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STRUCTURAL AND BIOGEOGRAPHICAL PATTERNS OF VEGETATION IN EQUATORIAL SUDAN

II. PHYSIOGNOMIC TRENDS

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Abstract. A selection of major floristic communities from a transect across the equatorial catenary-mosaic vegetation complex is analysed structurally and in an ecological context. In addition to the cover-dominance of general vegetation growth forms (bush, tree, grass, forb), other aspects of the vegetation structure (leaf size, tallness) respond in a recognisable, repetitive way to soil type and topographic variation. However, the major role in dictating both floristic and general structural trends appears to be played by combinations of edaphic and climatic factors. Three major structural complexes are recognised: a) *Anogeissus* Woodland/Grass-woodland communities dominated by the tallest height class and the medium leaf size classes; b) *Terminalia* and/or *Isoberlinia* Grass-woodland communities well represented in all height and leaf size classes; and c) *Grewia* and *Hyparrhenia* Grassland/Grass-bushland communities dominated by medium and short height classes, and medium and large leaf classes.

Introduction

Some well-defined zonal trends have been recognised within the apparently rather uniform catenary mosaic vegetation complex of the equatorial Sudan (Guillet and Moll, in press).

The floristic distribution of plant communities appears to be consistent with and help delucidating some general zoogeographical patterns identified elsewhere. The same analysis suggests that general vegetation growth form (tree, bush, grass, forb) changes within the floristic communities across subtle environmental gradients. For example, the bush to tree cover ratio increases with gradually decreasing rainfall precipitation northwards from a bush cover of 70% less than tree cover to one of 20% more than tree cover. These trends appear to be related primarily to differences in soil type and topography as suggested by the parallel SW-NE changes from eluvial-colluvial loamy soils to illuvial clayey soils.

This study aims at assessing whether similar patterns can be found also for other aspects of vegetation structure (*e.g.* tallness and leaf size), and possibly, at identifying any relationship with major environmental factors.

Methods

Data collection

Thirty five plots were placed in the most common communities recognised within 1750 observations in a ca 2000 km transect across equatorial Sudan west of the White Nile. Plot size ranged from 4-25 m^2 for grassland, to 100-900 m^2 for woody vegetation types, reflecting differences in the size of reasonably discrete vegetation assemblages within the mosaic. Details of structural and environmental data collected are given in Fig. 1. When latin names are not available, the analysed taxa have been given their local vernaculars names.

Numerical methods

Two-way indicator species analysis (TWINSPAN, Hill 1979a) was used to classify separately floristic and structural data. Detrended correspondence analysis (DECORANA, Hill 1979b) was used to ordinate floristic data both with a view to testing group robustness, as well as to uncover possible biotic-abiotic relationships. The ordination plots of samples according to pairs of axes obtained using DECORANA were studied to investigate intergroup relationships and to obtain a picture of possible vegetation/environmental interactions. For example, these relationships are shown whenever the relative position of clusters identified by TWINSPAN scatters according to an environmental gradient.

Results and discussion

Results of the TWINSPAN structural analysis are synthesised in Fig. 1. Similar plot clusterings in Fig. 2 suggest that the identified physiognomic clusters are confirmed floristically. Moreover, individual plots in

