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Ecological interpretation of plant communities by classification and ordination of quantitative soil characteristics

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ABSTRACT

An agglomerative cluster analysis and a principal components analysis of habitat, based on 27 quantitative soil variables, are compared with a Braun-Blanquet classification of the vegetation of the Manyeleti Game Reserve in the eastern Transvaal. The results indicate that these techniques can be successfully used to obtain relatively homogeneous habitat classes, characterized by sets of environmental (soil) variables and not only single variables individually, and which are furthermore significantly correlated with the recognized plant communities of the area.

RÉSUMÉ

INTERPRÉTATION ÉCOLOGIQUE DES FORMATIONS VEGETALES PAR LA CLASSIFICATION ET PAR L'ORDINATION DES CARACTÉRISTIQUES QUANTITATIVES DU SOL

Une analyse de groupage par agglomérations successives et une analyse des composantes principales de l'habitat, basée sur 27 variables quantitatives du sol, sont comparées avec une classification suivant la méthode de Braun-Blanquet de la végétation de la Réserve de Faune de Manyeleti dans l'est du Transvaal. Les résultats indiquent que ces méthodes peuvent être valablement utilisées pour obtenir des classes relativement homogènes d'habitats, caractérisées par des ensembles de variables du milieu (sol) et pas seulement par de simples variables considérées individuellement, et qui sont en outre en corrélation significative avec les formations végétales reconnues dans la région.

INTRODUCTION

For the establishment of efficient wildlife management programmes and conservation policies for any area, a sound knowledge of the ecology of the area is an essential prerequisite (Edwards, 1972). It has often been demonstrated that different ecosystems of a particular area can be recognized by the delimitation of the plant communities within the area (Major, 1969; Küchler, 1973; Bredenkamp & Theron, 1978). For this reason, and as part of a vegetation survey programme for conservation areas in South Africa, a study of the vegetation of the Manyeleti Game Reserve was undertaken. Although great diversity and variation occur in the vegetation, there is little conspicuous variation in the topography of the slightly undulating landscape, especially within the relatively small study area. The importance of soil characteristics as a principal ecological factor determining the distribution of plant species and plant communities in the Transvaal Lowveld has been emphasized by, *inter alia,* Van der Schijff (1957), Gertenbach (1978) and Bredenkamp (1982). It has often been shown that the distribution of plant species and, especially, plant communities, is the result of the totality of the present environmental factors rather than of single factors (e.g. Roberts, 1971; D. Scott, 1974; J. T. Scott, 1974; Bredenkamp, 1977).

This paper summarizes the results of an attempt to correlate the plant communities of the Manyeleti Game Reserve to unique sets of soil variables, rather than to certain variables individually. Simultaneously, however, an attempt is made to identify individual variables which could be important for the distribution of the plant communities.

THE STUDY AREA

The Manyeleti Game Reserve, which covers approximately 22 700 hectares, is situated in the Arid Lowveld Veld Type (Acocks, 1975), adjacent to the Kruger National Park, immediately south of the Orpen Gate, between 24°29′ and 24°42′ S and 31°23′ and 31°36′ E (Fig. 1).

The slightly undulating plains of the study area are situated at an altitude of 350–450 m with a slight rise towards the west. Numerous dry drainage lines dissect the area. Archaean granite covers most of the Reserve, but portions of a large dolerite dyke are exposed in the western parts. The soils of the uplands sites on granite are coarse, sandy, acid, leached and dystrophic whereas the soils of the bottomland sites are fine textured, neutral, mesotrophic and calcareous, and sometimes brackish. The soils of doleritic origin are very clayey, alkaline, eutrophic and calcareous.

The climate of the study area is, according to the Köppen index, a BShw climate (Schulze, 1947) where BS = arid steppe climate; h = hot and dry, with mean annual temperature exceeding 18°C; and w = dry winter. The average annual rainfall for the period 1967 to 1979 is 614,6 mm.

Temperatures recorded for Skukuza range from mean daily maximum temperatures of 32,3°C in December and January to mean daily minimum temperatures of 5,6°C in July (Weather Bureau, 1954).

