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An application of multivariate analysis techniques to dry-weight-rank data from a Bankenveld nature reserve

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Botanical composition data obtained by the dry-weight-rank method of botanical analysis are ordered and classified by DECORANA and TWINSPAN. Four grassland communities on the Jack Scott Nature Reserve were studied and gradients of disturbance, ungulate utilization and geological influence were found to exist.

Die plantsamestelling soos verkry uit droëmassa-rangordebepalings vir grasveld is deur middel van DECORANA en TWINSPAN georden en geklassifiseer. Vier grasveldgemeenskappe op die Jack Scott-natuurreservaat is bestudeer en gradiënte van versteuring, hoefdiergebruik en geologie is gevind.

Keywords: Classification, grasslands, ordination, rank data

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Introduction

Ordination and classification techniques have been used recently to analyse data obtained by the dry-weight-rank method of 't Mannetje & Haydock (1963). Ben-Shahar (1988) used such methods of statistical analysis on dry-weight-rank data to determine patterns of association in Sour Bushveld and Scott (1989) has shown that rank data can be statistically analysed by ordination and classification techniques.

The aim of this paper is to describe an application of ordination and classification to dry-weight-rank data in Bankenveld vegetation. This application enabled the authors to distinguish between ecologically interpretable vegetation types and to correlate plant species composition with environmental gradients, despite the statistical limitations of non-normally distributed data such as obtained by dry-weight-ranking.

Study area

The study area covers the 2 100-ha southern grasslands of Jack Scott Nature Reserve (25°54′S 27°45′E) in the Krugersdorp District of the Transvaal. The study area is therefore situated in the Central Variation of the Bankenveld (Acocks 1975).

From south to north across the study area, the geological succession is ascended from the older, dolomite–chert formations of the Malmani Subgroup to the shale and quartzite units of the Timeball Hill Formation in the Pretoria Group.

The study area experiences a hot, wet season from October to April and a cold, dry season from May to September. The mean annual temperature and mean annual precipitation for Krugersdorp, 21 km south of the study area, are 15.7°C and 767 mm. For Pelindaba, 22 km north-east of the study area, the respective values are 18.0°C and 673 mm (Weather Bureau, Department of Environment Affairs).

Methods

Communities and sample sites

The 11 grassland communities described by Coetzee (1974) in the study area were grouped into four broader communities for the purpose of the present study, based on the map of Coetzee (1974). These four grassland communities are presently referred to as the dolomite community (on chert-poor dolomite), the chert community (on chert-rich dolomite), the shale community and the old lands community (on shale).

As part of a more extensive botanical survey in the study area, 10 sample sites were randomly placed in each of the four above-mentioned communities during April 1986. At each site a 1-m iron stake was erected to mark the intersection of four 100-m transects at right angles to each other. The first transect was directed down the slope of the land surface and originated at the iron stake. Another transect was directed up the slope from the iron stake and was therefore back-to-back with the first transect. The remaining two transects were then placed at right angles to the other two and they each originated from the iron stake as well. The down-slope direction from the stake was measured from true north using a magnetic compass and this direction was recorded as the orientation direction for future reference.

Dry-weight-rank analysis

The dry-weight-rank method of botanical analysis, developed by 't Mannetje & Haydock (1963) and improved by Jones & Hargreaves (1979), has not been used extensively in southern Africa. Walker (1970) and Kelly & McNeill (1980) have used the method successfully in Zimbabwe, while Barnes *et al.* (1982) and Ben-Shahar (1988) have had success in the Transvaal. This method was used to determine the botanical composition of the grasslands on Jack Scott Nature Reserve between 10 February and 6 March 1987.

At each randomly selected sample site (10 per community), except one site on dolomite that was burnt in October 1986, each of the four transects was walked and a 0.5 × 0.5-m quadrat was evaluated every 10 paces. Dry-weight-ranking was therefore applied to 39 of the 40 sample sites in the study area. Forty quadrats (10 per transect) were examined at each sample site, in other words, 400 in each community, except the dolomite community where 360 quadrats were examined. Non-grass species were ranked as separate species as opposed to treating them together as one 'species'. The species were identified by comparison with herbarium specimens housed on the reserve and by G.K. Theron. The species names follow Gibbs Russel *et al.* (1985; 1987).

Dry-weight-ranking was not applied to areas burnt during spring 1985 or 1986 and the calculations of percentage dry mass were done using the original multiplying ratios of 't Mannetje & Haydock (1963), namely 8.04, 2.41 and 1.00.

