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SPECIES-HABITAT RELATIONSHIPS IN THE SERENGETI SHORT GRASSLANDS, TANZANIA

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Abstract. An improved principal components analysis ordination is used to study grass-habitat relationships in the Serengeti short grasslands. Species distribution is found to be influenced by soil factors along a topographic gradient.

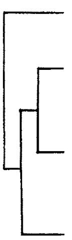
Introduction

The Serengeti National Park in northern Tanzania includes the Serengeti Plains where huge migratory ungulates numbering about 2.5 million animals congregate during the rainy season (Sinclair and Norton-Griffiths 1982). Such a large concentration of herbivores in 6,500 km sq of open grasslands create vegetation changes whose nature is unknown. For the conservation of the Serengeti National Park, it is important to know the structure of the vegetation and to detect some of the important environmental factors influencing the patterns observed. This is because the overall structure of the vegetation on the Serengeti Plains is influenced by an interplay of climatic, edaphic and biotic factors especially grazing and trampling (McNaughton 1983, 1984, 1985; Belsky 1985, 1988). Such data are needed to formulate long term management programs for the Serengeti National Park. The objective of this study therefore is to provide a description of the complex grass-habitat patterns in a small "homogeneous short grassland", by collecting soil samples from the centers of the grass mosaics. In an earlier study meant to describe the gross structure of the short grasslands (Banyikwa and McNaughton 1981, Bannyikwa et al. 1989) it proved difficult to relate the distribution of the grasses to the soil factors because the soil samples were combined per stand. It was thought that soil data collected in this manner would easily explain the complex grass distribution patterns in relation to the soil factors.

Materials and Methods

Species composition was measured as percentage cover from 32 random stands as described in Banyikwa et al. (1989). Soil samples were collected from 5 different quadrats for each species. The soil samples describing the habitat of a species were combined to form a composite sample and the analysed for pH, sodium, potassium, and magnesium using standard methods described by Koehler and Moodie (1978). The 21 species by 32 stands data matrix and the 4 soil factors by 21 species data matrix were first ordered by principal components analysis (PCA) using correlation matrices obtained from standardized centered data (Orloci 1978). Since this traditional PCA method proved to have low resolving power, the data sets were re-ordinated using their eigenvectors. The two sample ordinations were combined in a single ordination space using pH as the horizontal axis and magnesium as the vertical axis. Magnesium and pH were used as axes because they were the most discriminating factors in the environmental factors first ordination space. Pearsons product moment partial correlation coefficients were calculated in order to test the relationships between the species and soil factors within the principal components projections. All computations were done using the programs of Lagonegro and Feoli (1985).

Table 1. Relative percentage species abundance and mean analytic data of soil factors per species. Grouping of species is according to species classification as shown in the dendrogram.



	Species name	Species code	Abundance	Soil factors pH	Na	K	Mg
I	Sporobolus iocladus	SIOD	19.0	8.6	3.1	16.2	7.3
	Kyllinga nervosa	KYNE	17.9	8.5	1.5	17.9	9.9
	Eragrostis papposa	ERPA	5.1	8.5	1.6	14.2	9.2
II	Eustachys paspaloides	EUPA	15.3	8.4	2.9	13.3	6.2
	Microchloa kunthii	MIKU	1.4	8.1	1.1	10.7	6.9
	Sporobolus fimbriatus	SFIM	7.0	8.2	1.2	11.3	9.9
	Digitaria macroblephara	DIMA	3.3	8.4	3.2	15.3	8.6
	Digitaria abyssinica	DIAB	6.7	8.3	1.5	13.1	8.9
III	Sporobolus kentrophyllus	SKEN	12.6	8.1	2.8	13.6	7.9
	Harpachne schimperi	HARS	2.2	7.9	1.5	13.5	3.5
	Andropogon greenwayi	AGRE	0.7	7.9	1.9	13.0	11.1
	Chloris pycnothrix	CPYC	0.2	8.3	1.8	18.3	6.0
IV	Undifferentiated dicots	UNDI	6.3	9.5	11.6	9.4	6.8
	Cynodon dactylon	CYDA	2.7	8.7	5.2	12.2	8.1
	Oropetium capense	ORCA	0.9	8.5	5.1	12.8	5.1
	Sporobolus spicatus	SPIC	1.9	9.9	19.9	28.1	5.8
	Chloris gayana	CHGA	1.3	9.7	13.2	8.5	7.2
	Pennisetum clandestinum	PCLA	0.4	9.7	13.2	8.5	7.2
	Cenchrus ciliaris	CECI	0.1	9.9	12.2	8.5	7.2
	Psilolema jaegeri	PSJA	0.2	9.9	11.4	9.4	6.8
	Sporobolus sanguineus	SPSA	1.6	9.0	11.8	17.9	9.2

