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VEGETATION/ENVIRONMENT RELATIONSHIPS IN THE CENTRAL AREA OF THE CAPE MIDLANDS, SOUTH AFRICA

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Abstract. A syntaxonomic classification of the grasslands, dwarf shrublands and succulent thicket of the semi-arid eastern Cape midlands was prepared using two-way indicator species analysis. The relationships between selected environmental variables and the vegetation gradients were examined. Median annual rainfall and altitude were investigated using linear regression. Surface soil samples were analyzed for field moisture content, organic matter content, pH, conductivity, Ca, Mg, K, Na, P and texture. The results were ordinated using principal component analysis and compared with the structural/floristic classification of the vegetation. A shallow precipitation gradient was exposed, but does not adequately explain the high structural and floristic diversity. Axis 1 of the ordination revealed a gradient of decreasing Ca, Mg and conductivity values from the minerally rich sites of the shrublands to the leached conditions of the grasslands and dwarf shrublands. Axis 2 revealed a soil texture gradient of high clay and silt in the succulent dwarf shrublands to the sandy soils of the dwarf shrublands and grasslands. The models provide a set of multiple working hypotheses for understanding vegetation/environment interactions in the region.

Introduction

Total floristic classifications using indirect gradient analysis techniques yield two-way tables in which the relevé sequence may parallel an environmental gradient. Traditionally, floristic data are collected without due regard for the availability of accompanying environmental data (particularly precipitation), and it has seldom been possible to evaluate the relationship between major gradients. Climatic modelling and the preparation of surface response models for precipitation provides an exciting source of ancillary data. Where phytosociologists have operated over long gradients, and prepared classifications in landscapes with small changes in indirect environmental gradients (e.g. elevation) (Austin and Smith 1989), their hypotheses are testable using direct gradient analysis. Studies which have kept certain environmental variables (e.g. substrate type, aspect, elevation and treatment) within narrow limits provide examples where the methods of direct gradient analysis may be employed to further reduce and understand the precipitation gradients (Kessell 1979).

In the interpretation of environmental gradients responsible for differentiating plant communities over short spans, Palmer *et al.* (1988) used principal component analysis (PCA) of surface soil characteristics. Similar studies in arid regions (Secor *et al.* 1983) and wetter climates (Huntley and Birks 1979), have helped further understand floristic gradients. The ordination elucidates short span environmental gradients in natural ecosystems (Gower 1969, Whittaker 1975, Kessel 1979, Webster 1979), and is statistically favoured over other ordination methods (Wartenberg *et al.* 1987).

A syntaxonomic classification of the vegetation of the study area had been prepared (Palmer 1991). The relationship between environmental variables and the classification was developed by preparing a linear model of median annual rainfall and altitude against relevé sequence. Soil variables from a sub-sample of relevés in each structural class were ordinated using PCA.

The study area

The study area is some 40.000 km^2 in extent, and is situated in the Nama-Karoo and Grassland Biomes (Rutherford and Westfall 1986) between 31°-33° S and 24°-26° E. Altitude varies from 375 m at Jansenville to 2502 m at Compassberg.

Triassic sandstones of the Beaufort Group are the most prominent geological formation (Visser 1986), and have been intruded by dolerite, giving rise to an uneven topography of mesas, hillocks and sharp ridges. Deep, Quaternary alluvial deposits occur on the bottomlands.

In common with the soils of the other arid and semi-arid regions of the world (Evenari 1985), the main soil orders are aridosols and alfisols (MacVicar *et al.* 1977, Vorster 1985). The aridosols contain layers of duripans within 1 metre of their surface. These calcareous hardpans were apparently formed during pluvial episodes (Evenari 1985) when active leaching occurred. The shallow aridosols are found on pedologically young landscapes (Ellis and Lambrechts 1986) that have developed under conditions of rainfall deficiency (Van der Merwe 1941). The pediments contain structureless to weakly structured soils, mainly developed from *in situ* weathering, with lime generally present in the entire landscape (Figure 1). The presence of lime is an

