Journal of Vegetation Science 1: 97-104, 1990
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Fuzzy set ordination and classification of Serengeti short grasslands, Tanzania

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Abstract. Species abundance data from 32 representative stands are used to evaluate the vegetation in the heavily grazed Serengeti short grasslands. The abundant species are: *Kyllinga nervosa*, *Sporobolus ioclados*, *S. kentrophyllus* and *Eustachys paspaloides*, all occurring in elevated areas, and *Hypoestes forskalei*, which is found in the drainage areas.

Numerical classification and fuzzy set ordination revealed four main grassland communities associated with a topographic gradient. The communities are considered distinct since their niches, as computed in the community and environmental fuzzy system space are not overlapping. Leaching, erosion and animal disturbance effects correlated with the topographic gradient are found to determine species composition and overall community structure in the grasslands.

Keywords: Disturbance; Grassland community; Grazing; Topographic gradient.

Nomenclature: Clayton et al. (1970, 1974, 1982).

Introduction

The Serengeti Plains in northern Tanzania represent the most extensive natural grasslands in East Africa (Vesey-Fitzgerald 1973). These grasslands are particularly known for the occurrence during the wet season of huge migratory populations of wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*) and Thomson's gazelle (*Gazella thomsonii*), totalling about 2.5 million animals (Sinclair & Norton-Griffiths 1982). The animal migrations have attracted much attention and have been the object of extensive research (e.g. Grzimek & Grzimek 1960; Watson & Kerfoot 1964; Anderson & Talbot 1965; Sinclair & Norton-Griffiths 1979). Most of these studies, however, were concerned with large mammals and little work was done on the vegetation.

The first botanical descriptions of these grasslands, which were mainly physiognomically based on grass height (Watson & Kerfoot 1964; Anderson & Talbot 1965; Herlocker & Dirschl 1972), identified three vegetation zones:
1) a long grassland in the northern and northwestern plains; 2) an intermediate grassland on the central plains; 3) a short grassland in the southern and eastern region (see Schmidt 1975 for a zonation map). According to the criterion of Pratt, Greenway & Gwynne (1966), the whole Serengeti Plains are currently described as short grasslands (McNaughton 1983). In this paper the short grasslands are defined according to Anderson & Talbot (1965).

To date there exists no quantitative description of the complex vegetation patterns found on the short grasslands apart from general surveys covering extensive areas. According to Anderson & Talbot (1965) and Herlocker & Dirschl (1972) the vegetation of the short grasslands has been described as two major communities:
1) a *Sporobolus ioclados - Digitaria macroblephara - Kyllinga nervosa* short grass community, occurring in the central and northern portion, and
2) a *Hypoestes forskalei* / *Sporobolus - Digitaria - Kyllinga* short grass community, occurring along drainage lines. However, this classification based on a large scale investigation covering the whole of the Serengeti Plains does not account for variations that are evident on the smaller scale, i.e. by considering in detail the short grasses only.

In this paper we report part of a long-term study designed to provide data on grassland community diversity in relation to bio-physical environment in the Serengeti short grasslands using fuzzy set ordination. Fuzzy set theory (Zadeh 1965; Zimmerman 1984) is an extension of classical set theory which has been introduced into plant ecology only recently (Marsili-Libelli 1986; Roberts 1986; Feoli & Zuccarello 1986, 1988). It combines clasdirect gradient analysis of Whittaker (1967) (Feoli &

