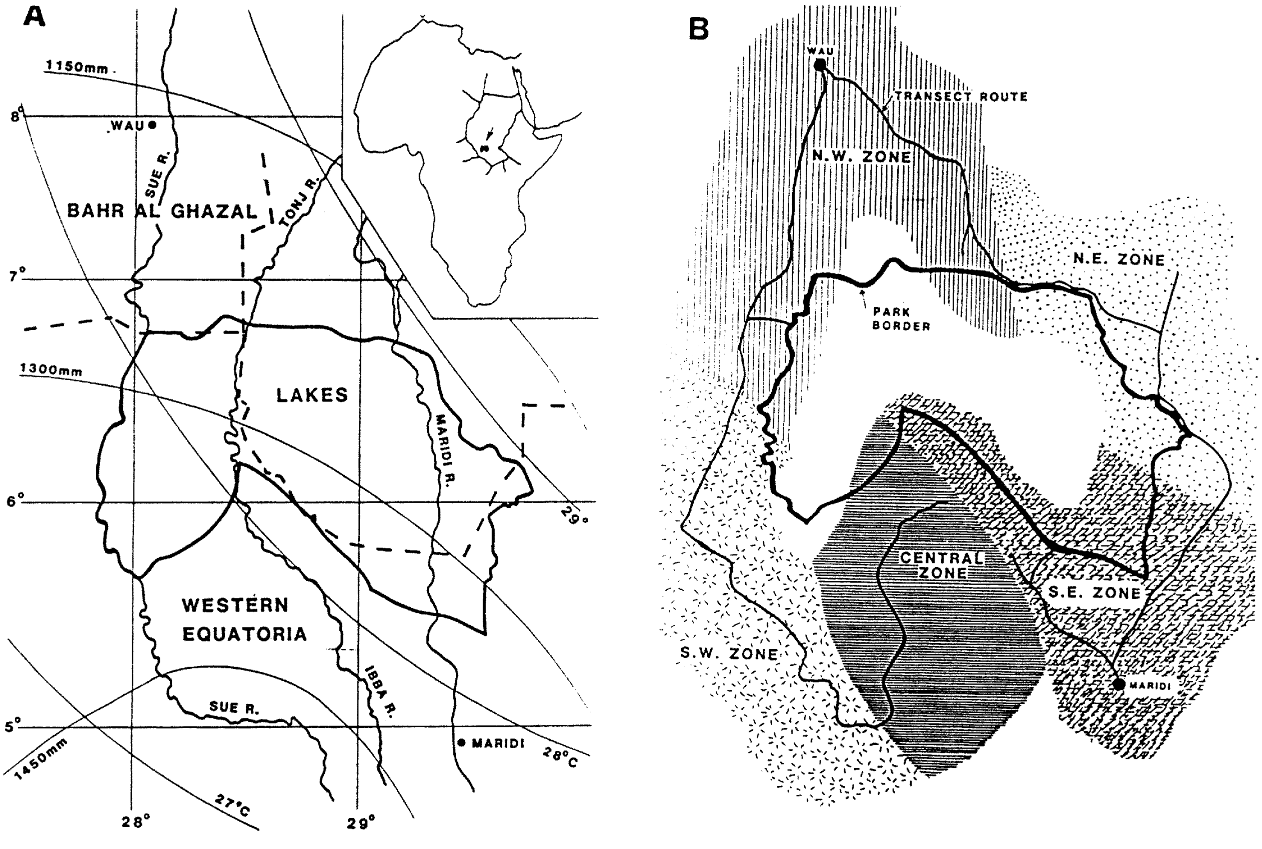

Figure 1. A: Location of the study area in the Sudan (inset); the location of the major river systems (~); the boundaries of the administrative provinces (- - -); the border of the Southern National Park (——) (see also B); and the mean annual rainfall and temperature isograms. B: The boundaries of the Southern National Park in relation to the phytogeographical zones delimited from the 1705 plots recorded on the transect route.

Guineo-Congolian 'mosaic of lowland rainforest and secondary grassland' towards the Zairean southern border, and the 'edaphic grassland of the Upper Nile' in the north.

Methods

Data collection

Observations were carried out during two field surveys for the Master Plan Programme of the Southern National Park during February-March 1980, and November-January 1980-81. Data were collected along a transect which roughly followed the boundaries of the Park (Fig. 1b). Relative cover values as well as the physiognomic type of dominant species were recorded at 1750 sites along the circuit. Approximately one observation per kilometer was made. The poor road through the study area, and the pattern of the catenary-mosaic vegetation (Milne 1935) hindered both random sampling and sampling at exact intervals. Data from a comprehensive aerial survey (methods in Boitani 1981) were used to achieve relative estimates of area covered by major vegetation types, as evaluated in the ground survey, and to quantify the overall relationships between grassy and woody vegetation. This is particularly relevant to cover descriptions of woody/non-woody relationships since (see *e.g.* the section on 'Open Vegetation type') our quantifications focus on patches of wooded vegetation. Patches of 'open' grassland were observed in a less regular manner because they were structurally and floristically simple. Vegetation types analysed comprised a modification of Pratt & Gwynne's (1978) categories: Riverine Communities, Open Vegetation, Grass-bushland, Grass-woodland, Closed Woodland, Thicket. Physiognomic forms analysed included: Grass, Bush, Tree.