Multivariate analyses

The botanical composition information from the dry-weight-rank analysis of the study area was subjected to ordination and classification, with the 39 sample sites as individuals and the plant species as attributes, quantified by percentage dry mass. The main multivariate approach was that of ordination using detrended correspondence analysis (DECORANA) (Hill 1979a), while classification by the polythetic divisive technique of two-way indicator species analysis (TWINSPAN) (Hill 1979b) was done supplementary to the ordination.

Two ordinations and classifications were done using standard procedures. Ordination and classification was done using the data from all four communities as well as the data from only the subclimax communities, excluding the old lands community.

Results

Botanical composition

The botanical composition of each grassland community in the study area is presented in Table 1. Non-grass species made up 5.3, 4.1, 4.6 and 2.6% of the composition of the chert, dolomite, old lands and shale communities respectively, in terms of dry mass.

The dry-weight-rank method of determining botanical composition does not indicate the distribution pattern of species through a community. For example, *Kohautia amatymbica* and *Stoebe vulgaris* both made up 0.7% of botanical composition in the old lands community but the former was more evenly distributed than the latter; *K. amatymbica* was recorded at six of the 10 old land sites while *S. vulgaris* was recorded at only two of the 10 old land sites. Similarly, in the shale community, *Indigofera arrecta* (0.5%) occurred in three of the 10 sample sites while *Senecio venosus* (0.4%) occurred in six of the 10 sample sites.

Perusal of Table 1 makes apparent the differences in botanical composition of the communities, but the ecological differences are better elucidated by the results of the multivariate analyses.

Multivariate analyses

The most noticeable feature indicated by the multivariate

Table 1 Botanical composition in terms of percentage dry mass for each grassland community of the study area on Jack Scott Nature Reserve. as measured by the dry-weight-rank method of 't Mannetje & Haydock (1963) during February/March 1987

		Percentage dry mass			
Number	Species	Chert	Dolomite	Old land	Shale
001	*Cassia mimosoides*	0.2	+		
002	*Crabbea angustifolia*	+	+	+	+
003	*Anthericum fasciculatum*		+		
004	*Kohautia amatymbica*	+		0.7	+
005	*Oldenlandia herbacea*			+	+
006	*Conyza podocephala*			0.3	
007	*Solanum incanum*		0.2	0.2	+
008	*Hermannia depressa*			+	
009	*Acanthospermum australe**			0.4	+
010	*Vernonia poskeana*	+			+
011	*Acalypha angustata*			+	+
012	*Vigna vexilata*			+	
013	*Solanum panduriforme*			0.4	+
014	*Helichrysum rugulosum*			0.3	
015	*Eriosema salignum*			0.1	
016	Unknown I			+	
017	*Rhynchosia totta*			+	
018	*Pentarrhinum insipidum*			+	
019	*Pollichia campestris*	+		0.2	
020	*Felicia muricatus*		+	+	
021	*Acacia ataxacantha*			+	
022	*Erigeron karvinskianus**			+	
023	*Hypoxis rigidula*		0.2	+	+
024	*Lippia javanica*			+	
025	*Verbena bonariensis**			+	
026	*Osteospermum muricatum*			+	
027	*Hermannia lancifolia*	+	0.2		
028	*Solanum supinum*		+		
029	*Helichrysum callicomum*		+		
030	*H.* cf. *oxyphyllum*	+	+		
031	*Bulbostylis burchellii*	0.8	0.2		
032	*Sphenostylis angustifolia*	0.1	+		+
033	*Senecio lydenbergensis*		+		
034	*Leucas neufliziana*	+	+		
035	*Polygonum* sp.		+		
036	*Rhus magalismontana*		0.3		
037	*Euphorbia* sp.		+		
038	*Plexipus pinnatifidus*		+		
039	*Cassine burkeana*		+		
040	*Barleria* sp.		+		
041	*Gnidia sericocephala*		+		
042	*Clutia pulchella*		+		
043	*Asparagus suaveolens*		+		
044	Unknown 2		+		
045	*Hermannia transvaalensis*		+		
046	*Ledebouria revoluta*		0.1		
047	*Kohautia virgata*	+	0.1		
048	*Limeum viscosum*	+	0.1		
049	*Fimbristylis hispidula*		0.2		
050	*Chaetacanthus costatus*		+		
051	*Dicoma anomala*	+	+		