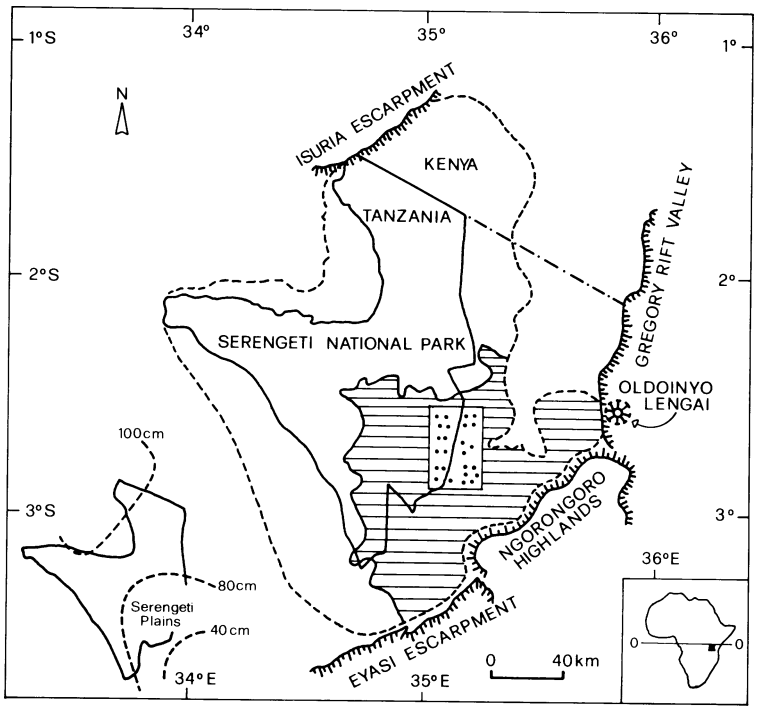


Fig. 1. Map of the Serengeti National Park (enclosed by solid line) in the Serengeti ecosystem (enclosed by dashed line) showing location of the study area (dotted) in the Serengeti Plains (shaded). The inset maps show the position of the Serengeti National Park in Africa (right) and rainfall isolines (left).

sification and ordination and provides direct ordinations with environmental fuzzy sets, in a manner similar to the direct gradient analysis of Whittaker (1967; Feoli & Zuccarello 1988). Fuzzy sets provide fuzzy axes which define a fuzzy system space. The application of fuzzy set theory to the problem that we want to study looks suitable since the community variation appears to be very gradual and the short grasslands may be considered as a system in which different vegetation states could be recognized as community types along gradients.

Materials and methods

Site description

The short grasslands studied constitute the eastern portion of the Serengeti Plains and extend from the Serengeti National Park into the Ngorongoro Conservation Area (Schmidt 1975; McNaughton 1983). They cover about 3 000 km^2 of gently rolling open grasslands between 35°00' and 35° 25' E and 2° 20' and 3° 20' S (Fig. 1). They are underlain by Precambrian basement rocks on which deep calcareous tuff from massive volcanic eruptions has been deposited (Pickering 1959). The soils are shallow, unstructured, saline and alkaline and have an impermeable hard pan of calcium carbonate at depths of 50-150 cm (de Wit 1978). The mean annual rainfall is 400 mm, and according to the moisture index of Thornthwaite (1948) the grasslands have a semi-arid climate (Norton-Griffiths, Herlocker & Pennycuik 1975). Other general descriptions of the Serengeti Plains which include the short grasslands are found in Schmidt (1975) and McNaughton (1983).

Sampling methods

Data for community analyses were obtained from 32 locations (stands) in the Serengeti short grasslands. Stand sites were located to represent the overall topographic and floristic range. Each stand was randomly sampled for species percentage cover using a rectangular grid (50 x 100 cm) of 50 equidistant wire intersections according to Floyd & Anderson (1982). After suspending the grid 10 cm above the ground, a record of top cover was made by counting the number of intersections directly above a plant species. The total number of grids (50) per stand was selected by applying Pielou's (1966) diversity criterion to preliminary samples collected during the reconnaissance survey. Topographic position and slope were noted for each stand. Soil samples were collected with a 5 cm diameter auger to a depth of 20 cm from five random grids in each stand. The samples were combined to form a composite sample per stand and analyzed for pH, sodium (Na), potassium (K), magnesium (Mg), calcium (Ca), cation exchange capacity (CEC) and moisture (MO), using standard methods (Koehler & Moodie 1978). The data reported in this