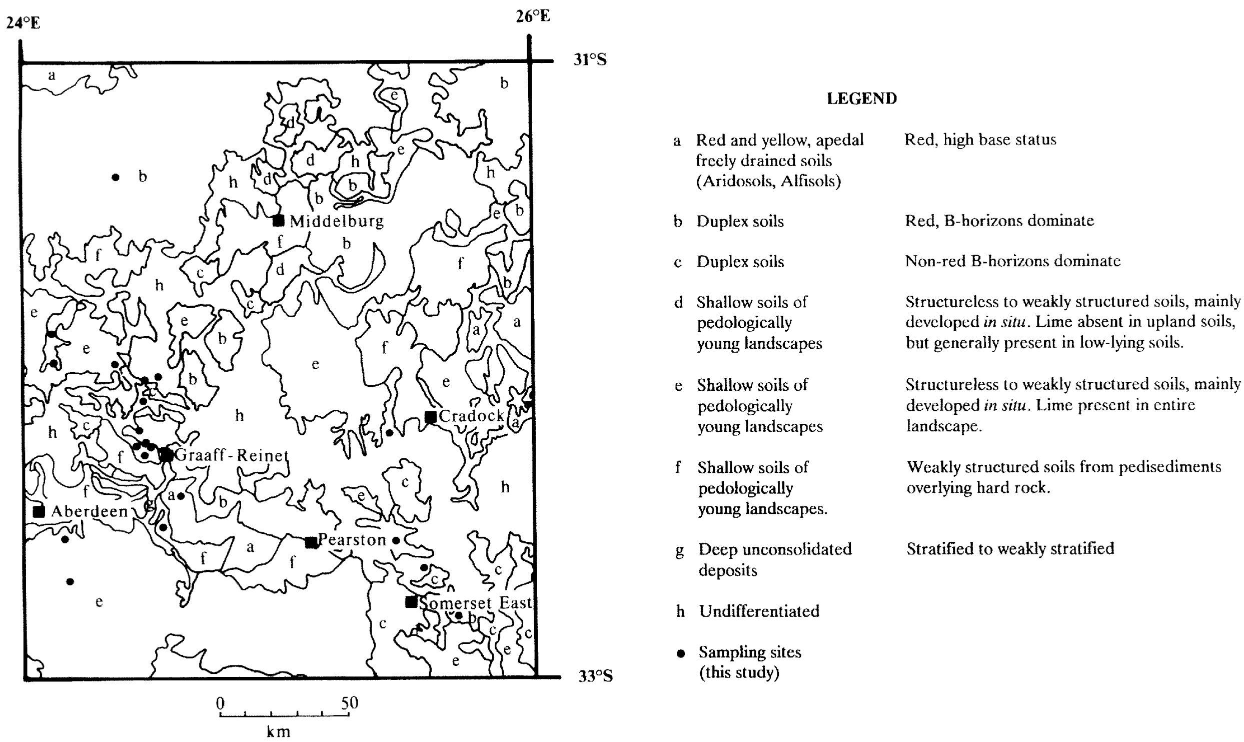

Fig. 1. Broad soil patterns in the study area (after Ellis and Lambrechts 1986) and the location of sampling sites.

indication of the limited extent to which these soils have been leached (Ellis and Lambrechts 1986).

The uplands contain rocky, shallow lithosols of the Mispah Form (MacVicar *et al.* 1977). The weathering of the plagioclase (mainly Ca, Na, Al, Si) and pyroxene (Ca, Na) (Mg, Fe, Al) $(Si, Al)_2 O_6$ may lead to a favourable environment for plant growth. The lithosols are found in three broad categories based on the geological origin of the dominant parent material: 1) the Mispah/rock complex of sloping landforms where dolerite overlies sandstone or mudstone (Van Riet and Minnaar 1977); 2) the Mispah soils on Beaufort Group sandstone on the convex sloping landforms; 3) the Mispah soils of the high-lying or raised plateaux of flat to gently sloping landforms. In all instances, the material underlying the A-horizon is hard rock, and the soil series classification of MacVicar *et al.* (1977) did not provide adequate classification classes for the purposes of this study. Ellis and Lambrechts (1986) regard much of the study area as "undifferentiated" (Figure 1).

The climate of the study area is influenced by altitude and distance from the moderating influence of the ocean. There is a rainfall gradient from east (591 mm at Somerset East) to west (284 mm at Aberdeen) and the area receives summer rain (October-March). The reliability of annual rainfall (expressed as a percentage of years with rainfall greater than or equal to 85% of the mean annual rainfall) is 65-70% (Venter *et al.* 1986). Large temperature fluctuations (both daily and seasonal) are an outstanding feature (Venter *et al.* 1986). Mean daily maximum temperature is 30° C in the hottest month, with a mean annual temperature of 15° C. The duration of frost at Middelburg is 158 days (Venter *et al.* 1986), one of the longest periods experienced by stations in the region.