Scientific nomenclature follows Andrews (1950-1956). At least one sample of each plant species was collected and identified at the Tropical Herbarium of Florence and/or Kew. The local vernacular names were obtained *in situ* from conservation officers. In the text these vernacular names have been used where the scientific names could not be obtained due to spoilage of specimens in transit.

When available, additional information on the plant-soil relationships as given by Morison *et al.* (1948) were collected to interpret species combinations in the communities identified.

Numerical methods

Both floristic and structural data were classified using two-way indicator species analysis (TWINSPAN, Hill 1979a). Data were ordinated using detrended correspondence analysis (DECORANA, Hill 1979b). The ordination plot of samples according to DECORANA sets of pairs of axes was studied to investigate inter-group relationships as well as to obtain a picture of possible vegetation/environmental interactions. Moreover, a program (P2R) of the BMDP series (Dixon 1983) was used to test DECORANA axes and their relative cover scores of each plant species in correlation analyses with climatic data. These included variables with the highest geographical variation over the study area, and for which published information was readily available (February mean temperature, and mean annual rainfall). Due to the repetitive complex pattern typical of the equatorial catenary-mosaic (Morison *et al.* 1948), different physiognomic vegetation types (Pratt and Gwynne 1978) might include plant groups characterized by similar, if not identical, species clusters which may vary only in combinations of dominance and/or form of the same species. The inherent risk of obscuring geographical variation in a floristic analysis based on all types combined was checked by performing separate analyses for each vegetation type in addition to that for all types combined. Complementary results of analyses of all floristic and structural types combined, and those of individual vegetation types, are discussed.

Results and discussion

Floristic taxa identified included 128 species. Of these, *Zenkerella* cf. *grotei* is a new species for the Sudan. Albeit with different patterns of dominance and association, identified species are all shared with other regions in the equatorial/sub-tropical realm, mainly to the west (Hall and Jenik 1968, Kershaw 1968, Lawson *et al.* 1968, Ramsay and de Leeuw 1965, Sillans 1958), but also to the south (Eggeling and Dale 1952, Langdale-Brown *et al.* 1964).

The TWINSPAN classification results in a very heterogeneous dendrogram in which branching appears to reflect differences in dominance rather than floristic "exclusiveness". The major species are widespread within dendrogram clusters albeit with different cover values; this could be a reflection of their wide ecological tolerance (White 1983) as suggested by their widespread distribution within the study area (Table 1a). This general trend of widespread species distributions in the catenary-mosaic complexities is also reflected by an absence of significant correlations between abundance values of individual species and climatic variables. On the other hand, significant correlations between axes from a DECORANA floristic ordination for all plots combined, and climatic variables (mean annual rainfall: $r = 0.37$, $P < 0.001$; February temperature: $r = -0.33$, $P < 0.001$) might reflect a tendency for plots to be ordinated along climatic gradients. Moreover, plots scatter according to vegetation types and, to a certain extent, also to geographical position (see below, section on relationships between vegetation types, and Fig. 2). Results of the TWINSPAN classification show good agreement

Table 1. List of major species, their percentage frequency within the study area as a whole, divided into the four cardinal sections, and according to vegetation types modified from Pratt and Gwynne (1978).

		A				B			
	Entire study area*	Cardinal sections				Vegetation types**			
		N	E	S	W	OV	GB	GW	CWT
Grewia mollis	37.6	46	53	25	23	20	56	46	19
Anogeissus leiocarpus	34.5	41	38	35	26	19	28	45	38
Combretum fragrans	21.3	26	18	14	26	38	29	19	21
Combretum collinum	20.4	21	29	19	11	21	29	20	12
Hymenocardia acida	19.9	23	16	15	28	19	31	17	26
Isoberlinia doka	19.7	20	16	19	6	16	6	36	13
Butyrospermum paradoxum	18.8	28	21	5	18	19	21	24	8
Terminalia 'Tabu'	18.1	20	15	15	22	27	26	16	15
Piliostigma thonningi	10.7	11	9	10	22	8	16	11	13
Hyparrhenia 'Kitipki'	10.2	9	6	12	28	20	12	9	2
Prosopis africana	9.4	11	6	7	11	11	12	10	12
Hyparrhenia 'Bagau'	7.4	3	5	13	18	8	9	7	-
Vitex doniana	6.8	5	8	9	13	2	7	6	8
Terminalia avicennoides	6.7	3	6	12	11	6	5	6	8
Khaya senegalensis	6.5	10	8	2	10	5	4	9	13
Bridelia micrantha	6.0	8	5	5	20	2	5	8	1