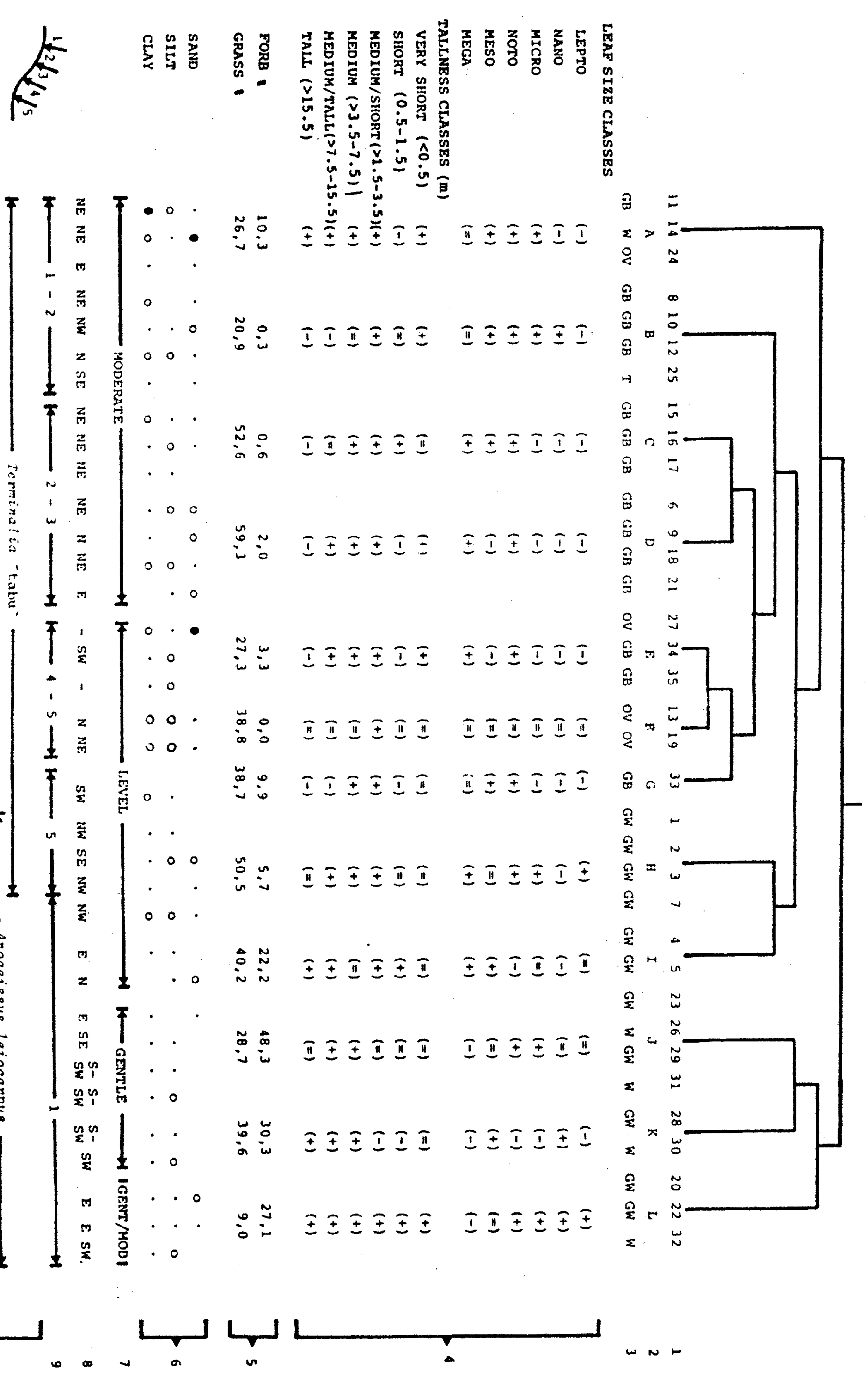


Figure 1. Synthesis of the vegetation structural classification from 35 detailed plots as given by TWINSPAN. Structural determinants and relationships of major clusters with floristic and environmental contributions. Life size classes after Raunkiaer (1934). 1) Plot numbers as given in Figs 2 and 3. 2) Major cluster labels as given in the text and in Fig. 2. 3) Vegetation types: OV: open vegetation, GB: grass-bushland, GW: Grass-woodland, T: thicket. 4) Summarized contribution of structural features to major plot clusters: (+): more than, (=): same as, and (-): less than predicted when compared to the 35 plots as a whole. 5) soil textural components, indicated by • >o> · . 7) Angle of slope (in degrees): level (0-3), gentle (4-8), moderate (9-16). 8) Aspect: North, South, East, West and intermediate orientations. 9) Situation in the landscape: plateau (1), top slope (2), mid-slope (3), bottom slope (4), plain (5). 10) Major characteristic taxa.