Table 1 Continued

Number	Species	Percentage dry mass			
		Chert	Dolomite	Old land	Shale
052	*Gnidia splendens*	0.4			
053	*Pentanisia angustifolia*	+			0.2
054	*Amaranthus thunbergii*	+			
055	*Rhynchosia monophylla*	0.1			
056	*Gnidia capitata*				0.2
057	*Tephrosia elongata*				0.2
058	*Walafrida densiflora*				+
059	*Phyllanthus incurvis*				+
060	*Justicia* sp.				+
061	*Blepharis* sp.				+
062	*Indigofera comosa*	+			
063	*Pearsonia sesillifolia*				+
064	*Ziziphus zeyheriana*				+
065	*Cyperus margaritaceus*				+
066	*Cassia biensis*	+			
067	*Sutera palustris*	0.2			
068	*Helichrysum nudifolium*	+			
069	*Ipomoea obscura*	+			
070	*Sida rhombifolia*			+	
071	*Stoebe vulgaris*			0.7	0.2
072	*Parinari capensis*	0.5	0.5	+	+
073	*Elephantorrhiza elephantina*	0.1	0.2	0.4	0.3
074	*Senecio venosus*	1.2	0.6	0.1	0.4
075	*Xerophyta retinervis*	1.0	0.2		
076	*Bidens pilosa**	+			
077	*Kalanchoe thyrsiflora*		+		
078	*Indigofera arrecta*				0.5
	Subtotal for non-grasses	5.3	4.1	4.6	2.6
079	*Andropogon schirensis*	7.7	1.2	1.9	10.2
080	*Aristida congesta* subsp. *congesta*	0.1	1.3	0.8	+
081	*Aristida* sp. 1	1.8	1.5		+
082	*Aristida* sp. 2	0.2	1.8		
083	*Bewsia biflora*	0.5	0.2		+
084	*Brachiaria serrata*	3.3	2.8		4.4
085	*Cymbopogon excavatus*	+		11.0	0.7
086	*C. validus*			0.4	
087	*Cynodon dactylon*	0.2	+	2.3	0.5
088	*Diheteropogon amplectens*	8.6	5.4	0.3	12.3
089	*Digitaria brazzae*	4.4	0.5		
090	*D. diagonalis*				0.1
091	*D. monodactyla*	2.7	5.1		
092	*D. tricholaenoides*	1.5	1.2	0.2	0.1
093	*Elionurus muticus*	4.7	5.5	0.8	11.4
094	*Eragrostis chloromelas*	0.8	5.0	3.2	0.1
095	*E. curvula*	1.2	5.1	11.9	1.3
096	*E. gummiflua*	0.4	0.4	3.1	0.7
097	*E. racemosa*	1.4	1.1	1.0	1.7
098	*E. rigidior*			+	
099	*Eustachys paspaloides*		0.4		
100	*Fingerhuthia sesleriiformis*		1.1		
101	*Heteropogon contortus*	0.2	0.6	3.1	0.6
102	*Hyparrhenia hirta*			24.5	
103	*Loudetia simplex*	5.4	1.7		2.3
104	*Microchloa caffra*	+	+		

Table 1 Continued

Number	Species	Percentage dry mass			
		Chert	Dolomite	Old land	Shale
105	*Monocymbium ceresiiforme*	2.3	1.2		0.5
106	*Panicum natalense*	0.2	0.4		3.8
107	*Paspalum scrobiculatum*			2.4	
108	*Pogonarthria squarrosa*	0.1	+		
109	*Rhynchelytrum nerviglume*	4.0	0.7	0.6	7.5
110	*R. repens*	1.0	0.5	+	1.2
111	*Schizachyrium sanguineum*	10.2	1.9	3.0	10.9
112	*S. ursulus*	0.3			
113	*Setaria sphacelata*	13.0	34.8	10.7	2.6
114	*Sporobolus africanus*			1.0	0.2
115	*S. fimbriatus*	0.2		11.3	0.8
116	*S. pectinatus*	0.9	0.5		
117	*Stipagrostis zeyheri*	0.2	1.1		
118	*Themeda triandra*	3.7	3.8	1.2	6.4
119	*Trachypogon spicatus*	3.1	4.3	0.9	14.0
120	*Tristachya rehmannii*	8.2	3.6		1.0
121	*Triraphis andropogonoides*	0.4	1.1		
122	*Urelytrum agropyroides*	1.0	0.8		1.8
123	*Trichoneura grandiglumis*	0.6			
124	*Tragus berteronianus*		+		
125	*Eragrostis* sp. 1			+	
126	*Eragrostis* sp. 2		+		
127	*Hyparrhenia* sp. 1			0.2	
	Subtotal for grasses	94.7	95.9	95.4	97.4

*exotic

+ = 0.01 to 0.09 % dry mass

analyses was the separation of the old lands community from the other communities, as evident to the right of Figure 1. The application of TWINSPAN to all the data revealed that samples 20 to 29 were separated from the other samples at the first level by *Hyparrhenia hirta* (Figure 2). The dolomite community was separated from the shale and chert communities at level two by *Setaria sphacelata*, the latter two communities being characterized by *Rhynchelytrum nerviglume* and *Andropogon schirensis*, while the chert community was separated from the shale community by *Digitaria monodactyla* and *Tristachya rehmannii* at the third level.