* Cut off point is 5%

** OV: Open vegetation, GB: Grass bushland, GW: Grass woodland, CWT: Closed woodland and thicket

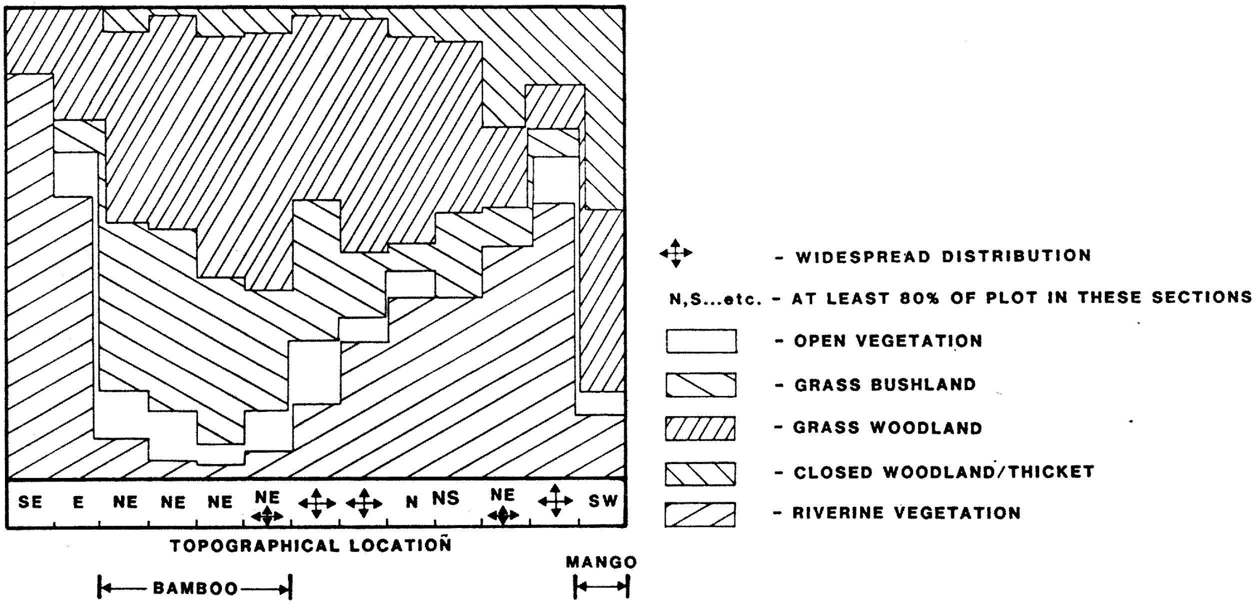

Figure 2. Schematic representation of relative contribution of vegetation types to groups of plots along a pair of DECORANA axes (all 1705 plots) indicating their relationship to topographical location and the distribution of Bamboo and Mango communities.

and suggest that similar groups of biotic and/or abiotic synergs are reflected by the two independent approaches. Comparing individual TWINSPAN dendrogram branches in terms of the contributions of vegetation types (Fig. 3a) and that of vegetation form (Fig. 3b), shows that the major TWINSPAN branches reflect differences in vegetation types and forms. As with taxa, these are differences in dominance and not in exclusiveness; however, branching relationships are more readily distinguished here than on a mere floristic basis. This might suggest that although vegetation types and forms, like taxa, are widespread throughout the study