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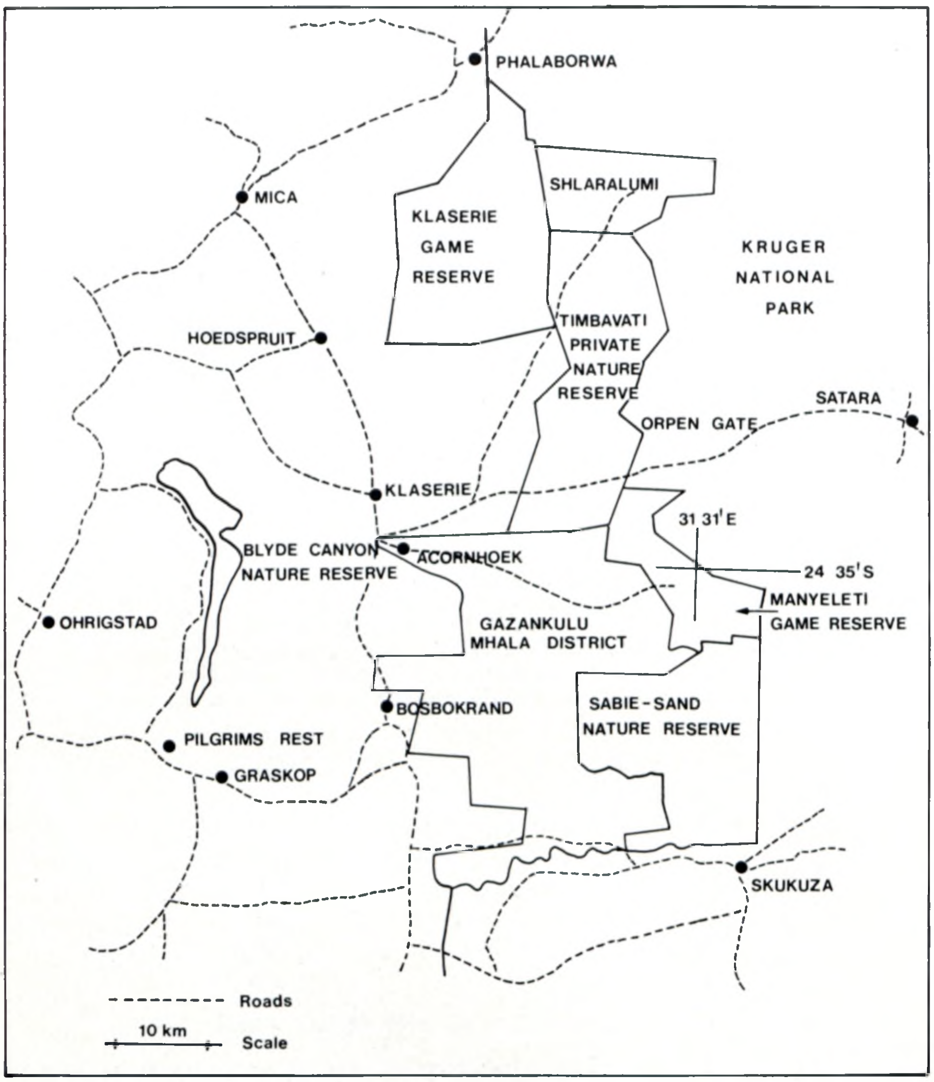

FIG. 1.—Map indicating the position of the Manyeleti Game Reserve.

METHODS

Floristic and habitat data were obtained from 245 stratified random sample plots (Bredenkamp & Theron, 1980).

A Braun-Blanquet analysis of the floristic data from the relevés was carried out independently and before cluster analysis and principal components analysis of soil habitat data (Table 1).

Quantitative data for 27 soil variables were obtained by analysis of soil samples from the 245 relevés (Table 2). The soil variables include:

percentage gravel in the soil sample in the A as well as B soil horizons; percentage coarse sand, medium sand, fine sand, total sand and clay (particle sizes according to MacVicar *et. al.*, 1977) in the A as well as B soil horizons, after the gravel has been removed;

the amounts of exchangeable K^+, Na^+, Mg^{2+}, Ca^{2+} and the S-values (mg/100 g soil) of the A and B soil horizons;

the soil conductivity (u mho/cm) of the A and B soil horizons;

TABLE 1.—The seven plant associations of the Manyeleti Game Reserve (Bredenkamp & Theron, 1980)

Symbol	Association	Habitat
A	*Perotis patens – Terminalia sericea* Association	sandy upland granitic soils
B	*Euclea divinorum – Acacia nigrescens* Association	black clayey bottomland granitic soils
C	*Themeda triandra – Acacia gerrardii* Association	red clayey granitic and doleritic soils
D	*Euclea divinorum – Albizia harveyi* Association	black clayey, brackish bottomland granitic soils
E	*Themeda triandra – Setaria woodii* Association	black clayey doleritic soils
F	*Cardiospermum corindum – Acacia nigrescens* Association	rocky hills
G	*Spirostachys africana – Diospyros mespiliformis* Association	river banks

the soil pH (transformed to H^+ ($X10^{-6}$), Haylett (1962), of the A and B soil horizons;

and the soil depth (cm).