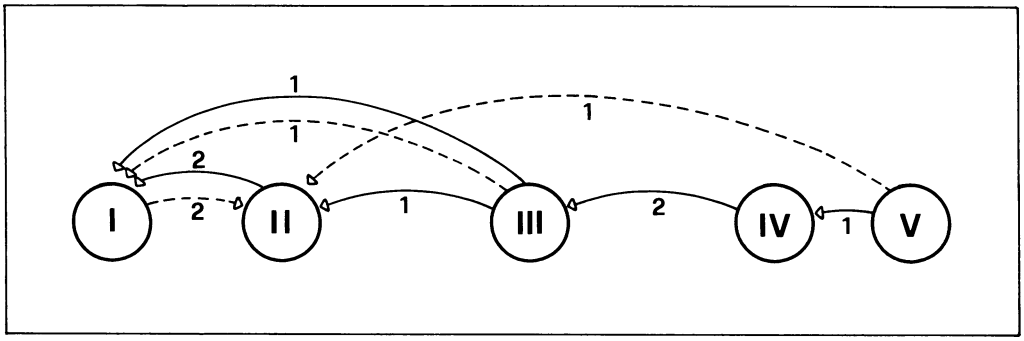


Fig. 2. The inter-connections between the five grassland communities from the Serengeti according to AFFINC measured as the number of stands in a cluster that are more similar to another cluster. Significant connections are indicated by a solid line while weak connections are shown by a dashed line.

paper were collected during the rainy seasons of 1974, 1975 and 1982.

Data analysis

A 32 stands by 21 species matrix contains the vegetation data while a matrix of 7 soil variables and 32 stands contains the soil data. Species have been classified by average linkage clustering based on the correlation coefficient. Stands were classified by sum of squares clustering using the chord distance, and by average linkage clustering using the cosine of the angle as a similarity measure (Orlóci 1978). Classifications have been tested by analysis of concentration at different hierarchical levels (Feoli & Orlóci 1979). The clusters have been compared by the probabilistic method suggested by Goodall & Feoli 1988) using the program AFFINC (Goodall, Ganis & Feoli 1987). This method is a modification of the one proposed by Goodall (1968) in which the affinity index is computed as the probability that a particular sample in a set would have attribute values as close to those of a specified subset, if its values were a random sample of those not in the subset.

The clusters of stands defined by the classification methods have been used to obtain fuzzy sets on the basis of the method suggested by Feoli & Zuccarello (1986, 1988), and used by Zerihun, Feoli & Lisanework (1989). We distinguished four types of fuzzy sets:
a) community fuzzy sets of stands;
b) community fuzzy sets of species;
c) environmental fuzzy sets of stands;
d) environmental fuzzy sets of species.

Community fuzzy sets are those derived directly by community data, while environmental fuzzy sets are those obtained by combining the community fuzzy sets with environmental data (Feoli & Zuccarello 1988). All four types of fuzzy sets are computed on the basis of the same stand classification as derived by the clustering techniques. The ordinations based on the fuzzy axes have been analyzed by the method of ellipses of equal concentration (Lagonegro & Feoli 1985a). The hypervolumes and cluster niche overlaps in the fuzzy system space have been computed according to Feoli, Ganis & Zerihun (1988), while taking the individual environmental fuzzy sets into account. Diversity measures have been computed for each vegetation type in order to correlate the hypervolumes to the diversity. For computation programs, see Lagonegro & Feoli (1985b), Scimone, Ganis & Feoli (1987), Ganis (1989) and Zuccarello (in prep.).