The vegetation contains examples from three phytochoria: the Dwarf Shrublands of the Nama-Karoo biome (Rutherford and Westfall 1986); the Succulent Thicket of the Subtropical Transitional Thicket (Cowling 1984); and the Grasslands and Shrublands of the Sudano-Zambezian Region (Werger and Coetzee 1978). An abridged constancy table (Table 1) summarizes the hierarchical classification.

Grasslands (communities 1A1-1B1) in the study area are characterized by high constancies of *Melica racemosa, Eragrostis chloromelas, E. curvula* and *Passerina montana*. Differential species of the three grassland communities include *Pelargonium abrotanifolium, Tetrachne dregei* and *Merxmuellera disticha*.

Shrublands (communities 2A1-2A5) consist of bushclumps containing woody shrubs *(Rhus undulata, R. erosa, Euclea undulata, E. crispa, Diospyros austro-africanus)* separated from one another by grasses *(Heteropogon contortus, Ehrharta calycina)* and dwarf shrubs *(Euryops spathaceus, Felicia filifolia, Helichrysum rosum)*.

Dwarf shrublands, dominated by low-growing (<0,4 m) perennial woody plants, are represented by three formations, with varying proportions of succulence and grassiness distinguishing between formations. Grassy dwarf shrubland (communities

Table 1. An abridged constancy tabel for the differential and abundant species in the grasslands (●), shrublands (◢), grassy dwarf shrublands (○), dwarf shrublands (▲), succulent dwarf shrublands (■) and succulent thicket (□) in the Cape midlands. 1 = 0-20% constancy; 2 = 21-40%; 3 = 41-60%; 4 = 61-80% and 5 = 81-100%.

Community number	1A1	1A2	1B1	2A1	2A2	2A3	2A4	2A5	3A1	3A2	3B1	3C1	3D1	4A1	4A2	4A3
Structure	●	●	●	◢	◢	◢	◢	◢	○	○	○	▲	■	□	□	□
Number of relevés	3	4	12	11	4	5	14	16	15	13	40	14	11	10	13	5
Differential species of Community 1A1																
Helichrysum nudifolium	3															
Indigofera rugosa	3															
Schismus inermis	3		1				1				1					
Protasparagus thunbergii	3															
Pelargonium abrotanifolium	3															
Differential species of Community 1A2																
Aloe arborescens		2												1		
Tarconanthus camphoratus		2														
Euryops tenuissimus		2														
Tetrachne dregei		2	1									1				
Pteronia glauca		2						1			1	1	1			
Hyparhennia hirta		2														
Differential species of Community 1B1																
Merxmuellera disticha		2	5		3		1	1		1	1	1				
Elytropappus rhinocerotis			2		2	1	1	1			1	1				
Pentzia globosa			2					1			1	1				
Differential species of Communities 1A1-1B1 & 2A4																
Eragrostis chloromelas	3	5	4				3	1			1			1		
Melica racemosa	3	2	1				2			1	1	1				
Digitaria eriantha	3		1			1	4	2	1	1	1	1				
Eragrostis curvula	3	2	1	1			1	1	1	1	1	2				
Passerina montana	3	2	2													
Differential species of Community 2A1																
Euryops spathaceus				3		5	1	1						1		
Ehrharta calycina			1	2	2	3	2	1				1				
Differential species of Community 2A2																
Sutera mollis			1		3		1					1				
Euclea crispa			1		3		1									
Buddleja saligna				1	2	1	2									
Protasparagus subulatus					2	1								1	1	
Pellaea sp.					2	1										
Indigofera denudata					2	1						1				
Solanum coccineum			1		2		2							1		
Eustachys paspaloides					2		2									
Solanum tomentosum				1	2		1		1	1		1		1	1	
Eriocephalus umbellatus			1		2			1	1	1		1				
Felicia filifolia			2		2		2	1		1	1	2	1			
Aloe broomii			1	1	2	1										
Mestoklema albanicum			1		2	2						1				
Nenax microphylla			2		2		1	1	1		1	1				