Classification and ordination of the habitat were done on standardized data (Seal, 1964) obtained from the absolute quantitative values of these variables.

Classification was done using Orloci's agglomerative cluster analysis (Orloci, 1967) in order to obtain definite and relatively homogeneous habitat classes, based on the variation within the sets of quantitative soil characteristics. This classification was compared

TABLE 2.—Average values for the 27 soil variables in the six soil habitat classes obtained by cluster analysis of habitat data

	Soil variables (A = A soil horizon; B = B soil horizon)	Soil habitat classes CA	CB	CC	CD	CE	CF
percentage	gravel A	9,1	6,8	5,3	0,9	0,8	4,2
	gravel B	42,3	36,5	9,8	2,4	12,6	14,3
	coarse sand A	32,7	26,8	26,8	10,5	9,3	18,5
	coarse sand B	41,0	28,9	25,3	17,7	27,5	24,0
	medium sand A	24,5	22,1	23,0	31,2	10,9	16,4
	medium sand B	22,5	15,0	15,6	33,3	13,7	13,9
	fine sand A	26,7	24,0	24,7	32,6	19,7	23,0
	fine sand B	18,3	16,2	15,8	27,2	17,3	17,5
	total sand A	84,0	73,0	74,7	73,7	37,9	58,2
	total sand B	81,8	60,2	56,5	78,2	58,5	55,6
	clay A	12,8	23,2	20,5	21,8	55,1	35,8
	clay B	15,3	35,0	37,8	18,6	36,3	37,8
	Summary	sandy	clayey	clayey	sandy	very clayey	clayey
mg/100g soil	potassium A	283,8	179,2	189,3	354,4	408,3	337,0
	potassium B	225,0	103,0	101,3	117,6	200,0	193,0
	sodium A	57,7	89,3	107,0	85,3	241,7	122,0
	sodium B	142,6	309,4	385,7	102,9	516,7	204,0
	magnesium A	246,5	538,7	463,3	948,5	4341,7	1545,0
	magnesium B	339,8	1264,9	1136,7	889,7	4683,3	1820,0
	calcium A	190,1	395,8	305,0	1139,7	1958,3	1255,0
	calcium B	128,5	770,8	550,0	580,9	3083,3	1840,0
	S-value A	770,1	1203,0	1065,0	2527,9	6950,0	3556,0
	S-value B	832,4	2447,6	2173,7	1691,2	8481,7	4507,0
	Summary	dystrophic	mesotrophic	mesotrophic	mesotrophic	eutrophic	eutrophic
umho	soil conductivity A	100,7	135,0	150,3	232,6	258,8	212,0
	soil conductivity B	73,8	377,6	1059,7	130,6	1021,3	294,8
	Summary	leached	normal	brackish	normal	brackish	normal
cm	soil depth	108,5	71,7	28,7	88,5	54,0	37,6
	Summary	deep	moderately deep	very-shallow	moderately deep	shallow	very shallow
	pH A	5,6	5,8	5,8	6,7	7,4	7,1
	pH B	6,2	7,0	7,3	7,4	8,2	8,0
	Summary	acid	moderately acid	neutral	neutral	alkaline	alkaline

TABLE 3.—A comparison between the distribution of 245 relevés in the seven Braun-Blanquet plant associations and the six habitat classes obtained by cluster analysis of habitat data

Braun-Blanquet plant associations	Cluster analysis habitat classes (see Fig. 2)						Total relevés
	CA	CB	CC	CD	CE	CF	
A	52	2					54
B	9	20	31	1		1	62
C	4	14	12	1		7	38
D	2	3	32		1	2	40
E					14	9	23
F		2				4	6
G	4	1		15		2	22
Total relevés	71	42	75	17	15	25	245

to and correlated with the seven plant associations of the Braun-Blanquet classification (Table 3).

Ordination by principal components analysis was done to indicate possible gradients in the soil habitat and, by locating the position of each plant assocation in the habitat gradient, it was determined whether or not the associations are restricted to certain areas within the gradient (Table 4). From the results of this ordination, the individual soil variables which could be important with regard to the distribution of the plant communities, were also determined (Table 5).

RESULTS

Classification of the soil habitat by cluster analysis

The dendrogram (Fig. 2) summarizes the results of the cluster analysis. Six soil habitat classes (CA-CF) were obtained at a similarity value of 88%. This high similarity value indicates the relatively small variation in habitat within each class. The average values for each variable in the six classes are given in Table 2.