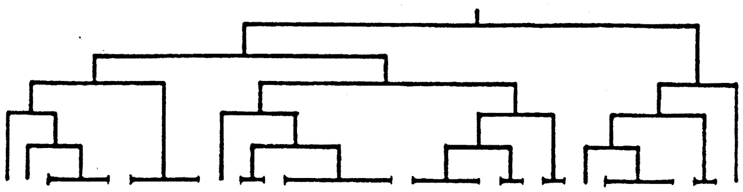
the DECORANA ordination (Fig. 3) form discrete assemblages which correspond to plot clusters recognised in both TWINSPAN classifications (Figs 1 and 2). The scatter divides a Woodland/Grass-woodland cluster from two other clusters comprising respectively Grass-woodland and Thicket, Grass-bushland and Open Vegetation plots. The relative position of the identified intercluster dichotomies appears to reflect the prevailing influence of specific abiotic factors rather than clear gradients between environmental opposites. For example, a 'xeric' Woodland/Grass-woodland cluster of plots splits from a 'mesic' Grass-woodland group, and within the Thicket/Grass-bushland/Open Vegetation cluster, plots on more clayey soils are easily distinguishable from those on more sandy soils (Fig. 3).

Some physiognomic vegetation clustering might also reflect a cardinal 'aspect' influence. The small latitudinal values in the study area might not be conducive to typical (*e.g.* south-north) solar radiation "gradient correlations". Yet an orientation effect could still arise from the influence of the prevailing winds which is conducive to seasonally opposite ecological extremes. These arise mainly from the impact of the hot, dry north-eastern Harmattan which are well discussed in both botanical and agricultural literature (Jenik and Hall 1966). Besides desiccating effects, boosting of fire spread, deficiency of soil moisture, additional effects such as soil erosion, lack of humus, litter accumulation and drift of herbaceous plants could be reflected in the identified structural clustering (see below). For example, in northeast-facing plots forbs are virtually absent and sand is present in the soil, whereas, forbs are well represented and sand virtually undetectable in those facing southwest. On the other hand, in neighbouring central African savannas Sillans (1958) suggests that it is worth investigating also the potential effects of moist, rain bearing winds. In our study area southwestern moist winds could, in fact, favourably influence the distribution of the relatively xeric woodland communities and may explain their opposed 'aspect' tendency when compared to that of more mesic Woodland/Grass-woodland communities and of the Grass-bushland communities in general (see section (i) below). This suggestion is also consistent with the relatively major slopes and upper position in the landscape characterizing the xeric Woodland/Grass-woodland communities. Both characteristics can, in fact, be conducive to better exposure to moist winds when complementing appropriate 'aspect' orientation. These results suggest a need for phenotypical analyses (*e.g.* of stomatical structure and density) of major species across an aridity gradient. These would help assessing the possibility that a single major species might have a number of different forms ('ecotypes') within the area. Two considerations support this contention: the widespread distribution of major species across the climatic variance of the study area, and the fact that, while the ordination axes of the 1750 floristic plots have been found significantly correlated with climatic variables, abundance values of individual species have not (Guillet and Moll, in press).

Several scatter correlations can be observed in Fig. 3 between structural clusters and soil and physiographic types. This re-emphasises the primary role played by soil conditions (*e.g.* the water-holding capacity and/or nutrient status) not only in exercising a controlling influence on the equatorial Sudan vegetation in general (Chipp 1930, Morison et al. 1948), but also on its structural features. On the other hand, their scatter is consistent with that of other analysed factors (see *e.g.* the case of darker soil colours scattering towards more clayey, illuvial soils, and *vice versa* that of lighter soil colours). These combinations also complement some biotic correlations (*e.g.* the understory forb/grass positive ratio dominating the xeric woodland communities clusters) and help to define and characterise structural assemblages (see (i-iii) below).