Table 1 - continued

Community number	1A1	1A2	1B1	2A1	2A2	2A3	2A4	2A5	3A1	3A2	3B1	3C1	3D1	4A1	4A2	4A3
Structure	●	●	●	◢	◢	◢	◢	◢	○	○	○	▲	■	□	□	□
Number of relevés	3	4	12	11	4	5	14	16	15	13	40	14	11	10	13	5
Differential species of Community 2A3																
Diospyros austro-africanus		2	2			5	2	1						1	1	
Euclea undulata				1		3		1						2	1	
Selago corymbosa						2										
Viscum obscurum						2									1	
Differential species of Community 2A4																
Teucrium africanum				1			3							1	1	
Walafrida saxatilis			1	1			3					1				
Indigofera sessilifolia			1				3	1		1	1	1			1	1
Sporobolus fimbriatus				1			2				1					
Eriocephalus africanus							2		1							
Lantana rugosa							2							1	1	
Helichrysum cymosum							2									
Indigofera heterophylla				1			2					1			1	
Cymbopogon marginatus			1				2	1								
Grewia occidentalis				1			2				1			1	1	
Differential species of Community 2A5																
Becium burchellianum				1				3	2		1	1			1	
Helichrysum dregeanum			1					2			1	1				
Differential species of Communities 2A1 - 2A5																
Rhus undulata				5	2	4	3	1		2				1	1	
Rhus erosa		2	2		2	2	1	2								
Differential species of Communities 3A1 & 3A2																
Enneapogon scoparius						1	2	2	4	5	1				1	
Tragus racemosus			1					2	3	2	1	2				
Differential species of Community 3A2																
Crassula obovata								1		2						
Setaria sphacellata			1							2			1			
Aptosimum procumbens							1	1		2	1	2	1			
Anacampseros telephiastrum										1	1	1	1			
Differential species of Community 3C1																
Euryops anthemoides			1	1			1					2				
Bulbine abyssinica							1				1	2	1			
Senecio radicans			1	1		1	1					2	2		1	
Sutera halimifolia			1			1						2			1	
Mesembryanthemum karrooense												2				
Gnidia polycephala								1		1		2				
Psilocaulon articulatum											1	1	1			

Table 1 - continued

Community number	1A1	1A2	1B1	2A1	2A2	2A3	2A4	2A5	3A1	3A2	3B1	3C1	3D1	4A1	4A2	4A3
Structure	●	●	●	◢	◢	◢	◢	◢	○	○	○	▲	■	□	□	□
Number of relevés	3	4	12	11	4	5	14	16	15	13	40	14	11	10	13	5
Differential species of Community 3D1																
Sarcocaulon camdeboense										1	1		4	1	1	
Senecio acutifolius											1		3			
Haworthia viscosa												2	3			
Senecio longiflorus												1	2		1	4
Pachypodium succulentum											1	2	3		1	1
Pegolettia retrofracta							1	1		1	1	1	2			
Euphorbia ferox								1			1		2		1	
Mestoklema tuberosum											1	1	2			
Galenia sarcophylla											1	1	2			2
Gazania krebsiana							1				1	1	2			
Differential species of Communities 3B1, 3C1 & 3D1																
Eberlanzia spinosa							1	1	1	1	3	3	2			1
Rosenia humulis			1			1	1				3	2	2			1
Trichodiadema pygmaeum			1						1	1	1	2	3		1	
Differential species of Communities 2A3-3D1																
Tragus koeleroides			2	1		1	5	2	2	2	2	2	1		1	
Eragrostis lehmanniana			1	1		3	1	3	4	3	2	4		1	1	
Eragrostis obtusa				1		1	3	2	2	3	3	3	2	2	2	
Aristida diffusa			2		3		3	4	3	3	1	2	1	1	2	
Blepharis villosa				1		3	3	1		1	2	3	2		1	
Heteropogon contortus				2				4	4	1	1					1
Felicia muricata			1	1			2	2	2		3		1		1	
Hibiscus pusillus			1	1		2	4	2		1	1					
Differential species of Community 4A2																
Boscia oleoides														1	2	
Aloe ferox				1						1				1	3	1
Diospyros lycioides			1				1			1			1		2	
Differential species of Community 4A3																
Peliostomum origanoides												1		1	1	4
Aizoon rigidum															1	4
Aloe striata																4
Euphorbia heptagona																2
Differential species of Communities 4A1, 4A2 & 4A3																
Portulacaria afra														3	3	5
Pappea capensis														4	4	2
Grewia robusta				3			1	1						3	5	5
Maytenus polyacantha		2	1	1	2	3	1	1						3	4	2
Rhoicissus tridentata													1	2	1	2
Carissa haematocarpa							1						1	2	2	
Abutilon sonneratianum														2		
Panicum maximum										1				2	1	