Comparison of the values of the different soil habitat variables within and between the classes enabled the following soil habitat index to be compiled (for average values and explanation of the terms, see Table 2):

- Class CA: deep, acid, dystrophic, leached, sandy (granitic) soils.
- Class CB: moderately deep, moderately acid, mesotrophic, normal, clayey (granitic) soils.
- Class CC: very shallow, neutral, mesotrophic, brackish, clayey (granitic) soils.
- Class CD: moderately deep, neutral, mesotrophic, normal, sandy (granitic) soils.
- Class CE: shallow, alkaline, eutrophic, brackish, very clayey (doleritic) soils.
- Class CF: very shallow, alkaline, eutrophic, normal, clayey (doleritic soils).

From Table 3 it is clear that the *Perotis patens – Terminalia sericea* Association, the *Euclea divinorum – Albizia harveyi* Association and the *Spirostachys africana – Diospyros mespiliformis* Association are chiefly represented by soil habitat classes CA, CC and CD, respectively. Both the *Euclea*

TABLE 4.—A comparison between the distribution of 245 relevés in the seven Braun-Blanquet plant associations and the seven habitat groups obtained by Principal Components Analysis of habitat data

Braun Blanquet plant associations (see Table 1)	Principal Components Analysis : habitat groups (see Fig. 3)							Total relevés
	OA	OB	OC	OD	OE	OF	OG	
A	50	1	1				2	54
B	4	48	2	5	1	1	1	62
C	2	13	18	3		1	1	38
D		11	5	24				40
E					23			23
F		1			1	4		6
G	1			1			20	22
Total relevés	57	74	26	33	25	6	24	245

TABLE 5.—Eigen values of the soil variables in the first and second components of the ordination

Soil variables (A = A soil horizon; B = B soil horizon)	first component	second component
gravel A	0,398	−0,142
gravel B	0,536	−0,472
coarse sand A	0,707	0,277
coarse sand B	0,568	−0,598
medium sand A	0,685	0,218
medium sand B	0,505	−0,761
fine sand A	0,341	−0,058
fine sand B	0,044	−0,483
total sand A	1,000	0,307
total sand B	0,692	−0,998
clay A	−0,999	−0,316
clay B	−0,686	1,000
potassium A	−0,276	−0,712
potassium B	−0,032	−0,616
sodium A	−0,631	−0,297
sodium B	−0,381	0,900
magnesium A	−0,867	−0,675
magnesium B	−0,841	−0,140
calcium A	−0,810	−0,743
calcium B	−0,749	−0,335
s-value A	−0,903	−0,751
s-value B	−0,878	−0,172
soil conductivity A	−0,546	−0,108
soil conductivity B	−0,374	0,917
soil depth	0,483	−0,748
pH A	−0,721	−0,430
pH B	−0,721	−0,381

divinorum – Acacia nigrescens Association and the *Themeda triandra – Acacia gerrardii* Association are mainly represented by classes CB and CC. The *Themeda triandra – Setaria woodii* Association is restricted to classes CE and CF, whereas the *Cardiospermum corindum – Acacia nigrescens* Association occurs in classes CB and CF.

Concerning the division of the relevés within the soil habitat classes, it is clear that soil habitat class CA is mainly associated with the *Perotis patens – Terminalia sericea* Association, class CD with the *Spirostachys africana – Diospyros mespiliformis* Association, and class CE with the *Themeda triandra – Setaria woodii* Association. Soil habitat class CB is mainly represented in both the *Euclea divinorum – Acacia nigrescens* Association and the *Themeda triandra – Acacia gerrardii* Association, and class CC is also represented in these two associations as well as the *Euclea divinorum – Albizia harveyi* Association. Although the relevés of soil class CF are present in almost all the associations, this class is best represented in the *Themeda triandra – Acacia gerrardii*, the *Themeda triandra – Setaria woodii*, and the *Cardiospermum corindum – Acacia*

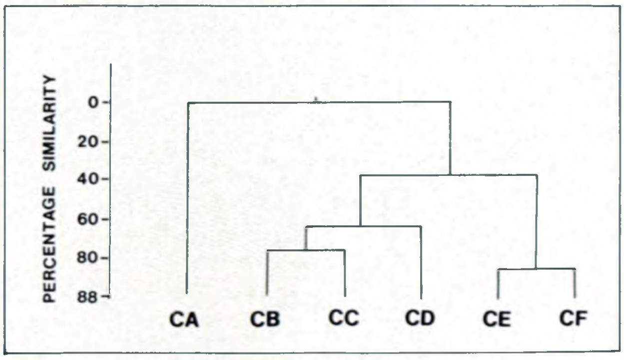

FIG. 2.—A dendrogram indicating the classification of the habitat by cluster analysis.

nigrescens Associations. The statistical chi-square method of Bailey (1974) was used to measure coincidence between the classification of the soil habitat by means of the numerical cluster analysis, based on quantitative soil habitat data and the Braun-Blanquet classification of the vegetation based on qualitative floristic composition. Despite theoretical limitations of the method, the chi-square value of 526,4 (p=0,001 at χ^2 = 59,7, 30°f) indicates that the two classifications are indeed highly significantly correlated.