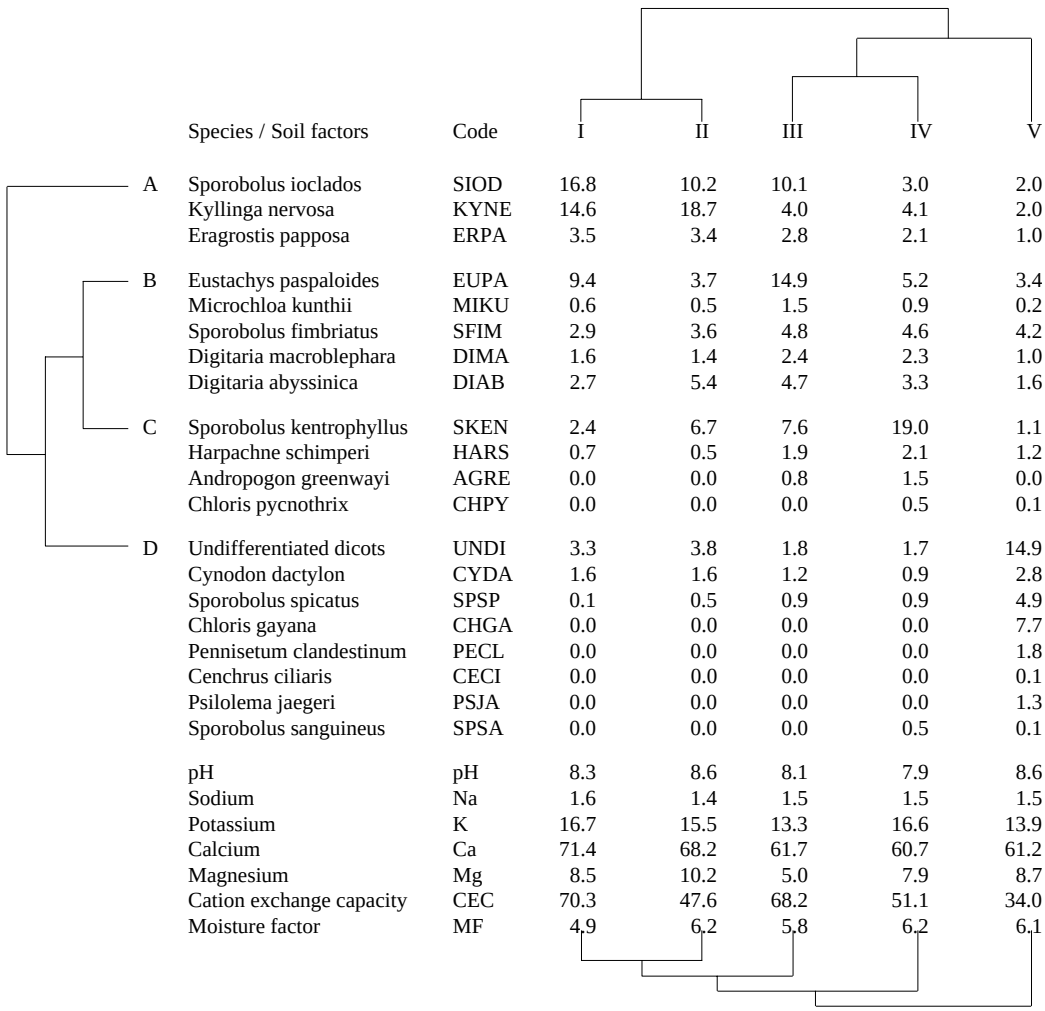
Results and discussion

Classification

The classification of the species and stands, and the soil data for the clusters are presented in Table 1. The clusters are described by the average values of the species and the average values for soil factors. The two methods of classification used for stands resulted in five main clusters with the same content. The hierarchical structure is different however. The classification based on cosine and average linkage (dendrogram at the base of Table 1) demonstrates the gradual variation of vegetation while the classification based on sum of squares and chord distance (dendrogram at the top of Table 1) would suggest a discontinuity between clusters I+II and clusters III+IV+V.

The analysis of concentration indicates that the optimal classification in terms of overall cluster separation is the one based on four species groups and two stand groups (clusters I+II+III+IV versus cluster V). This result would confirm the classification of Anderson & Talbot (1965) and that of Herlocker & Dirschl (1972)

Table 1. Mean percent cover of species and average soil factor values for five clusters of stands from Serengeti short grasslands. Classification of the stands based on cosine and average linkage (base dendrogram) and that based on sum of squares and chord distance (top dendrogram) are shown. The dendrogram on the left shows species classification in four groups based on average linkage clustering and correlation coefficient. Associations between clusters and topography are: I = hilltops, II = upper hillslopes, III = middle hillslopes, IV = lower hillslopes, V = drainage areas.