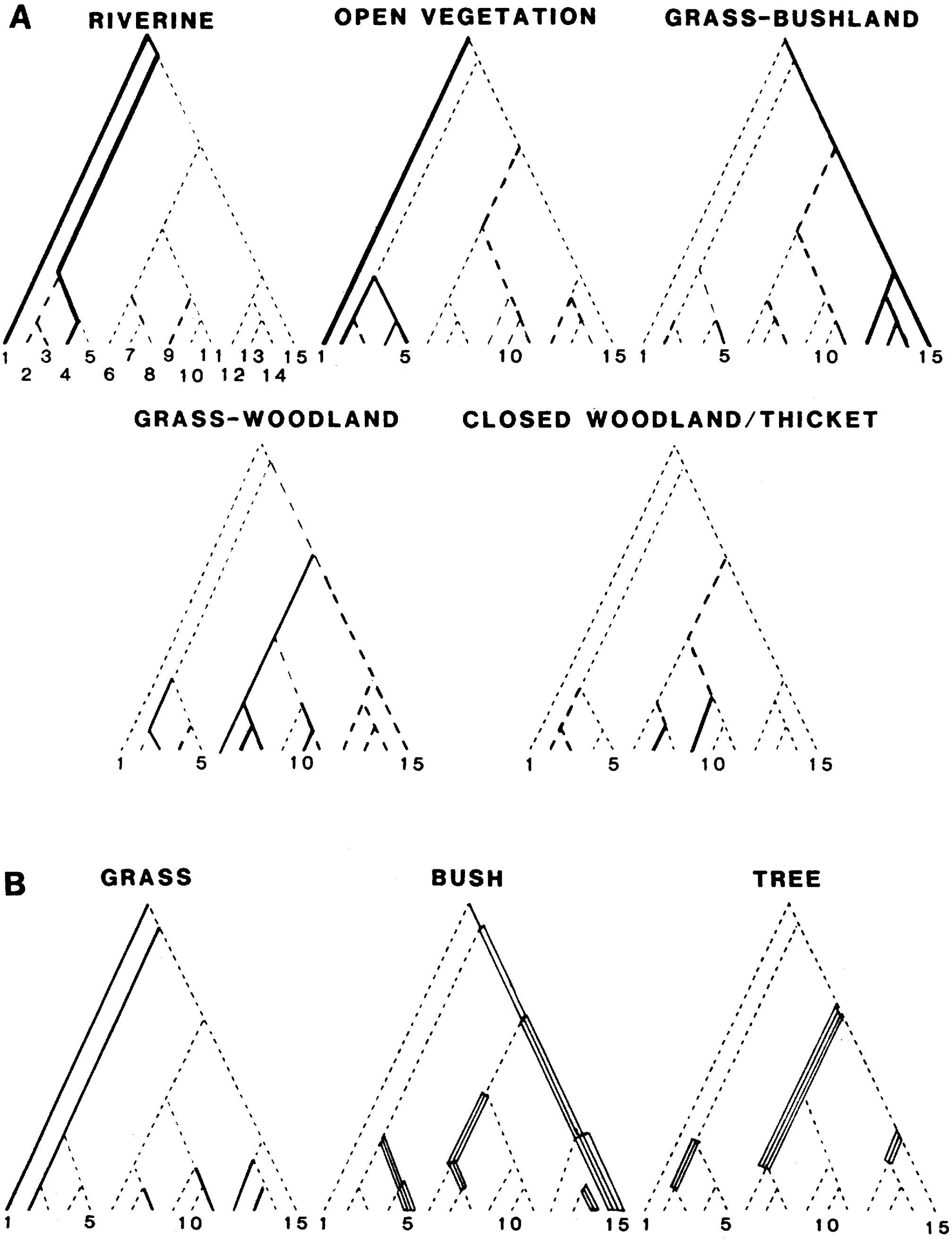

Figure 3. Highly synthesized and compressed dendrograms as given by the TWINSPAN classification of the 1705 plots. A: Proportional contribution of the different vegetation types: (——) more than, (- - -) same as, and (. . .) less than predicted, when compared to the 1705 plots as a whole. B: The relative dominance of vegetation forms is indicated by the number of lines.

area, their distribution pattern is modelled according to partitions identifiable in the clusters of taxa. As supported by differences in the contribution of major species to different vegetation types (Table 1b), it appears that the explanatory contribution and potential of a floristic classification is better achieved when characterizing differences within vegetation types. Consistently, in the TWINSPAN classification of floristic data for each vegetation type, we can identify differences within each type in relationship to their characteristic taxonomic communities. Recognized communities are discussed below, in relationship to their more typical cover in terms of various vegetation growth forms (grass, bush, tree).

Vegetation types

In the present classification, taxa are defined as "characteristic" of a given vegetation type (Table 2) if they are: a) a TWINSPAN 'indicator' species, *i.e.,* if they are widespread and/or dominant within, and therefore characterize a cluster of plots, but also b) a TWINSPAN 'non preferential' species when equally well represented within, although not exclusive to a cluster, *i.e.,* not characterizing one cluster from the other within non-relevant branching pairs, but characteristic relative to clusters selected at different branching levels.

The genus *Hyparrhenia* is the main grass taxon and occurs virtually throughout the study area, but it is only mentioned in the text when it is diagnostic for a particular community type.

Cover-dominance position for each vegetation form here refers to the respective cumulative total values of cover. Therefore, a vegetation form may be classed as typically 'dominant' within a given community, if it is widespread and/or frequently dominant within its respective cluster of plots.

In addition to providing crude total cover values we specify whether a vegetation form is dominant overall because it is more widespread or because it is more frequently dominant, in those instances when these two contributions are not equally responsible for the achieved cover score.

Cover descriptions are only given for sub-communities when their ratios are significantly different from those of their mother community.

Communities that occur less frequently are undersampled relative to others. However, all communities studied were common and therefore characteristic taxa are considered representative of 'true' communities. The management usability of their cover quantifications is however limited because it is based on a reduced number of samples, and is provided here mainly as a reference for further study.

Excluding Closed Woodland and Thicket which are by definition composed almost entirely of woody plants, the grass to tree cover ratio approaches the mean of ca 23% for all vegetation types, with only a few significant exceptions within vegetation types. The bush to tree cover ratio is instead much more variable, not only and obviously between, but also within vegetation types.

Open Vegetation. This category includes patches of more wooded vegetation within Pratt & Gwynne's (1978) bush/wooded grassland vegetation type. Our definition comprises relatively sparse (low density) woody vegetation, sometimes fringing and/or intercalating with (but excluding) pure'grassland' such as those embanked riverine 'opens' and/or relatively broad, seasonally waterlogged valleys or 'dambos'. This vegetation type is characterized by *Combretum* communities, and is prevalent in the northern and central zones (NW, NE and CENT). That is the area excluding the cooler, more mesic section. However, field observations indicate that the low density cover of this type is more frequently associated with, and therefore possibly reflects, localized patches of stressed environment (*e.g.* eroded soils), soil depth and topography rather than any particular climatic zone. For example, in the northwestern zone (NW) Open Vegetation, unlike Mixed Thicket (see (iii) below), often comprises species associated with short period fallow areas (White 1983) including *Anogeissus leiocarpus, Terminalia avicennoides, Nauclea latifolia,* 'degbe', *Gardenia ternifolia* and *Terminalia* 'tabu'. The woody vegetation cover is then typified by a 300% bush to tree cover ratio; bush being both generally dominant and widespread. Grass accounts for 10% of the total vegetation cover.

Two major associations of Open Vegetation are here identified with the help of TWINSPAN classification: the *Combretum fragrans, Canthium crassum* community primarily associated with shallow/coarse soils, and the *Combretum collinum* subsp. *binderianum, Anogeissus leiocarpus* community mainly associated with deeper and/or less drained soils (Table 2a-b).

Grass-bushland. Floristically, the TWINSPAN clustering helped to identify three principle Grass-bushland communities: the *Combretum collinum* subsp. *binderianum*; the *Butyrospermum, Terminalia* and *Combretum fragrans*; and the *Hymenocardia, Canthium, Terminalia* and *Hyparrhenia* communities (Table 3c-d).

Grass-woodland. The TWINSPAN floristic classification helped distinguish three major clusters of Grass-woodland association, the *Terminalia, Isoberlinia* and *Anogeissus* communities (Table 2e-f).