It may be concluded that the soil habitat classes CA, CE and CD and the *Perotis patens – Terminalia sericea* Association, the *Themeda triandra – Setaria woodii* Association and the *Spirostachys africana – Diospyros mespiliformis* Association respectively, are mutually restricted to one another, within the study area. The soil habitats of the *Euclea divinorum – Acacia nigrescens, Themeda triandra – Acacia gerrardii* and *Euclea divinorum – Albizia harveyi* Associations are fairly closely related (soil habitat classes CB and CC, Fig. 2), at least as far as the measured quantitative soil characteristics are concerned. These three associations occur on mesotrophic clayey soils mainly of granitic origin. Although typical stands of these associations can easily be recognized, transitions in vegetation and habitat are frequently found (Bredenkamp, 1982), which could hamper identification. These transitions (gradients) are also indicated in the results of the ordination which follow.

Ordination of soil habitat by principal components analysis

The results of the principal components analysis of soil habitat data show that the first two components explain 48,9% of the variation in the soil data, and these two components are therefore considered adequate to indicate possible soil habitat gradients and also to show whether there is an associated distribution of plant associations (Table 4).

The arrangement of relevés along the first two components of the soil habitat ordination represents gradients without consistent discontinuities (Fig. 3). Gradients in soil habitat variables (Fig. 3) were established by superimposing the quantitative values of those variables with relatively high eigen values (Table 5) and which contribute greatly to the

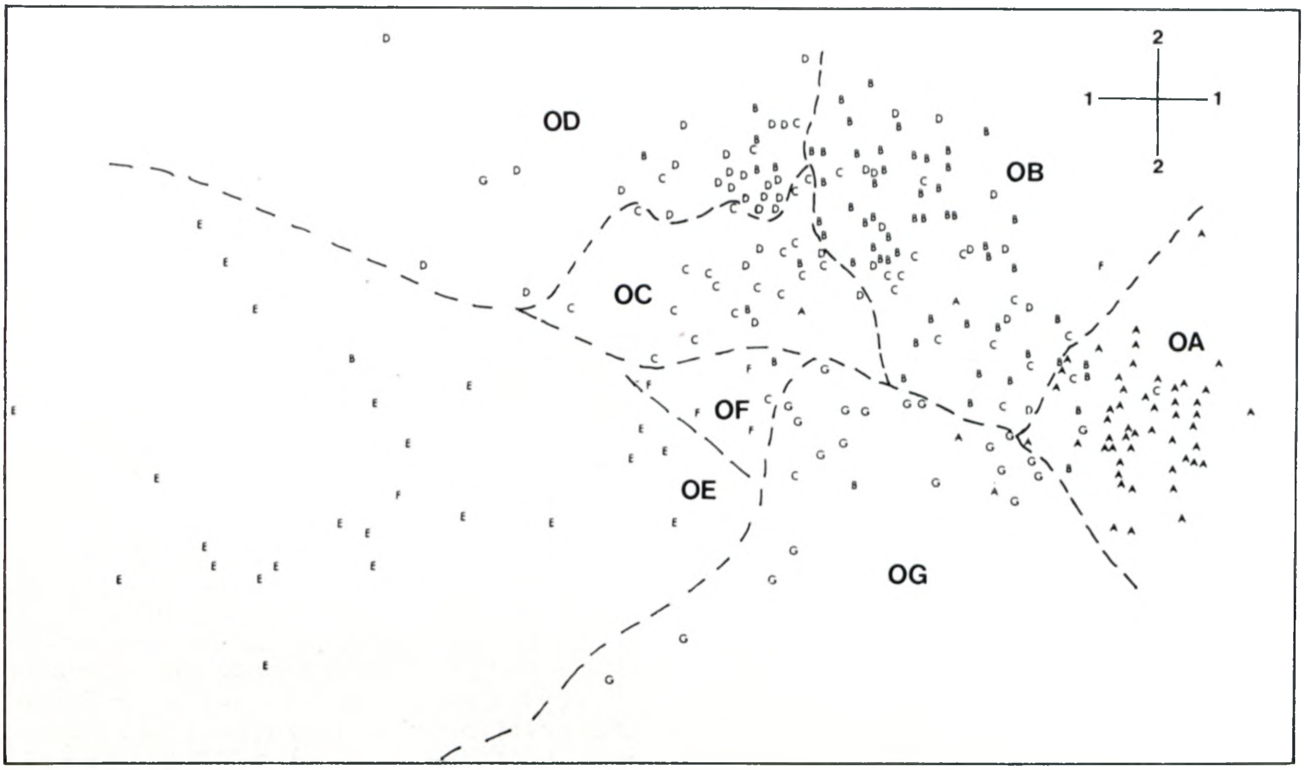

FIG. 3.—The distribution of the Braun-Blanquet Associations in relation to the first and second components of the ordination (Symbols are explained in Table 1.)

distribution pattern of the relevés along the first two components of ordination.