	Species / Soil factors	Code	I	II	III	IV	V	Mean
A	Sporobolus ioclados	SIOD	16.8	10.2	10.1	3.0	2.0	9.4
	Kyllinga nervosa	KYNE	14.6	18.7	4.0	4.1	2.0	8.7
	Eragrostis papposa	ERPA	3.5	3.4	2.8	2.1	1.0	2.6
B	Eustachys paspaloides	EUPA	9.4	3.7	14.9	5.2	3.4	7.3
	Microchloa kunthii	MIKU	0.6	0.5	1.5	0.9	0.2	0.7
	Sporobolus fimbriatus	SFIM	2.9	3.6	4.8	4.6	4.2	4.0
	Digitaria macroblephara	DIMA	1.6	1.4	2.4	2.3	1.0	1.7
	Digitaria abyssinica	DIAB	2.7	5.4	4.7	3.3	1.6	3.5
C	Sporobolus kentrophyllus	SKEN	2.4	6.7	7.6	19.0	1.1	7.4
	Harpachne schimperi	HARS	0.7	0.5	1.9	2.1	1.2	1.2
	Andropogon greenwayi	AGRE	0.0	0.0	0.8	1.5	0.0	0.5
	Chloris pycnothrix	CHPY	0.0	0.0	0.0	0.5	0.1	0.1
D	Undifferentiated dicots	UNDI	3.3	3.8	1.8	1.7	14.9	5.0
	Cynodon dactylon	CYDA	1.6	1.6	1.2	0.9	2.8	1.8
	Sporobolus spicatus	SPSP	0.1	0.5	0.9	0.9	4.9	1.5
	Chloris gayana	CHGA	0.0	0.0	0.0	0.0	7.7	1.5
	Pennisetum clandestinum	PECL	0.0	0.0	0.0	0.0	1.8	0.4
	Cenchrus ciliaris	CECI	0.0	0.0	0.0	0.0	0.1	0.0
	Psilolema jaegeri	PSJA	0.0	0.0	0.0	0.0	1.3	0.0
	Sporobolus sanguineus	SPSA	0.0	0.0	0.0	0.5	0.1	0.1
	pH	pH	8.3	8.6	8.1	7.9	8.6	8.3
	Sodium	Na	1.6	1.4	1.5	1.5	1.5	1.0
	Potassium	K	16.7	15.5	13.3	16.6	13.9	15.0
	Calcium	Ca	71.4	68.2	61.7	60.7	61.2	64.6
	Magnesium	Mg	8.5	10.2	5.0	7.9	8.7	8.1
	Cation exchange capacity	CEC	70.3	47.6	68.2	51.1	34.0	54.3
	Moisture factor	MF	4.9	6.2	5.8	6.2	6.1	5.8

since cluster V is very different from the set of the other four. However, a classification in five clusters is justifiable because the probabilistic method (AFFINC) shows that the five clusters are significantly distinguishable (Fig. 2) and because they are ecologically interpretable in terms of species abundance and the topographic location (Table 1). The five clusters represent communities which are sequentially arranged along the topographic gradient from hill tops (clusters I and II) through the hill slopes (clusters III and IV) to the drainage areas (cluster V). On the basis of average soil data in Table 1, it is difficult to explain the vegetation variation since according to the Mann-Witney test no significant differences were found between the clusters.