Table 1 - continued

Community number	1A1	1A2	1B1	2A1	2A2	2A3	2A4	2A5	3A1	3A2	3B1	3C1	3D1	4A1	4A2	4A3
Structure	●	●	●	◢	◢	◢	◢	◢	○	○	○	▲	■	□	□	□
Number of relevés	3	4	12	11	4	5	14	16	15	13	40	14	11	10	13	5
Frequent species																
Themeda triandra	5	3	3	1	2	2	4	4	1	1						
Lycium schizocalyx		2	1	1	2		3	1	1	1	4	2	4		1	4
Chrysocoma ciliata		2	3	1	5	5	4	3	2	4	3	3		2	1	
Pentzia incana		2	1	5	2	3	4	3	5	5	5	5	5	3	5	4
Walafrida geniculata		2	1	2		3		2		1	1	1		1		1
Protasparagus striatus				2			2				1		2	1	3	2
Protaspargus suaveolens			1	1			2	1		1	1	3	1	1	2	
Blepharis capensis							1	1	1	1	1	2			2	2
Lycium oxycarpum				1				1	1	1	1			3	1	2
Helichrysum rosum			1	2	2	1	2	2	1	2	1	1	1		1	
Eriocephalus ericoides			1	1			3	1			2	2	2	1	1	
Aristida congesta			1				2	1	3	1	4	5	5	1	4	1
Crassula muscosa				1	2	2		1	1	1	1	2	2	1	1	2
Cymbopogon plurinodis			2			1	1	1	1	1					1	
Thesium rigidum								2	2	2	1	1	2	1		
Rhigozum obovatum									1	1	1	2	3	2	4	5
Rhus longispina				2										2	1	
Cadaba aphylla									1			1	1	1	1	

3A1-3B1) occurs on the pediments on shallow soils with a calcrete hardpan at 0,2-0,3 m from the surface. Grasses in these communities include *Aristida diffusa, Enneapogon scoparius, Eragrostis lehmanniana, E. obtusa, Tragus racemosus* with the dwarf shrubs *Aptosimum procumbens* and *Blepharis villosa.*

Typical dwarf shrubland (community 3C1), located on the pediments on shallow, pedologically young soils, is dominated by *Eberlanzia spinosa* and *Rosenia humulis*. Differential species of this community include *Euryops anthemoides, Senecio radicans, S. halimifolia* and *Gnidia polycephala.*

Succulent dwarf shrubland (community 3D1) is dominated by leaf succulents and occurs on the deeper, pedologically young soils of the bottomlands and pediments. The succulent genera include *Mestoklema tuberosum, Haworthia viscosa, Pachypodium succulentum, Pegolettia retrofracta, Sarcocaulon camdeboense, Senecio longiflorus, S. acutifolius* and *Galenia sarcophylla.*

Succulent thicket (communities 4A1-4A3) is structurally and floristically distinctive, consisting of short to medium (1,5-3,0 m) succulent shrubs *(Portulacaria afra)*, short to medium woody shrubs *(Maytenus polyacantha, Carissa haematocarpa, Boscia oleoides, Pappea capensis)*, dwarf shrubs *(Peliostomum origanoides)* and climbers *(Rhoicissus tridentata).*

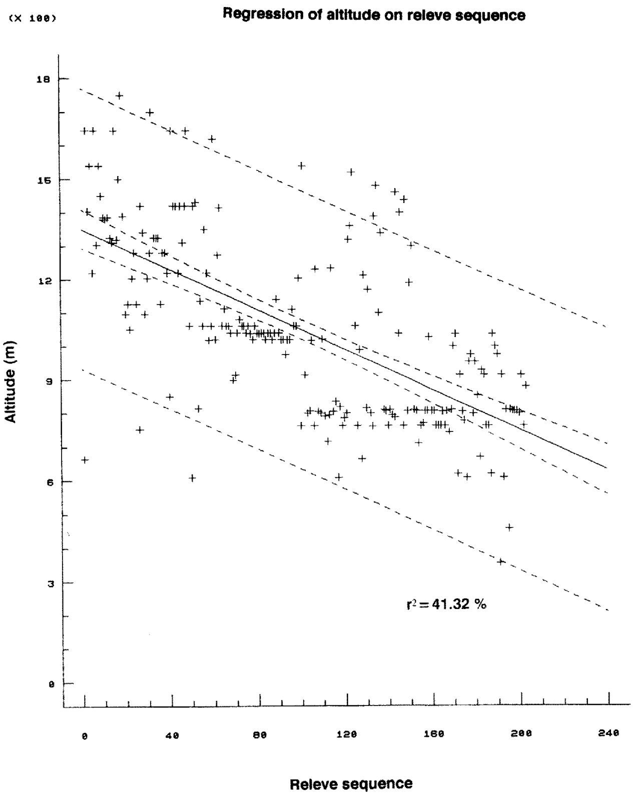

Figure 2. Linear regression of altitude on relevé sequence.