The different Braun-Blanquet plant associations (Table 1), represented by the same relevés than those used in the soil habitat ordination, were superimposed on this ordination and the results (Fig. 3) show that the different plant associations are indeed remarkably confined to certain areas within the soil habitat gradients and consequently the plant associations could easily be delimited (Fig. 3).

The grouping of relevés by principal components analysis of soil habitat data was compared to the Braun-Blanquet classification of these relevés. The results are given in Table 4. From Fig. 3 and Table 4 it is clear that the *Themeda triandra – Setaria woodii* Association is entirely restricted to soil group OE; the *Perotis patens – Terminalia sericea* Association is almost entirely restricted to soil group OA; the *Spirostachys africana – Diospyros mespiliformis* Association to soil group OG; and the *Cardiospermum corindum – Acacia nigrescens* Association to soil group OF. The soil groups OE, OA, OG and OF, furthermore, mainly contain relevés of the abovementioned four assocations respectively. These results indicate that the four groups of the soil habitat and four plant associations are mutually restricted to one another, and largely confirm the results of the cluster analysis.

The *Euclea divinorum – Acacia nigrescens* Association is principally confined to soil group OB (48 of the 62 relevés, that is 77,4%), but group OB also contains relevés from the *Themeda triandra – Acacia gerrardii* and the *Euclea divinorum – Albizia harveyi* Associations. The *Themeda triandra – Acacia gerrardii* Association is mostly limited to groups OB and OC whereas the *Euclea divinorum – Albizia harveyi* Association occurs in group OB and OD. These results indicate, as the results of the cluster analysis, the relationships and transitions between the habitat of the *Euclea divinorum – Acacia nigrescens*, the *Themeda triandra – Acacia gerrardii* and the *Euclea divinorum – Albizia harveyi* Associations.

Despite the somewhat arbitrary delimitations of the plant associations in this ordination, the classification obtained was correlated to the Braun-Blanquet classification by means of the chi-square test of Bailey (1974). The chi-square value of 824,8 ($p=0{,}001$ at $\varkappa^2 = 68{,}0$ 36°f) indicates a highly significant correlation between the two classifications.

For each plant association, the average values of the most important variables, i.e. those with relatively high eigen values in the first two components, are given in Figs 4 & 5. Variables with relatively high eigen values in the first component include total sand, coarse sand and clay contents of the A soil horizon and the S-value, magnesium and calcium contents and the pH of both A and B soil horizons (Table 5).

These variables contribute greatly to the distribution of the relevés in the first component. Only the total sand and coarse sand contents of the A soil horizon have positive eigen values and the quantitative values of these two variables mostly increase from left to right, whereas the quantitative