Figure 1 also highlights a good correspondence between the numerical partitioning of the TWINSPAN structural classification and the qualitative vegetation type categorization based on Pratt & Gwynne (1978). Similarly, as found in the more general floristic analyses (Guillet and Moll, in press) differences in dominance rather than exclusiveness of features tend to be the discriminating factors among the detailed plots under study here. These results are comparable to those obtained from the individual species and suggest that the geographical distribution of structural features/assemblages reflected in the TWINSPAN classes is widespread within the study area, albeit in different proportions. The correspondence between vegetation types and assemblages of structural features therefore enables us to discuss the contribution of various levels of the structural analysis, according to vegetation types and alongside the results from the floristic investigations in order to better understand environmental variation. Three major structural groups are recognised: i) dominated by the the tallest height class and medium leaf size classes (clusters J to L), ii) with a fair representation of all height and leaf size-classes (clusters H and I), and iii) dominated by medium and very short height classes and medium and large leaf sizes classes (clusters B to G) (Fig. 1). More particularly:

(i) The first structural group, clusters J to L, encompasses 'xeric' ($\leq$ 1225 mm $\bar{X}$ annual rainfall) Woodland/Grass-woodland communities. These are more frequently associated with southerly aspect, gentle slope, eluvial soils with relatively low clay and sand content, and large conical red termitaria. Floristically this structural group is characterized by *Anogeissus leiocarpus* and *Blighia unijugata* and, particularly when *Anogeissus leiocarpus* dominates, has a comparatively low number of species. A noteworthy subdivision appears to be cluster L from J and K. 'L' is associated



PLOT NUMBER	3	20	4	5	21	23	2	6	7	25	8	17	18	9	10	11	12	15	16	13	24	33	35	27	34	1	19	26	14	22	31	32	28	29	30
CLUSTER LABEL	H	L	I	I	D	J	H	D	H	B	B	C	D	D	B	A	B	C	C	F	A	G	E	E	E	H	F	J	A	L	J	L	K	J	K
SPECIES																																			
Hyparrhenia sp.			2	1			3	3	2																										2
Vitex doniana	1		1		1			1	1																	2		1							
Isoberlinia cf. doka		5	4	4	3	3																						3							
Parinari curatellifolia	1																																		
Imperata cylindrica			1	1																															
'Gbogbo'	1																																		
Aframomum sp.	3		2				1																			1									
Lophira cf. alata	2		1	1																															
Strychnos innocua								1																											
Prosopis africana	3	3	1			1	1	1	1	2				1																					
Annona senegalensis			1	1	1	1	1	1	1		1	1		1			1		1																
Chlorophora excelsa			1																							1									
Hymenocardia acida	1		1	1		1	1	1	1	1	1		1	1	1	1	1		1									1							
Combretum collinum		1			1				1	1		1	1		1	1		1	1			1		1	1							1			
75		3			1	2	1	1	1				1						1		2	1		1						1		2			
Butyrospermum paradoxum				1						1	1											2	3					1							
Hyparrhenia papillipes	1	1	2		2	2		2	2	1	1	2	3	3	1	2	3	3	3	2	2	2	2	1	2	2	2								
Grewia cf. mollis		3	1	1	1	1	1	1	1	1	1	2	1	2	2	1	2	2	1	3	3	1	2		1	1	1		1	1					
'Maronguc'		1													1	1	1																		
Asparagus racemosus					1			1				1	1	1		1																			
Nauclea latifolia								1					1				1																		
Canthium sp. (cf. crassum)							1		1	1	1					2								1											
Terminalia sp.	1						4	1		1	1	2	1	1	1	1			1			1	1												
'Imaakuri'											1																								
'Kpasamangua'												1																							
Dombeya sp.														1																					
'Morgel'														1			1																		
'Ngbinzakukiri'															1		1																		
Delonix cf. elata												1	1	1	1			1																	
'Rambanguodi'														1																					
Asteracantha longifolia																						1	1												
Ficus sp.																							1												
'59																									3										
Indigofera sp.	1					1						1	1																1						
Piliostigma thonningi	1											1	1				1	1								1							2	1	
Maytenus senegalensis														1	1	1	1	1	1			1	1		1			1	1	1					
Afzelia quanzensis									3	2																		2							
Bridelia micrantha	1	1	1		1	1	1				1	1	1	1	1		1		1			1	1				1	1			1	1	1		
Manniophytum africanum			1							1																						1			
'Bafukuyu'								1	1													1			2										5
Combretum fragrans								1					1	1	1	1	1	1								2			1	3			4	1	
Cissus sp. (?populnea?)												1														1					1			1	
cf. Justicia sp.			1	1				1																				3							
Ficus sp.				1		1											1														3				
Gardenia cf. jovis-tonantis					1					1																		1						1	
Khaya senegalensis																1												3							
Landolphia comorensis																												1							
Tamarindus indica																														4	1				
Ritchiea sp.																												1		1					
'Gitikiri'						1																						2	1	1	2	3			
'Memeango'									1																			2			2				
'Nvuoanzoro'																														1					
Irvingia smithii																															4				
'Pelelengu'																																1			
Anogeissus leiocarpus																										2		4	5	3	3	4	4	2	5
Rhus natalensis																															1			1	
Paullinia pinnata																																	1	1	
'Degbe'																																	1	1	
Beckeropsis uniseta																																	2	2	
Ziziphus abyssinica, Z. spinacchristi																																	1		
Terminalia avicennoides																																			4
'Nzawa'																																	2	2	1
Zenkerella cf. grotei						3																	1					1					3	5	