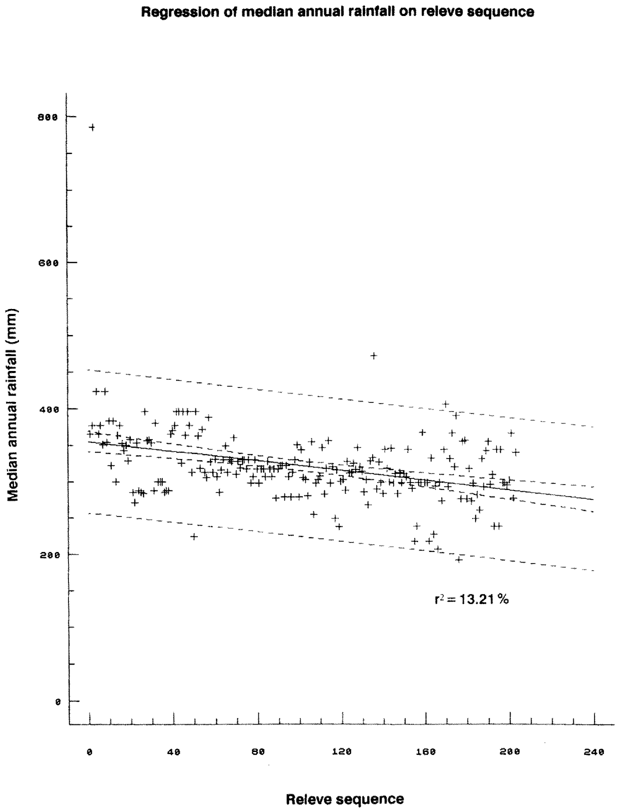

Fig. 3. Linear regression of median annual rainfall on relevé sequence.

Materials and methods

Median annual rainfall (MAR) (mm) for each relevé was extracted from a surface response model (Dent *et al.* 1988) of rainfall for southern Africa. Altitude for each relevé was obtained from a digital terrain model. Using the relevé sequence (Palmer 1991), a linear regression model was prepared for altitude (Figure 2) and median annual rainfall (Figure 3).

Twenty soil samples were collected from nineteen 100 m^2 quadrats in a single operation in May 1987 (Figure 1). The quadrats were subjectively selected from examples of the plant communities recognized by Palmer (1991), and were situated predominantly in undifferentiated (Ellis and Lambrechts 1986) soils. A sample of 100 cm^3 was collected from the surface to 0,3 m within each quadrat using a bucket-type soil auger. The surface litter was carefully removed before the sample was taken and placed in separate, watertight bags for transfer to the laboratory. Moisture content (%) was calculated according to Van Rooyen (1978). Organic content (%) was determined by heating samples at 550 °C for 1-2 hours in an electric muffle furnace. The pH was determined using a Metrohm pH meter Model E 280 A after 20 g of sieved (mesh size 2 mm), airdried soil had been transferred to beakers and 50 ml distilled watter addes. Available phosphorus was determined using the Bray No. 1 acid extraction procedure (FSSA 1974). Particle size distribution was determined by pipette analysis (Day 1965), and the air-dry colour of the samples was ascertained in the laboratory using a colour chart (Munsell Color Company 1971).

The soil data for the 20 samples consisted of twelve variables: moisture content (%); organic content (%); pH (H_2O); Mg; Ca; Na; K; Cond (μmohs/cm); available phosphorus; sand (%); silt (%) and clay (%). The variables were standardized to zero mean and unit variance because of the different measurement units. Ordination of the samples on the basis of the soil data was carried out using principal component analysis (PCA) (Anonymous 1989).