Ordination

The ordination based on community fuzzy sets corresponding to the most dissimilar clusters (I and V) is presented in Fig. 3. Fuzzy set I is plotted on the abscissa and fuzzy set V on the ordinate. The ordination shows that topography, accounted for by fuzzy set I, has an overriding effect on the arrangement of stands and that it is the most important environmental factor. Fuzzy set V

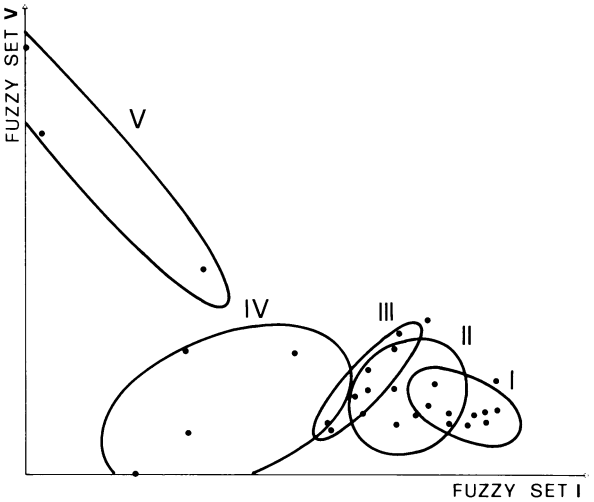


Fig. 3. Fuzzy set ordination of Serengeti short grasslands. The ellipses of equal concentration at 5% probability are drawn around the centroids of the five clusters of stands.

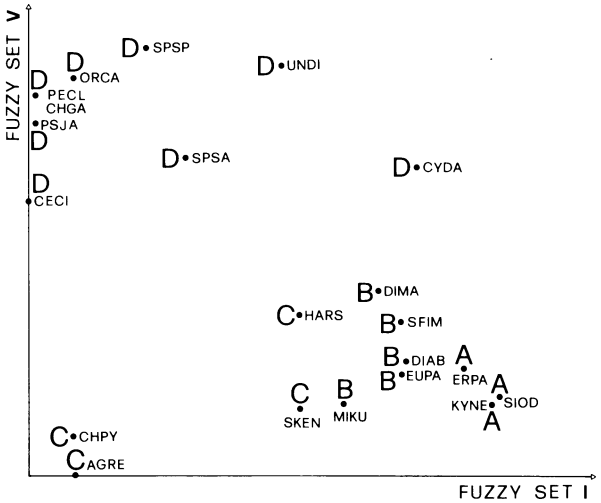


Fig. 4. The fuzzy set ordination of species. The clusters of species A, B, C, D, are indicated. For species names see Table 1.

separates only the stands associated with drainage areas.

The ordination of species according to community fuzzy sets I and V is presented in Fig. 4. The distribution pattern of species within the stand ordination (superimposition of Fig. 4 on Fig. 3) indicates that the arrangement of species groups follows the topographic gradient, with group A species occurring on the hill tops, group B and C species on the hill slopes and group D species in the drainage areas.

The ordinations based on environmental fuzzy sets (soil factors) are presented in Fig. 5 for calcium and cation exchange capacity, which were the most discriminating factors in the fuzzy system space. The arrangement of the stands along the topographic gradient is not fully retained. Clusters I and II overlap completely while cluster V shows high heterogeneity.

The hypervolumes of the clusters using primary data and fuzzy data are presented in Table 2. They offer a relative measure of the environmental heterogeneity of the vegetation types represented by the clusters in the study area. The largest hypervolume is the one of cluster III if primary data are considered, and that of cluster V in the case of fuzzy data. The smallest hypervolume is the one corresponding to cluster II in both cases. Measurements of niche overlap for the clusters using primary data are presented in Table 3. According to this measure, negative values indicate overlap. Only cluster II and IV are non-overlapping in the environmental space. If the environmental fuzzy space is considered, all the cluster-niches are non-overlapping except clusters I and II (Table 4). The overlap between clusters I and II suggests that the two clusters represent one community, which includes two vegetation types distinguishable on the basis of species abundances rather than on the basis of species composition.

Based on these results four main communities can be described as follows:

1. *Sporobolus ioclados - Kyllinga nervosa* community

This community occurs on the hill tops and upper hill slopes and is characterized by group A species,

Table 2. Niche hypervolumes (NH) and maximum niche width (NW) of stand clusters based on primary - and fuzzy set data.