Results and discussion

Table 1 shows the relative percentage abundance and mean analytical soil data for each species of the grasslands. The species classification is presented in the dendrogram at the left of Table 1. Cluster I of 3 species includes the two most abundant species: Sporobolus iocladus and Kyllinga nervosa. Cluster II consists of 5 spe-

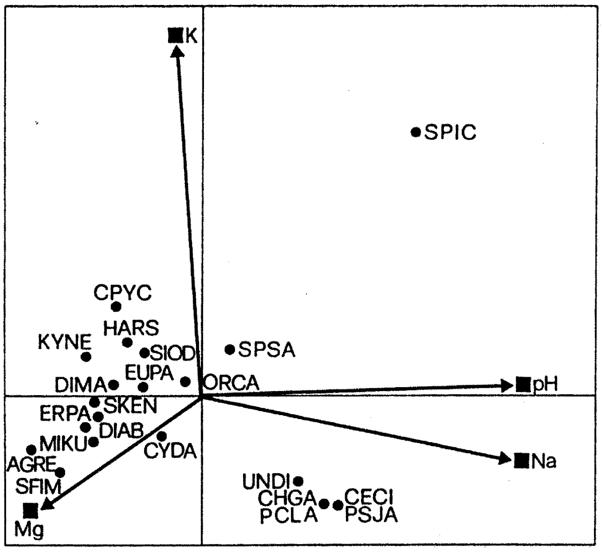


Fig. 1. Biplot of species and soil factors in a traditional principal components ordination.

cies which include the third abundant species, Eustachys paspaloides. Cluster III consists of 4 species which include the fourth abundant species, Sporobolus kentropylus. Cluster IV consists of rare species. The classification distinguished four intergrading grassland communites of overlapping species associations. Detailed descriptions of these communities have been provided (Banyikwa et al. 1989).

The results of biplotting species ans soil factors in a traditional principal components ordination are presented in Figure 1 and Table 2. The low resolving power of this method is indicated by the lack of clear association between the projections of the species and the soil factors although the soil samples were collected from

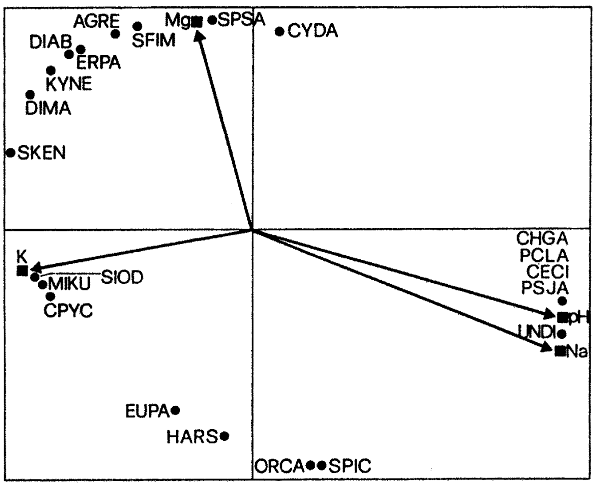


Fig. 2. Biplot of species and soil factors using correlation matrices derived from the eigen vectors. pH is plotted on the horizontal axis and Magnesium is plotted on the vertical axis.