Closed Woodland and Thicket. This vegetation type is more common in the western and central areas (NW, SW, CENT Zones) and less common in eastern areas especially to the south. Three major divisions are identified within these vegetation types with the help of TWINSPAN: *Mangifera indica* copses, *Oxytenanthera abyssinica* brakes and *Hymenocardia, Anogeissus, Combretum* and *Grewia* mixed thickets.

Table 2. TWINSPAN classification of four major vegetation types, characteristic taxa in descending order of cover dominance, relative contribution of vegetation growth form, typical soil type association and biogeographical zone. Semicolons separate groups of species with larger dominance differences. Vegetation type labels: OV=open vegetation; GB=grass-bushland; GW=grass-woodland; CW-T=Closed Woodland-Thicket. After labels the division number of TWINSPAN dendrogram branches and the number of plots are indicated.

a	(OV 40, 39 plots)	(OV 20, 71 plots)	(OV 41, 32 plots)	(OV 82, 15 plots)	(OV 83, 17 plots)
	Combretum fragrans; *Canthium crassum* *Isoberlinia acida* *Hymenocardia acida* *Prosopis africana*	*Combretum fragrans;* *Terminalia 'tabu'* *Canthium crassum* *Hyparrhenia 'kitipki'* *Hymenocardia acida* *Butyrosp. paradoxum*	*Terminalia* 'tabu' *Hyparrhenia* 'kitipki' *Butyrospermum paradoxum;* *Hymenocardia acida* *Canthium crassum* *Piliostigma thonningii*	*Butyrospermum paradoxum* *Canthium crassum* *Piliostigma thonningii* *Hymenocardia acida;* *Lophira alata*	*Hyparrhenia* 'bagau' *Combretum collinum subsp. binderianum*
bush to tree cover ratio	119%	129%		158%	129%
grass to total cover ratio	22%			31%	49%
widespread	B=G>T	T=B		T>B	G>B=T
dominant	T>B=G	B>T		G>B>T	G>B=T
eluvial soils	shallow +		shallow		
colluvial soils			coarse (patches)	coarse + +	
illuvial soils					poorly drained
zone	NW			NW and NE	CENT

+with localized patches of deeper soils

+ + at the bottom of steeper areas

b	(OV 21, 23 plots)	(OV 84, 15 plots)	(OV 85, 5 plots)	(OV 11, 6 plots)
	Combretum collinum ssp. binderianum *Anogeissus leiocarpus* *Grewia mollis* *Canthium crassum*	*Combretum collinum ssp. binderianum* *Grewia mollis* *Canthium crassum;* *Anogeissus leiocarpus* 'bafukuyu' *Khaya senegalensis* *Butyrosp. paradoxum*	*Anogeissus leiocarpus* *Isoberlinia doka;* *Combretum collinum ssp. binderianum* *Zenkerella grotei* *Hyparrhenia* 'bagau' *Parinari curatellifolia* *Afzelia quanzensis* *Saba florida* (syn. *Landolophiac omorensis)* *Prosopis africana*	*Combretum collinum ssp. binderianum* *Blighia unijugata* *Albizia sp.* *Ritchieia sp.*
bush to tree cover ratio	112%	114%	43%	188%
grass to total cover ratio	22%	25%	17%	17%
widespread	(B>T)=G	G=B>T	T>B	(T=B)>G
dominant	T>B>G	T=B>G	T>B=G	(T=B)=G
eluvial soils			deep + +	
colluvial soils				
illuvial soils		impeded +		
zone		NE	NW	SE (in poorly drained soils)

+ locally discontinued by better drained patches (*e.g.*, large terminate mounds)

+ + with patches of more abrupt slopes of the eluvial-colluvial transition at the edges of the eluvial mosaic

c	(GB 5, 168 plots) *Grewia mollis;* *Butyrospermum paradoxum* *Anogeissus leiocarpus* *Terminalia* 'tabu' *Combretum fragrans* *Hymenocardia acida;* *Piliostigma thonningii;* *Canthium crassum;* *Prosopis africana*	(GB 41, 36 plots) *Grewia mollis* *Terminalia* 'tabu' *Anogeissus leiocarpus;* *Combretum fragrans* *Butyrospermum paradoxum* *Canthium crassum*	(GB 43, 14 plots) *Combretum collinum* ssp. *binderianum* *Terminalia* 'tabu' *Grewia mollis;* *Butyrospermum paradoxum* *Piliostigma thonningii* *Entada africana* *Hymenocardia acida*	(GB 42, 45 plots) *Grewia mollis* *Butyrospermum paradoxum;* *Combretum fragrans* *Prosopis africana* *Terminalia* 'tabu'; *Hymenocardia acida,* *Gardenia ternifolia*	(GB 40, 34 plots) *Grewia mollis* *Piliostigma thonningii;* *Combretum fragrans* *Butyrospermum paradoxum;* *Acacia hockii* *Hyparrhenia* 'kitipki' *Bridelia micrantha*	(GB 11, 39 plots) *Grewia mollis* *Hymenocardia acida* *Anogeissus leiocarpus;* *Combretum fragrans* *Isoberlinia doka;* *Butyrospermum paradoxum*
bush to tree cover ratio	131%	68%	151%	119%	235%	178%
grass to total cover ratio	21%	19%	21%	19%	23%	30%
widespread		B=T		B=T	B>T	
dominant					B>T	B>T
eluvial soils		often shallow		deeper, eroded patches	coarse grained +	shallow, coarse ++
colluvial soils		coarse	transition	coarse		
illuvial soils						
zone		NE	NE	NE and NW	NW and SE	NE

+ where the narrowness of ridges allow species characteristic of well-drained sites to grow next to species typical of impeded areas.