Results and discussion

Neither regression model adequately explains the vegetation gradient developed using indirect methods. The MAR model (Figure 3) has a low co-efficient of determination (R-squadred = 13.21%) and there is a discernable trend of increasing aridity from the grasslands to the succulent dwarf shrublands (Y = —0.33× + 355.3). It was not possible to determine the point of differentiation between each community, suggesting that factors other than precipitation may be

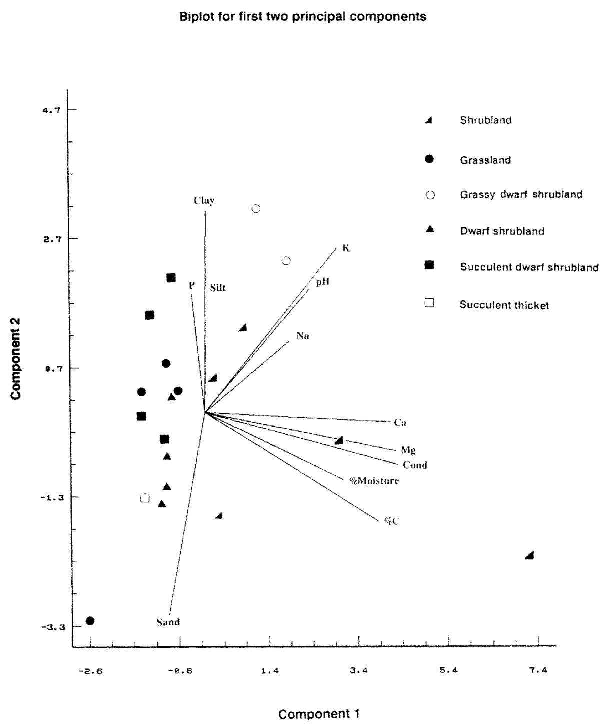

Fig. 4. A plot of the first and second principal component axes for twelve soil variables.

Table 2. Details of the site variables and vegetation type along the soil colour gradient in the study area.

Air-dy colour	Relevé numer	Vegetation type	Altitude (m)	Geology
10YR3/2	273	Shrubland	1667	Dolerite
10YR3/2	270	Shrubland	1348	Dolerite
*10YR3/2	270	Shrubland	1348	Dolerite
10YR3/3	199	Shrubland	1318	Dolerite
10YR4/3	272	Shrubland	1639	Dolerite
10YR4/4	217	Grassland	1500	Sandstone
10YR5/3	219	Shrubland	1576	Sandstone
10YR5/2	275	Grassland	1450	Sandstone
10YR5/2	274	Grassland	750	Sandstone
10YR5/3	271	Dwarf shrubland	1310	Dolerite
10YR5/4	230	Dwarf shrubland	1300	Dolerite
10YR5/4	269	Succulent thicket	909	Dolerite
7.5YR5/4	131	Succulent dwarf shrubland	750	Alluvium
7.5YR4/4	193	Dwarf shrubland	1640	Sandstone
7.5YR4/4	261	Succulent dwarf shrubland	630	Sandstone
7.5YR4/4	279	Grassy dwarf shrubland	1000	Alluvium
7.5YR5/6	267	Grassy dwarf shrubland	750	Sandstone
7.5YR5/4	258	Succulent dwarf shrubalnd	742	Alluvium
5YR5/6	268	Dwarf shrubland	850	Dolerite
5YR5/6	266	Succulent dwarf shrubland	790	Alluvium

* Sample from inside the bush-clump.

influencing floristic composition.

Altitude, an indirect environmental gradient (Austin 1980), is a surrogate for a range of environmental variables (Austin and Smith 1989). The regression model of altitude versus relevé sequence had a higher coefficient of determination (R-squared = 41.32%) than MAR. The relevé sequence paralleled the gradient of decreasing altitude. The highlands of the study area are situated on substrates of sandstone and dolerite origin, and this gradient may be an artifact of the dependence of the vegetation on substrate.

The first and second principal component provided a model of the relationship between vegetation classification and soil (Figure 4), and accounted for 38.2% and 21.3% of the total variance respectively. The samples along the first component axis have high Ca, Mg and conductivity values on the right hand side and lower values on the left. The extreme right contains minerally rich sites in the shrubland, and on the left are the leached soils of the dwarf shurblands and grassland. The grassy dwarf shrublands have higher Ca, Mg and conductivity levels than the succulent dwarf shrubland. The higher Ca levels in the grassy dwarf shrubland may be explained by the regular presence of a $CaCO_2$ (limestone) layer 0,2-0,3 m below the surface.

The second principal component axis parallels the soil texture gradient in the ecosystem. In the upper half of the diagram, the high clay and silt samples occur, with the sandier samples in the lower half. The succulent dwarf shrubland and the grassy dwarf shrubland on the pediments are higher in clay and silt than those of the shrubland, grasslands and succulent thicket and they have consistently more higher pH.

The soils of the mountain slope communities (shrublands and grasslands), where the rainfall is higher, are leached of K and Na which may have been transported to the pediments. Ca and Mg, derived from the plagioclase and pyroxene minerals in the dolerite parent material, have high levels. Moisture content of these soils was high.