* Quantitative classes after Braun-Blanquet (Werger 1974)

Figure 2. TWINSPAN classification of 35 detailed floristic plots. Quantitative classes after Braun-Blanquet (Werger 1974).

with relatively steeper slopes, more sandy soils and is better represented in smaller leaf size classes (including LEPTO) and well represented in all height classes. Floristically cluster L is dominated by *Anogeissus leiocarpus, Blighia unijugata* or *Isoberlinia doka* and *Grewia mollis,* The remaining two clusters (J and K) are in turn better represented in medium to tall height classes (> 3.5 m), and relatively less well represented in the smaller leaf size-class (LEPTO) with cluster K also poorly represented in medium leaf size-classes (MICRO and NOTO). These clusters are floristically dominated by *Anogeissus leiocarpus, Combretum fragrans* and *Anogeissus leiocarpus* or *Isoberlinia doka, Grewia mollis* and *Annona senegalensis*, respectively.

(ii) The second structural group, clusters H and I, comprises 'mesic' (≥1375 mm $\bar{X}$ annual rainfall) Grass-woodland communities, associated with 'LEVEL' ground, colluvial/illuvial soils, and floristically

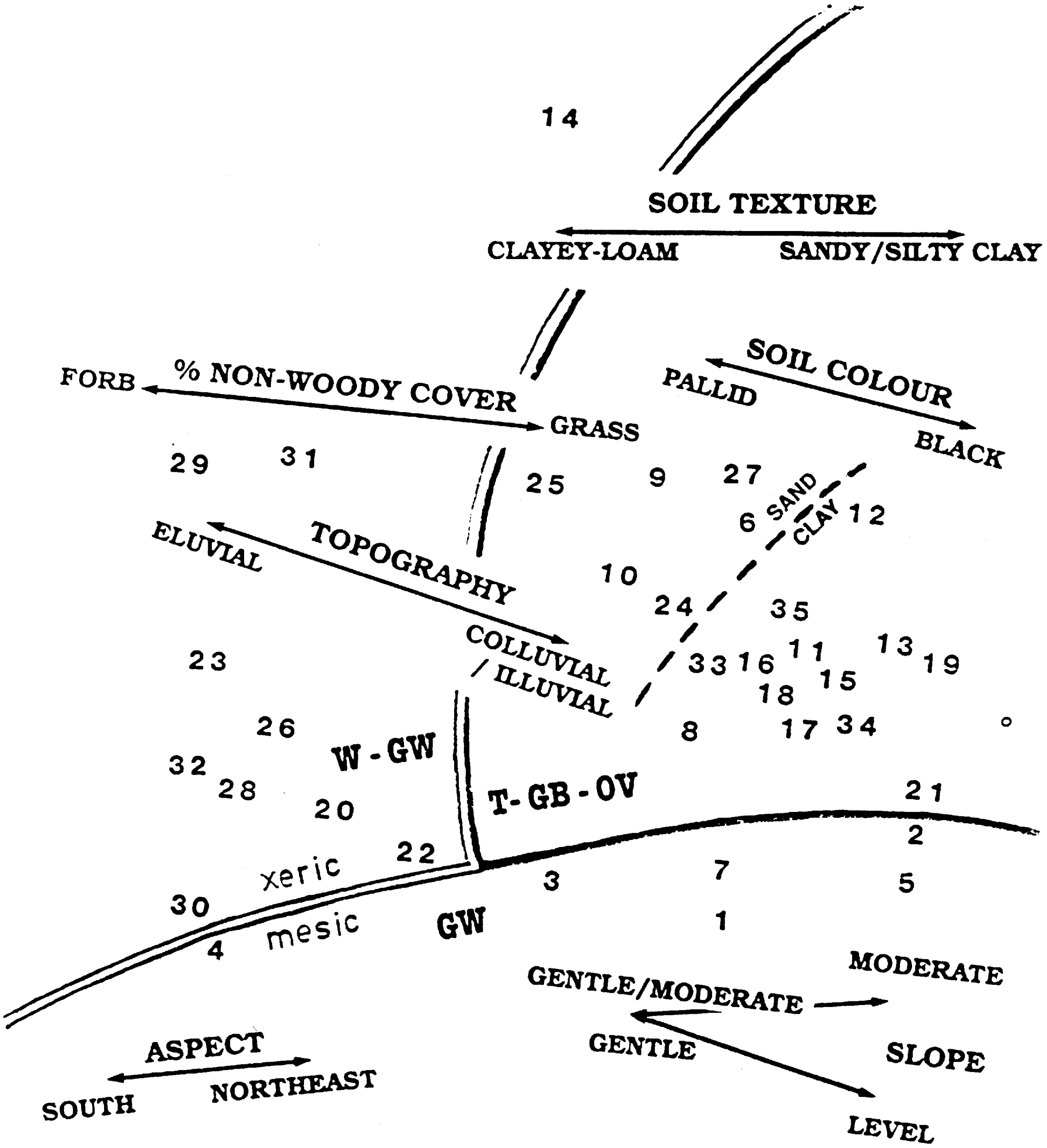


Figure 3. DECORANA ordination of 35 detailed structural plots, showing environmental scatter relationships.