an area where each species indicated the highest abundance. Figure 2 shows the biplot results of PCA using correlation matrices derived from the eigenvectors. The high resolving power of this method is shown by the clear association between the species and the soil factors. The extracted variances of the first four components are:

component	1	2	3	4
Extracted variance (%)	50.96	25.63	22.30	1.08

The first axis is determined by high levels of pH and Sodium, low levels of Potassium and is associated with drainage areas where animal grazing is the least. The second axis is comprised of high levels of Magnesium, hillslopes and heavy animal grazing. On the scale of the third axis, Potassium concentration, in association with hilltops and animal grazing are the important factors.

The grasses; Chloris gayana, Pennisetum clandestinum, Cenchrus ciliaris, and Psilolema jaegeri, and the undifferentiated dicots, mainly Hypoestes forskalei, positively correlate with the first axis, associating with drainage areas, high pH and Sodium, coincide with low overall species abundance (Table 1).

Eustachys paspaloides, Harpachne schimperi, Oropetium capense and Sporobolus spicatus which receive low projections along the second axis, negatively correlate with Magnesium. Eustachys paspaloides which attained high abundance on the sharp slopes is negatively correlated with the second axis while Sporobolus kentrophyllus which shows maximum abundance on the relatively flat hillslopes in negatively correlated with the first axis. Andropogon greenway; an established heavy grazing indicator grass (Vesey-

Table 2. Correlation coefficients between species and soil factors based on the first three components of principal components analysis.

Cluster	Species name	pH	Na	K	Mg
I	Sporobolus iocladoa	-0.89	-0.81	-0.99	-0.12
	Kyllinga nervosa	-0.84	-0.92	0.52	0.77
	Eragrostis papposa	-0.73	-0.83	0.36	0.87
II	Eustachys paspaloides	-0.40	-0.24	0.76	-0.74
	Microchloa kunthii	-0.88	-0.79	0.99	-0.17
	Sporobolus fimbriatus	-0.53	-0.66	0.10	0.97
	Digitaria macroblephara	-0.91	-0.96	0.65	0.66
	Digitaria abyssinica	-0.77	-0.86	0.42	0.84
III	Sporobolus kentrophyllus	-0.99	-0.99	0.84	0.42
	Harpachne schimperi	-0.22	-0.06	0.63	-0.85
	Andropogon greenwayi	-0.61	-0.73	0.94	0.94
	Chloris pycnothrix	-0.85	-0.76	0.99	-0.22
IV	Undifferenciated dicots	0.99	0.99	-0.87	-0.38
	Cynodon dactylon	-0.01	-0.17	-0.42	0.95
	Oropetium capense	0.10	0.26	0.35	-0.97
	Sporobolus spicatus	0.12	0.28	0.32	-0.98
	Chloris gayana	0.99	0.97	-0.93	-0.24
	Pennisetum clandestinum	0.99	0.97	-0.93	-0.24
	Cenchrus ciliaris	0.96	0.96	-0.93	-0.24
	Psilolema jaegeri	0.99	0.99	-0.93	-0.24
	Sporobolus sanguineus	-0.26	-0.41	-0.18	0.99
	Soil factors				
	pH	1.00			
	Sodium	0.99	1.00		
	Potassium	-0.90	-0.82	1.00	
	Magnesium	-0.32	-0.47	-0.13	1.00

Table 3. Extracted variances (%) on the first four components of PCA for primary data (PCA 1), and for data based on correlation coefficients between species and soil factors on the first three components (PCA 2).

Fitzgerald 1960, McNaughton 1983, 1985) attains high abundance on the flat hillslopes.