+ + with deeper patches

d	(GB 19, 49 plots) *Canthium crassum* *Combretum fragrans;* 'bafukuyu' *Terminalia* 'tabu'	(GB 4, 94 plots) *Combretum collinum* subsp. *binderianum;* *Grewia mollis* *Combretum fragrans* *Anogeissus leiocarpus;* *Canthium crassum*	(GB 18, 44 plots) *Anogeissus leiocarpus*	(GB 6, 60 plots) *Hymenocardia acida* *Canthium crassum;* *Terminalia* 'tabu' *Grewia mollis;* *Prosopis africana* *Piliostigma thonningii*	(GB 3, 89 plots) *Hymenocardia acida;* *Canthium crassum* *Hyparrhenia* 'kitipki' and/or *Hyparrhenia* 'bagau' *Terminalia* 'tabu' *Prosopis africana*	(GB 7, 29 plots) *Hyparrhenia* 'bagau' *Hyparrhenia sp.* *Hyparrhenia* 'kitipki'; *Hymenocardia acida* *Vitex doniana* *Combretum fragrans* *Annona senegalensis* *Prosopis africana;* *Lophira alata* *Afzelia quanzensis*
bush to tree cover ratio		200%		199%	167%	105%
grass to total cover ratio		21%		23%	30%	42%
widespread		B>T		B>T	G>(B>T)	(B>T)=G
dominant				B>T	B>T=G	B=T
eluvial soils	shallow	eroded patches	deeper			
colluvial soils						
illuvial soils		poorly drained				
zone	NE	NE and SE	SE	SW +		SW and CENT

+ primarily to the northeast of the Zone, *i.e.*, out of the relatively higher rainfall, lower temperature area

e	(GW 40, 62 plots) *Terminalia* 'tabu' *Hyparrhenia* 'kitipki'; *Lophira alata* *Isoberlinia doka* *Annona senegalensis* *Hymenocardia acida*	(GW 659, 81 plots) *Isoberlinia doka* *Grewia mollis* *Hymenocardia acida*	(GW 41, 316 plots) *Isoberlinia doka* *Grewia mollis* *Butyrospermum paradoxum;* *Anogeissus leiocarpus* *Combretum fragrans* *Hymenocardia acida*	(GW 165, 133 plots) *Grewia mollis* *Butyrospermum paradoxum;* *Anogeissus leiocarpus* *Terminalia* 'tabu'; *Zenkerella grotei* *Prosopis africana;* *Bridelia micrantha*
bush to tree cover ratio	52%	77%		75%
grass to total cover ratio	28%	18%		16%
widespread	B (scattered)	T=B=G		T>B
dominant		T>B		T>B
eluvial soils	} transition	} transition		shallow and patches of deep
colluvial soils				coarse
illuvial soils				
zone	NW, CENT and SE	NW and SE	NE	NW and NE

+ with pockets of shallow, eroded soils

f	(GW 42, 132 plots) *Anogeissus leiocarpus* *Grewia mollis* *Combretum collinum* ssp. *binderianum* *Khaya senegalensis*	(GW 84, 72 plots) *Anogeissus leiocarpus* *Combretum collinum ssp. binderianum* *Grewia mollis* *Khaya senegalensis;* *Butyrosp. paradoxum* *Canthioum crassum* *Manniophyton fulvum* (syn. *M. africanum)* *Zenkerella grotei* *Hymenocardia acida*	(GW 43, 10 plots) *Fluggea microcarpa* *Albizia sericocephala* *Ficus* 'ndairoko' *Anogeissus leiocarpus*	(GW 171, 19 plots) *Anogeissus leiocarpus* *Combretum collinum ssp. binderianum;* *Hyparrhenia* 'bagau' *Terminalia avicennoides* *Hymenocardia* 'kitipki' *Piliostigma thonningii*
bush to tree cover ratio				
grass to total cover ratio	22%			33%
widespread	T>B			G>T>B
dominant	T=B			
eluvial soils	deep		deep	
colluvial soils				
illuvial soils				poorly drained
zone	NE	NE	SE	SW

g	(CW-T 18, 10 plots) *Piliostigma thonningii* *Butyrospermum paradoxum* *Terminalia* 'tabu'; *Hymenocardia acida* *Manniophyton fulvum* (syn. *M. africanum*) ++ *Terminalia avicennoides*++ *Parinaria curatellifolia* ++ 'ngbingzakukiri' ++ *Isoberlinia doka* ++ *Khaya senegalensis* ++	(CW-T 4, 31 plots) *Hymenocardia acida;* *Combretum fragrans* *Anogeissus leiocarpus* *Grewia mollis;* *Terminalia* 'tabu' *Khaya senegalensis* *Piliostigma thonningii*	(CW-T 19, 18 plots) *Hymenocardia acida* *Combretum fragrans* *Anogeissus leiocarpus* *Grewia mollis;* *Combretum collinum* ssp. *binderianum* + *Canthium crassum* + *Khaya senegalensis* + *Prosopis africana* +	(CW-T 21, 8 plots) *Anogeissus leiocarpus* *Irvingia smithii* *Parinari curatellifolia* *Maytenus senegalensis* *Afzelia quanzensis* 'ngbiringbiri' *Vitex doniana*
bush to tree cover ratio	117%		87%	32%
grass to total cover ratio	16%		9%	0%
widespread	B=T		T=B	T>B
dominant	B>T		T>B	T>B
eluvial soils	++ in } transition		shallow, eroded (+ in deeper patches)	deep
colluvial soils				
illuvial soils				
zone	NW		NE and CENT	SW and CENT