characterized by *Lophira alata, Hyparrhenia* 'bagau' and *Vitex doniana*. Although only comprising the Grass-woodland vegetation type, this structural group splits from the dendrogram branch comprising the first structural group. This is possibly because it encompasses communities structurally intermediate between these last and the remaining Grass-bushland/Grassland communities. Consistently, it also shares characteristic species with a Grass-bushland community in Guillet and Moll (in press): the generally more mesic southeasterly distributed GB 7. This structural group is well represented, physiognomically, in all height and leaf size classes (with the minor exception of being less than predicted in the NOTO size class), and floristically, in the major component of the two other community types (*e.g. Terminalia* 'tabu' and *Anogeissus leiocarpus*). However, rather than *Anogeissus leiocarpus* which is never dominant in this structural group, its clusters are primarily dominated by various combinations of *Terminalia* 'tabu' or *Isoberlinia doka*. More particularly, cluster H, physiognomically characterised by medium height classes (1.5 < 15.5 m), is floristically dominated by *Terminalia* 'tabu'/*Annona senegalensis, Terminalia* 'tabu'/*Hymenocardia acida, Hymenocardia acida* and *Vitex doniana*; whereas cluster I, particularly well represented in larger leaf sizes and from the short to the tallest height classes (> 0.5 m), is floristically dominated by *Isoberlinia doka* in association with *Hymenocardia acida/Canthium crassum* or with *Terminalia* 'tabu'/*Butyrospermum paradoxum*.