Dolerite dykes adjacent to sandstone and mudstone parent material on the pediments may ameliorate the alkalinity, accounting for the *Eberlanzia*-dominated succulent dwarf shrubland. The ameliorating influence of the dolerite is also found on the concave slopes where *Portulacaria afra* occurs. Conditions of moderate acidity appear to favour the succulent thicket.

A laboratory determination of air-dry soil colour revealed a gradient from the dark brown soils (10YR 3/2) of the high-lying areas to the reddish brown soils (5 YR 5/6) of the bottomlands (Table 2). This parallels the gradient from the high altitude grasslands and shrublands to the low-lying succulent dwarf shrublands.

When comparing the soils from this study with the soil data from other biomes (Table 3), it is apparent that the pediments are covered by a thin layer of minerally-rich, eutrophic soils. High pH may be a consequence of high Na and K levels at or near the surface. The high mineral and base status is further aggravated by low precipitation and soil surface compaction. Leaching of minerals and salts is hampered by the presence of impermeable rock at shallow depths (0,3-0,5 m), as well

Table 3. A comparison of the soil characteristics from five broadly synonymous soil types in the Karoo and other biomes in South Africa.

Biome	Nama-Karoo			Savanna	Grassland	Fynbos
Formation*	1	1	2	3	4	5
Author**	a	a	b	c	d	e
Sample No.	6	6	258	58	183	3
Depth (cm)	0-6	6-25	0-30	0-30	0-30	0-30
Sand (%)	84.7	68.4	71.5	70.0	68.0	—
Silt (%)	5.8	6.6	12.1	16.0	15.0	—
Clay (%)	9.1	24.8	16.3	14.0	18.0	—
pH (H_2O)	8.3	8.0	7.1			7.7
pH (KCl)	—	—	5.8	6.8		
Na (me/100 g)	10	10	15.7	9.6	—	154
K (me/100 g)	50	20	82.3	87.4	71.7	77
Ca (me/100 g)	510	960	480	737	350	470
Mg (me/100 g)	80	200	266	269	260	1330
S-value	650	1190	844	1103	—	2030
CEC	600	1190	—	—	—	—
Conductivity	—	—	76	99	—	210
% oxidizable C	0.3	0.3	2	—	—	4
% moisture	—	—	2.7	3.1	—	—
P (mg/kg)	—	—	19	—	5	4
Soil form	Glenrosa		Swartland	Mispah	Sterkspruit	—
Soil texture***	l/sa	s/Cl/lm	sa/lm	s/cl/lm	—	sa/lm
Dominants	?	?	Eberlanzia	Cymbopogon Phyllanthus	Heteropogon Themeda	Cussonia

* (1) dwarf shrubland; (2) succulent dwarf shrubland; (3) succulent thicket; (4) lowland grassland; (5) dune fynbos
** (a) Ellis and Lambrechts (1986); (b) This study; (c) Palmer et al. (1988); (d) Bosch (1977); (e) Van der Merwe (1976)
*** (l/sa) loamy sand; (s/cl/lm) sandy clay loam; (sa/lm) sandy loam.

as the presence of the $CaCO_3$ layer. The high sand fraction for the study area appears to be one of the major features distinguishing these from soils in other biomes (Table 3).

Many of the lithosol profiles display a structural integrity associated with well-preserved conditions, suggesting that erosion of the A-horizon is not a major perturbation. Soil nutrients are not limited, and single precipitation events may determine fluctuations in production levels. The importance of available P in PCA axis 2 suggests that research should be undertaken on the role of nutrient enrichment in determining plant community distribution.

No single environmental variable succeeded in explaining the floristic gradients within the system. The precipitation gradient is shallow, and median annual rainfall is probably not a major differentiating variable. Changes in elevation strongly influence floristic composition, but these may be linked to associated changes in the substrate in the high lying landforms. The soil texture gradient is steep and is responsible for differentiating communities from one another on the pediments.

Evidence for a warm, wet period in the middle Holocene provides an explanation for the presence of woody shrubs and succulents of subtropical affinity (Palmer 1990). This helps explain the poor differentiation of the succulent thicket along a precipitation gradient.

In this study, a stepwise approach has been used to further understand vegetation/environment interactions. Environmental variables associated with all samples were analyzed whenever possible. However restricted environmental data were also analyzed, further enhancing our understanding of the variables associated with plant communities, and enabling the preparation of testable hypotheses.

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