(i) Mango *(Mangifera indica)* Copse

This community occurs as virtually pure stands in the CENT and SW zones where Mango trees were planted along major district roads. It is likely that dispersal from these areas was facilitated by wildlife, mainly elephants, sometimes resulting in large patches. These copses are more common in the southwestern areas where they can be considered to be true 'forests': more than 35 m high, with crown diameters of ca. 6 m which form an inter-individual continuum. Several individuals have zero branching height with small branching angles. The distance between the bases of the trees is ca. 2 m. The only other species occurring in these Mango forests are climbers (*e.g.* 'abakpa', *Combretum aculeatum,* 'mere', *Saba florida*, mostly with broad leaves and thin, branching stems which often creep horizontally. On the other hand, several bush and tree species may intermix with sparser or isolated Mangoes which are often found at the edges or away from patches of pure stands. Common species include *Terminalia avicennoides, Ficus* 'ndairodo', *Anogeissus leiocarpus, Irvingia smithii, Hymenocardia acida,* 'gbutunga'. The distance between individual Mangoes is larger and their crowns often do not touch. The individual trees usually have a greater branching degree and branching height (2 m) and their almost horizontally spreading crowns are ca. 25 m in diameter. They reach 25-30 m height and have grass and forbs rather than climbers as a non-woody understorey. The cover of mixed Mango consociations is two-thirds trees and one-third bush, usually of only one to a few species at any single location.

(ii) Bamboo *(Oxytenanthera abyssinica)* 'Brake'

The bamboo 'brake' typically characterizes the colluvial soil complex. It also occurs in shallow eroded eluvial soils (*e.g. Hymenocardia acida* dominated, but then less frequently and/or only locally. As also indicated by results of the DECORANA ordination (see above, and Fig. 2), this community is restricted to northern zones of which more than 60% refers to the NE Zone. Species with which it is more often associated include *Anogeissuss leiocarpus, Grewia mollis* and *Isoberlinia doka* or *Khaya senegalensis, Butyrospermum paradoxum; Zenkerella grotei* and *Canthium crassum*, in the northeast; *Isoberlinia doka* and/or *Anogeissus leiocarpus* with *Prosopis africana, Zenkerella grotei, Terminalia* 'tabu', *Combretum fragrans, Hymenocardia acida, Terminalia avicennoides* and *Khaya senegalensis* are more common associates in the northwest.

This species composition of associates is remarkably close to that of major central African dry forest types, *e.g.* the 'Isoberlinia dense dry forest' of which *Oxytenanthera* sp. is a typical understorey species (Sillans 1954). This would suggest that, as in central Africa (Sillans 1954), the equatorial Sudan bamboo brake formations could be derived from these dry forest types.

The woody vegetation cover, when bamboo is in association with other species, is typified by a 93% bush to tree cover ratio; the two forms being equally widespread and as frequently dominant, with neither grass nor forbs recorded.

(iii) Mixed Thicket

A part of this community type includes patches of impenetrably thick, medium height, structurally uniform and species-rich woody assemblages which have frequently been observed where evidence was available of past fires and/or long-abandoned cultivation areas ('bush fallow' sensu White 1983). These may represent successional phases of woody establishment, contrasting markedly with 'open' areas on degraded soils and/or regrowth areas of 'short period fallows' which are instead typified by rather homogeneous although dense, shorter and species-poor communities. These are usually dominated by single fire-adapted species such as *Combretum* spp. (see *'Open Vegetation'*, above).

Two major Mixed Thicket communities are recognised: the Northern and the Southern Mixed Thicket (Table 2g).

General vegetation distribution pattern

Both TWINSPAN analyses, that for all plots combined and that for separate vegetation types, divide the study transect into similar sections. This was inferred by labelling each plot according to its geographical location and finding that (as for results of the DECORANA ordination of all plots combined, Fig. 2) clusters generally had at least 80% of plots belonging to one or the other geographical section. Therefore, to describe the contribution of each cluster community to the definition of botanical/ecological zones, each cluster community has also been described in relation to the geographical distribution of the majority (>80%) of its plots (Table 2). While plant communities define their boundaries, and therefore characterize these zones, only few taxa do so, for example by being virtually confined to and well distributed within the zone (*e.g. Entada africana* in the warmer, more xeric NE zone); or by 'default' sensu Guillet and Crowe (1985 and 1986), *i.e.,* by being generally widespread and yet not occurring in the zone (*e.g. Combretum collinum* subsp. *binderianum*, observed in all but the cooler, more mesic SW zone).

The geographical positions of major zone boundaries and their relationship to climate are shown in Fig. 1. The TWINSPAN analyses helped to divide the study area into five major zones with the 1300 mm isohyet and/or the 28 °C isotherm roughly dividing relatively more mesic, cooler zones: the southwestern, central and southeastern zones (SW, CENT, SE) from relatively more xeric and/or warmer zones the northeastern/northwestern zones (NE/NW). This boundary generally confirms described zoogeographical zones (*e.g.* Mackenzie 1954, Lewis 1949) and agrees with the generalized divide of two of Chipp (1930)'s 'vegetation belts', namely the *Afzelia-Butyrospermum-Lophira* and the Combretaceae 'Grass-woodlands'. However, rather than merely climatically correlated zonations, interzonal boundaries appear to reflect more complex environmental interlinkings. For example, an altitude gradient could support division of the southwestern zone (SW) which comprises the highest band of the ironstone plateau, from the northwestern (NW), central (CENT) and southeastern (SE) zones, which include its lower reaches, and from the northeastern (NE) zone which encompasses riverine fringes of the alluvial plains marking the boundaries between the ironstone plateau and the lowland flood plains and Sudd swamps.