(iii) The third structural group, clusters C to G, encompasses Grass-bushland/Grassland vegetation types. This group spans from LEVEL slopes with illuvial/colluvial soils, to MODERATE slopes with eluvial/colluvial soils; these soils are often more sandy clays. Characteristic species are *Terminalia* 'tabu' and *Maytenus senegalensis* (both of which are less frequent only in more open grassland areas), whereas the generally dominant species comprise the *Grewia mollis/Hyparrhenia* 'kitipki' association. Physiognomically, this group is characteristically under-represented in smaller leaf size-classes (from LEPTO to MICRO) and the tallest height class (> 15.5 m). Two community subdivisions appear appropriate here on the basis of differences in site topography, soil texture and slope classes. These differences span from the MODERATE slopes with the eluvial/colluvial soils of the Grass-bushlands comprised in clusters C and D, to the LEVEL slopes and colluvial/illuvial soils of the relatively species poorer Grass-bushlands typical of clusters E to G. Clusters C and D, which are characterized floristically by *Delonix elata*, are dominated by associations of *Piliostigma thonningii/Combretum collinum* subsp. *binderianum/Grewia mollis, Terminalia* 'tabu', *Maytenus senegalensis, Grewia mollis, Combretum fragrans, Annona senegalensis, Hymenocardia acida* and/or *Combretum collinum* subsp. *binderianum*. Clusters E to G are instead dominated by *Hyparrhenia* 'kitipki', *Grewia mollis, Combretum collinum* subsp. *binderianum* and *Butyrospermum paradoxum*, or *Hyparrhenia* 'kitipki' and *Grewia mollis* (in Grasslands).

Although the 'chaining' dendrogram branch of cluster B indicates a less definable and separable structural community (see also Fig. 3) this is worth separate treatment because it comprises a discrete vegetation type: the Thicket. This 'pseudocommunity' is frequently associated with eluvial-eluvial/colluvial sites and MODERATE slopes, is well represented in all but the extreme leaf size classes (LEPTO and MEGA), and in short and medium height classes (< 7.5m). Its cluster encompasses relatively species rich plots, more typically dominated by *Maytenus senegalensis, Annona senegalensis* and/or *Terminalia* 'tabu', *Grewia mollis, Hymenocardia acida* and *Combretum collinum* subsp. *binderianum*, respectively corresponding to the southern and northern phases of 'Mixed Thicket' communities identified in Guillet and Moll (in press).

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REFERENCES

Chipp, T. F. 1930. Forests and plants of the Anglo-Egyptian Sudan. Geographical Journal 75: 123-143.

Guillet, A. and E. J. Moll. 1992. Structural and biogeographical patterns of vegetation in equatorial Sudan I. Terrestrial communities. Coenoses 7: 61-73.

Hill, M. O. 1979a. *TWINSPAN - A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes*. Cornell University, Ithaca.

Hill, M. O. 1979b. *DECORANA - A FORTRAN program for detrended correspondence analysis and reciprocal averaging*. Cornell University, Ithaca.

Jenik, J. and J. B. Hall. 1966. The ecological effects of the Harmattan winds in the Djebobo Massif (Togo Mountains, Ghana). J. Ecol. 54: 767-79.

Morison, C. G. T., A. C. Hoyle and J. M. Hope-Simpson. 1948. Tropical soil-vegetation catenas and mosaics: a study in the south-western part of the Anglo-Egyptian Sudan. J. Ecol. 36: 1-84.

Pratt, D. J. and M. D. Gwynne. 1978. *Rangeland management and ecology in East Africa*. Hodder and Stoughton, London.

Raunkiaer, C. 1934. *The life forms of plants and statistical plant geography*. Oxford.

Sillans, R. 1958. *Les savanes de l'Afrique centrale*. Le Chevalier, Paris.

Werger, M. J. A. 1974. On concepts and techniques applied in the Zurich-Montpellier method of vegetation survey. Bothalia 11: 309-323.

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