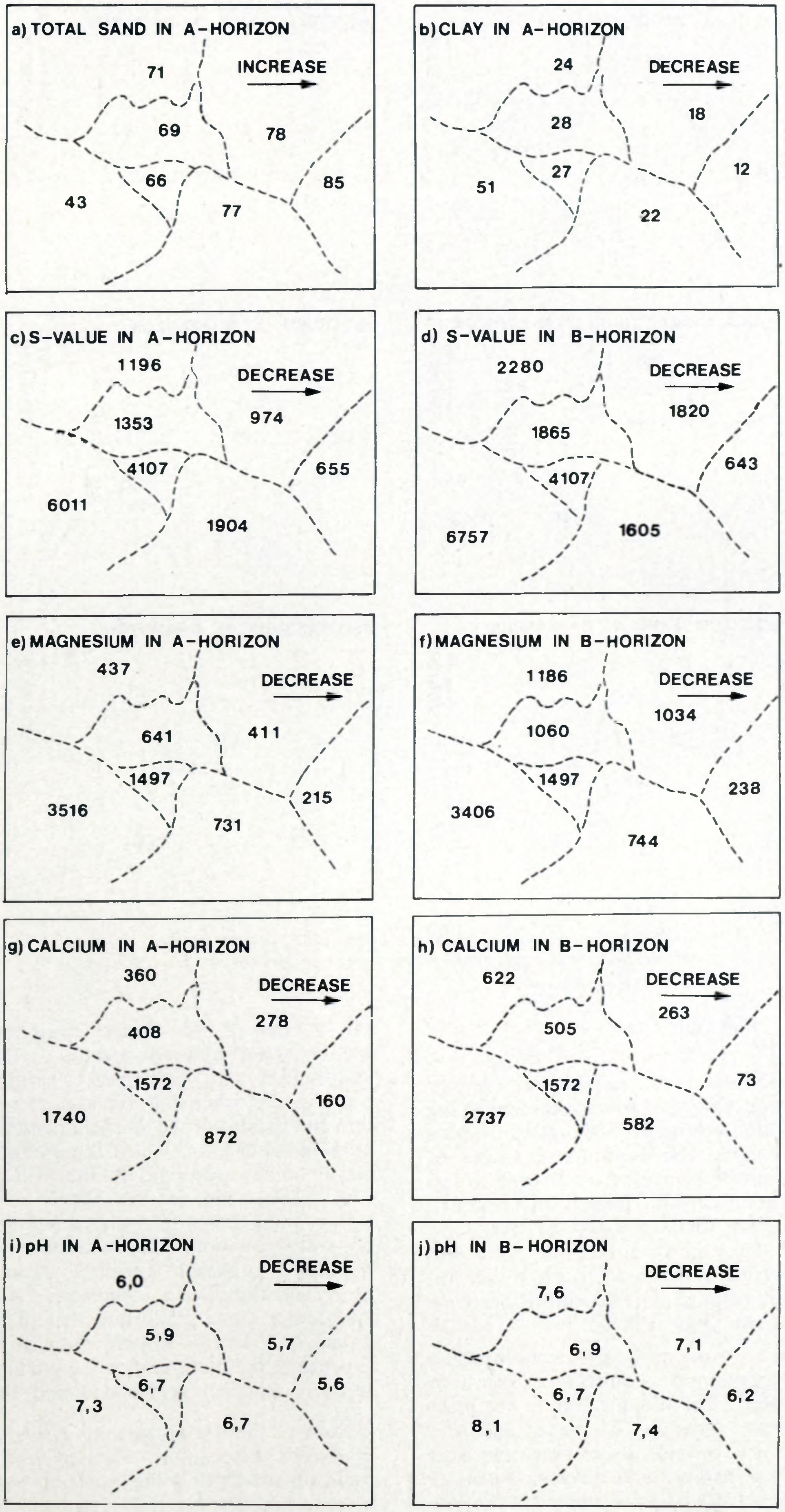

FIG. 4.—Distribution of average quantitative values in each Association of the soil variables with high eigen values in the first component of the ordination.