The grasses; Sporobolus ioclados, Microchloa kunthii and Chloris pycnorhrix, negatively correlate with the first axis, associating with hilltops on relatively low pH level in soils, are positively correlated with Potassium. Digitaria macroblephara and the sedge: Kyllinga nervosa negatively correlate with pH and high Sodium concentration.

Sporobolus fimbriatus, Sporobolus sanguineus and Cynodon dactylon receive high projections along the second axis, associated with high concentrations of Magnesium, occur on relatively flat hillslopes. Digitaria abyssinica and Eragrostis papposa are positively correlated with the second axis in soils with high Magnesium (Table 2).

The ordination reveal the four grassland communities exhibited by the species classification. Starting from the hill tops where the characteristic species is Sporobolus ioclados (cluster I), there are two species distribution projections along the hilltops-drainage areas first axis. Species associated with relatively flat hillslopes, on high Magnesium soils, follow the high second axis projections route, with the leading spe cies being Sporobolus kentrophyllus (cluster II). Species correlated with low Magnesium soils on relatively sharp slopes follow the low second axis projections direction and the characteristic species is Eustachys paspaloides (cluster III). Drainage areas grassland community is indicated by high pH and Sodium with a high abundance of dicots (cluster IV).

Conclusion

The ordination has described species abundance gradients related to a variety of bio-edaphic factors. As cautioned by Greig-Smith (1983) relationships between environmental gradients and species suggested by the ordination should not be interpreted as causes underlying species behaviour. Ordination primarily exposes compositional gradients that are related to a factor complex which may arise from many factor gradients (Whittaker 1978). The results of ordination therefore suggest some of the probable overall patterns of bio-edaphic interrelationships. Furthermore, factors like microclimate, interspecific interactions and grazing which are known to influence the abundance of the grasses on the Serengeti Plains (Banyikwa 1976, 1981, 1987, 1988, McNaughton 1979, 1984, 1985, Belsky 1983, 1988) were not investigated in details. Nevertheless, the combination of classification, ordination and partial correlation analyses provide an overview of the grass-habitat relationships and give an opportunity to evaluate the importance of different environmental factors influencing individual species behavior within the constraints of the factors measured.

A topographic complex was found by ordination and classification to be the primary environmental component associated with the spatial distribution of edaphic factors and the plant species. Since, (1) volcanic ash blown by the easterly winds and deposited on these grasslands was the primary source of edaphic factors; (2) records show that the volcanic ash was rich in sodium and potassium and relatively poor in magnesium (Pickering 1959); and (3) distribution of ash was uniform depending on wind direction and speed, only extrinsic factors must have caused the spatial distribution of edaphic factors. Based on the field observations and data contained in this paper, I suggest three major factors; (1) rain associated infiltration, (2) rain and wind correlated erosion, and (3) animal disturbance associated effects. The bio-edaphic factors spatial distribution as influenced by the topographic gradient define four habitats: (1) a relatively non leached Potassium rich hill tops region, (2) a relatively heavily leached steep hill slopes part with low Magnesium, (3) a relatively flat hill slopes landscape with high Magnesium, and (4) a sodic and alkaline drainage area. Plant species occupy certain zones within this bio-edaphic factors gradient in accordance with their level to tolerate certain ranges of salinity and alkalinity (Banyikwa 1976; Banyikwa and McNaughton 1981; Banyikwa et al. 1989; Belsky 1987, 1988).

The biplot of the modified version of principal components analysis (PCA) in which the eigenvectors arising from the first PCA analysis are used as derived data for the calculation of a secondary correlation matrix which is then used in the ordination, made it possible to display relationships between the spatial distribution of grasses and soil factors in a clearer way than has been possible using traditional methods. In provisional analyses of the data using canonical correspondence analysis (Ter Braak 1986) and traditional PCA (Orloci 1978), it was not possible to relate the distribution of the species and the measured soil factors. Therefore it is recommended that in situations where an attempt is being made to partition the complexity of a fine scale vegetation mosaic in relation to the soil factors a PCA on derived scores should be done.

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