Cluster	Primary data		Fuzzy data	
	NH	NW	NH	NW
I	3.45	4.62	0.99E-5	0.63
II	0.61	5.65	0.13E-6	0.51
III	5.83	4.72	0.32E-6	0.55
IV	2.14	5.35	0.32E-3	1.08
V	1.76	3.13	0.17	2.19

Table 3. Niche overlap between the five clusters of stands computed on primary data (negative values indicate overlap).

cluster	I	II	III	IV	V
I					
II	– 0.71				
III	– 0.43	– 0.49			
IV	– 0.70	0.07	– 0.58		
V	– 0.55	– 0.47	– 0.72	– 0.47	

Table 4. Niche overlap between the five clusters of stands based on fuzzy set data (negative values indicate overlap).

Cluster	I	II	III	IV	V
I	-1.00				
II	-0.74	–1.00			
III	0.02	0.32	–1.00		
IV	0.04	0.24	0.03	–1.00	
V	0.17	0.24	0.22	0.02	–1.00

Table 5. Species diversity in five clusters of stands of Serengeti short grasslands measured as total number of species per cluster *S*, Shannon's entropy *H'* and species evenness *J*.

Cluster	*S*	*H'*	*J*
I	16	2.045	0.74
II	15	2.134	0.79
III	17	2.360	0.82
IV	17	2.310	0.82
V	20	2.510	0.84

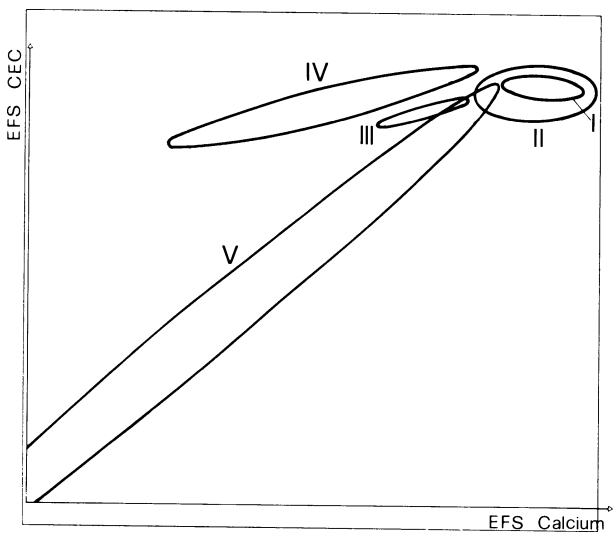


Fig. 5. Environmental fuzzy set ordination of Serengeti short grasslands. The abscissa represents the calcium fuzzy axis while the ordinate represents the CEC fuzzy axis. Ellipses of equal concentration at 5 % probability are drawn around the centroids of the 5 clusters of stands.

especially the two most abundant ones: *Sporobolus ioclados* (on hill tops) and *Kyllinga nervosa* (on upper hill slopes). This grassland community is the most extensive one within the Serengeti short grassland (Herlocker & Dirschl 1972; Banyikwa 1976; McNaughton 1983). The soils in this community are relatively saline and alkaline because they have been least affected by leaching because of the low permeability of the soil (de Wit 1978; Belsky 1988). The soils in this community may be regarded as net 'holders' of soil minerals because they occur on the plateau where the topography is flat and erosion low. This interpretation would correspond with that of a topography gradient in a desert watershed made by Olsvig-Whittaker, Shachak & Yair (1983).

2. *Eustachys paspaloides* community

This community occurs on the middle hill slopes and is characterized by group B species. The characteristic species of this community *Eustachys paspaloides*, occurs where the slopes are relatively steep, and around inselbergs where erosion is relatively high. The low magnesium level in the soils of this community is attributed to leaching and erosion. The soils of this community may be regarded as net soil mineral 'movers' caused by run-off erosion, which is generated from the inselbergs and relatively steep slopes (Olsvig-Whittaker, Shachak & Yair 1983).