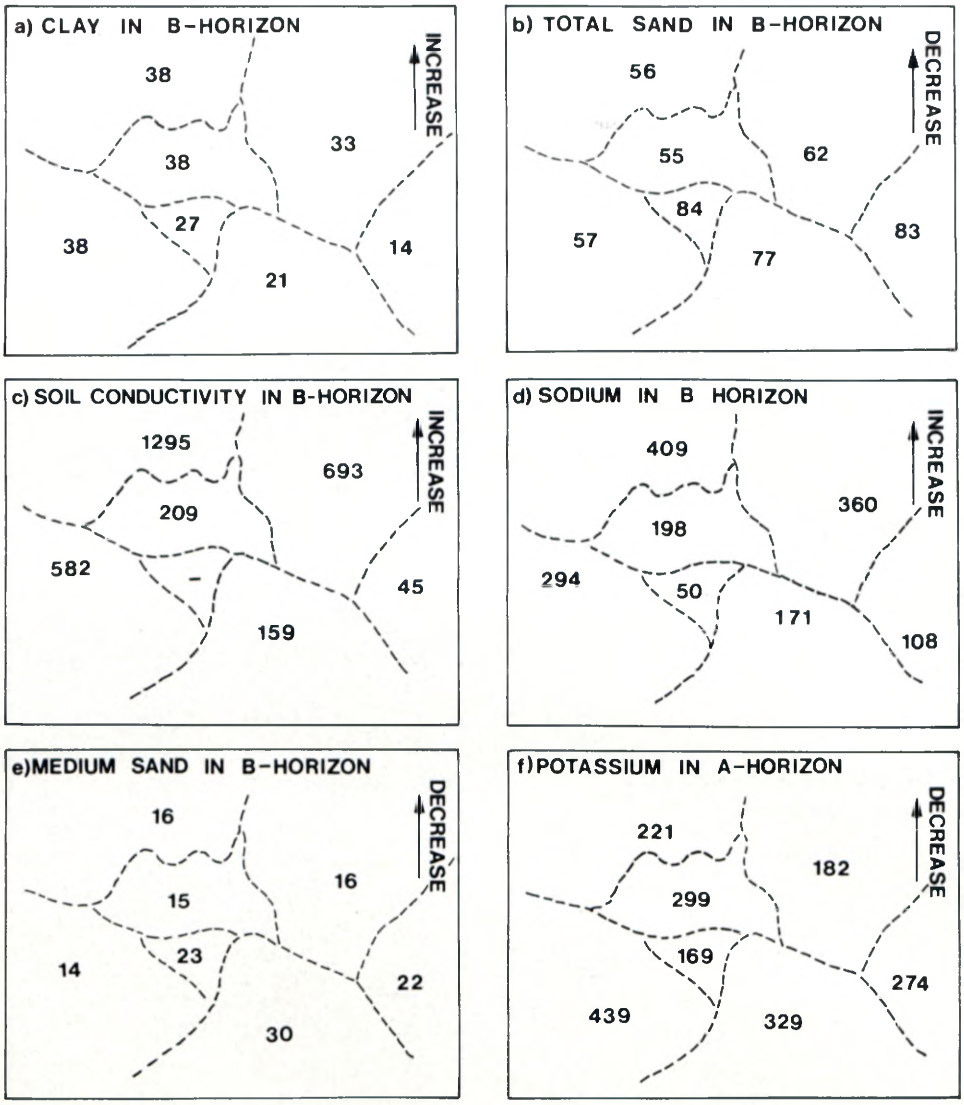

FIG. 5.—Distribution of average quantitative values in each Association of the soil variables with high eigen values in the second component of the ordination.

values of the other important variables mostly decrease from left to right (Figs 3 & 4).

For the second component, variables such as clay content, soil conductivity and sodium content of the B soil horizon are important. With relatively high positive eigen values, the quantitative values of these variables mostly increase from bottom to top in Figs 3 & 5. Variables with relatively high negative eigen values include total sand and medium sand contents in the B soil horizon, calcium, potassium contents and S-value in the A soil horizon and soil depth. The values of these variables mostly decrease from bottom to top (Figs 3 & 5).

According to the zone in the gradients to which the different associations are confined, a suggestion of the relationships of each assocation to the most important habitat variables is made and the transitions between related associations are also indicated. The soil habitat of the *Perotis patens – Terminalia sericea* Association is situated at the one end of the soil gradient where it represents acid, coarse, sandy soils, especially low in calcium and magnesium content. This habitat grades mainly into the habitat of the *Euclea divinorum – Acacia nigrescens* and *Themeda triandra – Acacia gerrardii* Associations with slightly acid to neutral, clayey and nutritionally richer soils, but also, to a lesser degree, into the habitat of the *Euclea divinorum – Albizia harveyi* Association which represents the neutral, clayey and mesotrophic but brackish (sodium-rich) soils. The soils of the three last mentioned Associations are closely related and gradual transitions are common. The habitats of the *Themeda triandra – Acacia gerrardii* Association and, especially, the *Euclea divinorum – Albizia harveyi* Association, also grade into that of the *Themeda triandra – Setaria woodii* Association, which is situated at the other end of the gradient where the soils are alkaline, very clayey and eutrophic.

Soils of the *Cardiospermum corindum – Acacia nigrescens* Association, which is restricted to the rocky doleritic hills in the transitional areas between dolerite and granite, show relationships with those of the *Themeda triandra – Acacia gerrardii* and *Themeda triandra – Setaria woodii* Associations. The widely scattered distribution pattern of the relevés of the *Spirostachys africana – Diospyros mespiliformis* Association of the riverbanks (group OG, Fig. 3) indicates the great variation in soil character of this Association. These different soils show relationships with the soils of most other Associations through which the rivers flow. In spite of this variation, these soils could easily be united into a single group (group OG, Fig. 3) which indicate the relationship of these soils to each other.

The results indicate that, although the habitat often represents a complex continuum, soil groups which largely represent the floristic Associations can be established within the gradient.

In conclusion the following can be emphasized:

1. The use of classification and ordination techniques on quantitative soil characteristics proved very successful in obtaining relatively homogeneous soil habitat classes which are (i) characterized by sets of environmental (soil) variables rather than of individual single variables and are (ii) significantly correlated with the recognized plant communities of the area.

2. The soil habitat and distribution of the plant communities were successfully interpreted and the reality of these communities as ecologically significant units emphasized.

3. The transitions in vegetation can also be explained by gradients in the habitat (e.g. Bredenkamp, 1982).

4. Some individual environmental variables which may influence the distribution of the plant communities can also be identified from the results of the principal components analysis.

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