Relationships between vegetation types

Figure 2 summarizes the relative partitioning of all plots in terms of vegetation types and their distributional tendencies. If one compares the transect results with those of the concurrent aerial survey of the whole area (Table 3), there is a general agreement, despite some differences at a more detailed level. More particularly, this suggests that the tree rather than the bush component is the dominant vegetation form throughout the study area, and supports the contention that the sampling procedure was representative. Fig. 2 also shows that while communities characterized by low dominance of bushland are typical of both northern and southern zones, those with higher bush cover tend to occur primarily in the northern zones. This distributional trend would agree with the recognition of two distinct groups of riverine communities in Fig. 2.

While the generalized mixed thicket is widespread, the *Oxytenanthera abyssynica* 'Bamboo' brake (see below) tends to occur in the north. If one can generalize the observation of Morison *et al.* (1948) that in Western Equatoria the Bamboo brake is characteristically associated with a type of colluvial soil, this would indicate a possible northern distributional tendency of the colluvial complex (see below, under soil-plant relationships). Two (above discussed) community types in the Closed Woodland and Thicket group have a southern distributional tendency: the *Mangifera indica* copses and the mixed thicket typified by a dominance of the 'tree' form. The *Mangifera indica* disappears as a community in the north where it virtually occurs only as isolated individuals. The tree-dominated Mixed-thicket community (GW-T 21) is instead replaced by the bush dominated GW-T 4 when moving northeasterly (Table 2). This represents the only observed manifestation of a subtraction effect acting on a specific vegetation type as one moves at increasing latitudes away from the edges of the more diverse and species richer tropical forest towards more xeric northern woodland communities. The combined northerly diluting effect of shifting cultivation and increasing impact of fires could be behind this distribution trend and correspond to Rose Innes's (1977) distinction, in western Africa, of a derived savanna-mosaic transitional between high closed forest and open tree savanna, and a fire proclimax Guinea-savanna. Excluding the heavily man-in-

Table 3. Comparative relationships of vegetation types from percentage frequency of plots in the ground survey and numerical estimate of percentage area from a comprehensive aerial survey*

Ground survey (plot frequency)		Aerial survey (estimate of area)		
Open vegetation	9%	Grassland	3%	14% **
Grass-bushland	33%	Bushed-grassland	26%	
Grass-woodland	52%	Wooded-grassland	27%	
Closed-woodland/ Thicket	6%	Woodland	45%	63% **
Cumulative woodland vegetation types	58%		72%	

* Methods in Biotani (1981)

** Southern edges only

fluenced distribution of *Mangifera indica*, one could think that such a subtraction effect has not been detected for major/dominant species (*e.g.* Table 1), because the more typical species composition of the study savanna-woodland includes species occurring both in drier and wetter parts of the Sudanian Region (White 1983). On the other hand, even allowing for Smith's (1949) certain 'belting of species across the isohyets', only few major species display a northerly decreasing distributional frequency trend, *e.g. Terminalia avicennoides*, whereas the bulk of other major species' distribution tend to dilute towards the south, *e.g. Grewia mollis, Butyrospermum paradoxum* and *Khaya senegalensis* (Table 1). This may support the contention put forward elsewhere in Africa (*e.g.* Rose Innes 1977 and Sillans 1954) that often, in Equatoria, the present day closed savanna-woodland vegetation is represented by associations of northern species replacing southern communities, rather than relict of retreating southern communities. These relicts would now only survive in restricted favourable pockets such as some riverine strips. Other derived communities, such as the above discussed bamboo formations, would instead derive from local xeric vegetation types, *e.g.* the 'dry dense forest', and/or have a restricted northerly distribution.

Community successional transition spans various vegetation types both within and across different climatic zones whenever soil conditions, such as drainage, promote it. The transition of OV 21 (Table 2) may, for example, be reflecting a soil drainage gradient and respectively occurs within same north-eastern climatic zones (through OV 24 to GW 84), or between the north-eastern and the central and southern zones (through GB 4 to GW-T 19).

Soil-plant relationships

The Grass-woodland/Grass-bushland distributional patterns discussed above can also help elucidating some physiographical and pedological correlates. Woody vegetation tends to be associated with deeper eluvial soil, or illuvial soil in the south, and with shallower eluvial soil and colluvial/illuvial or colluvial/eluvial transition soil in the north (Table 2). Moreover, the distribution of communities associated with hollows and valleys, as inferred by relevant plant-soil relationships (Table 2), indicates that the illuvial component is rare, limited in surface area and often intermixed with other soil types in the south, especially the SW district. Both tendencies are a reflection of the better drainage of the southwestern valleys which, relative to those in the northeast, are narrower, have steeper slopes, and are not conducive to widespread flooding. Consistently, the transition from the illuvial type is generally abrupt and the illuvial/colluvial transitional soil type is poorly represented in southern areas, and its only characteristic community (an *Entada africana* association) was found in the NE zone.

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