3. *Sporobolus kentrophyllus* community

This community occurs on the lower hill slopes where the topography is relatively flat, and is characterrized by group C species, especially *Sporobolus kentrophyllus*. *Andropogon greenwayi* and *Chloris pycnothrix* , which are separated from other group C species in Fig. 4, indicate areas of heavy grazing and animal disturbance (McNaughton 1983; Belsky 1988).

4. *Hypoestes forskalei* community

This community occurs in the drainage areas and is characterized by group D species. The drainage areas have a relatively high landscape diversity. Where erosion has reduced soil depth, the shallow-rooting *Oropetium capense* and *Microchloa kunthii* are dominant. Where surface run-off and the associated salts accumulate during the rainy season salt pools are formed, which dry out in the dry season leaving white crusts of salts (Banyikwa 1976; de Wit 1978). Here *Sporobolus spicatus* and *S. sanguineus* are dominant.

Diversity

Data on species diversity are presented in Table 5. Diversity progressively increases from the hilltop stands to the drainage areas stands. The *Sporobolus ioclados* - *Kyllinga nervosa* community of the hill tops has a low species diversity and is dominated by few patchily distributed species (Banyikwa & Ganis subm.). The *Hypoe-*

stes forskalei community of the drainage areas has a high species diversity, arising from a high number of species per stand and overall high landscape heterogeneity. The *Eustachys paspaloides* and *Sporobolus kentrophyllus* communities are intermediate in this respect. A comparison of Tables 2 and 5 reveals that niche hypervolumes are not correlated with species diversity, although the most heterogeneous environment represented by community 4 (Cluster V) has the highest diversity and the largest hypervolume in the fuzzy system space.

Conclusions

The ordination in the fuzzy system space has indicated that topography is an important factor influencing overall structural organization in the Serengeti short grasslands. The importance of topography in influencing vegetation structure in East Africa has been evident since Milne (1935) introduced the catena concept. Grazing patterns (McNaughton 1985), soil properties (de Wit 1978) and vegetation patterns in the Serengeti ecosystem (McNaughton 1983) are greatly influenced by topography. The influence of topography on the structure and composition of grasslands is interpreted as arising from its effect on the distribution of the soil-physical and mineralogical factors (Banyikwa 1989), which effect is again influenced by animal disturbance effects (Banyikwa & Ganis subm.), surface run-off and leaching (Perring 1959; de Wit 1978; Olsvig-Whittaker, Shachak & Yair 1983).

Grazing in relation to topography would also explain the patchy distribution of the grasses in these grasslands. Grazing as well as trampling and the regular use of certain tracks by the migratory ungulate populations (Vesey-Fitzgerald 1960; McNaughton1983, 1985), damage and eliminate the more sensitive species from the grasslands as well as breaking the larger tussocks and patches. The broken patches become separated by lanes of dusty soil which are eroded; this process increases vegetation patchiness (Banyikwa & Ganis subm.).

The results obtained, apart from elucidating the structure and composition of the Serengeti short grasslands, provide an insight into the general nature of variation in tropical grassland vegetation. The distribution of stands in the ordination is essentially continuous and the species attain maximum abundance within limited zones defined by the bio-physical environment. Gradual environmental change and the associated vegetation continuum represent broad scale vegetation structure. On a fine scale, however, discontinuity is ubiquitous and pattern diversity and pattern intensity become an important characteristic of the vegetation as it is related to discontinuities in the physico-chemical environment.

The application of fuzzy set theory in this study confirmed ideas that are suggested by field observations but are not easily quantified and explained by traditional methods of data analysis. In a preliminary analysis of the data using Bray-Curtis ordination, principal components analysis and detrended correspondence analysis, it proved difficult to relate observed community trends to the pattern of edaphic factors. Thus, fuzzy set ordination is recommended in situations where the communities under investigation are not clearly defined, as is often the case in the tropics.

Acknowledgements. The first author thanks the Third World Academy of Science (TWAS) for financial support and the University of Dar es Salaam for funding the field work.

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Received 27 July 1989;
Revision received 7 November 1989;
Accepted 21 November 1989.