Species such as *Andropogon schirensis*, *Rhynchelytrum nerviglume*, *Schizachyrium sanguineum*, *Eragrostis racemosa* and *Themeda triandra*, which were common across all the communities, were more abundant in the shale community while *Aristida congesta* subsp. *congesta*, *Eragrostis chloromelas* and *E. curvula* were more abundant in the dolomite and old lands communities where commoner species were less abundant.

The first sample ordination axis in Figure 1 represents a gradient from natural, undisturbed range to disturbed range. Within the first axis there is a subgradient across the old land samples representing an increase in *Cymbopogon excavatus*, *Paspalum scrobiculatum* and *Eragrostis chloromelas* from

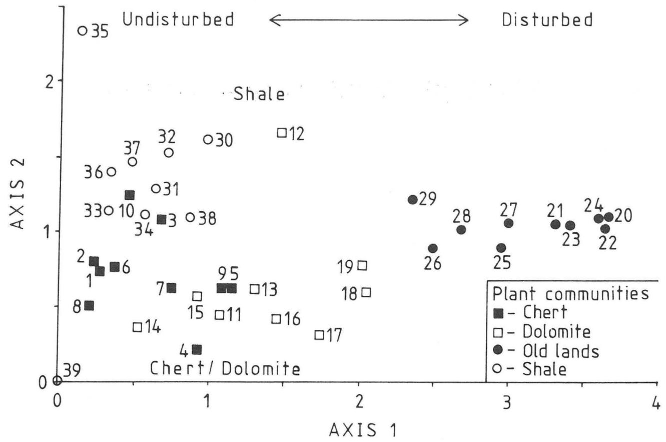

Figure 1 DECORANA ordination of all the vegetation samples in the study area. Eigenvalues for the first and second axes are 0.673 and 0.230 respectively and sample numbers are as follows: 1 to 10 = chert community, 11 to 19 = dolomite community, 20 to 29 = old lands community and 30 to 39 = shale community.

left to right. Along the second axis, samples on chert and dolomite (1–19) tend to plot at the lower end except for samples 10 and 12, while samples on shale (20–39), including the old lands (which were on shale), tend to plot at the upper end, except for sample 39.

The shale–chert–dolomite gradient may be explained by the fact that dolomite-derived soils in the area are more base-rich and physiologically drier, than the chert- and shale-derived soils in the area (Werger & Coetzee 1978). In other words, dolomite-derived soils are poorer in acid elements such as Si and Al and richer in base elements such as Ca and Mg than shale-derived soils. It may therefore be expected that soils derived from the dolomite would have higher pH values than soils derived from the shale.

The occurrence of species such as the geophytic *Anthericum fasciculatum*, *Hypoxis rigidula* and *Ledebouria revoluta*, as well as the crassulacean *Kalanchoe thyrsiflora*, and the succulent *Euphorbia* sp. on dolomite indicates the physiological dryness of dolomite-derived soil.

The species ordination for all four communities reflected the corresponding sample ordination. The strongest gradient

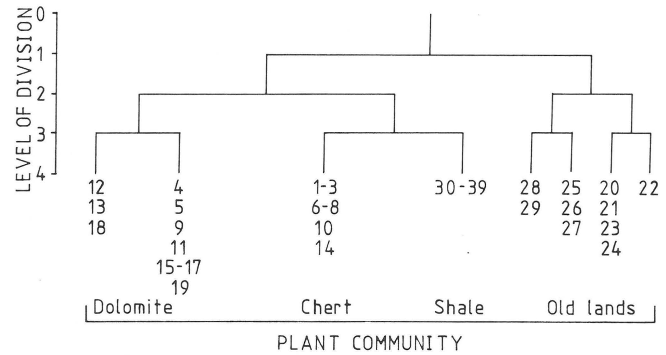

Figure 2 TWINSPAN classification of all the vegetation samples in the study area. Sample numbers are as follows: 1 to 10 = chert community, 11 to 19 = dolomite community, 20 to 29 = old lands community and 30 to 39 = shale community.

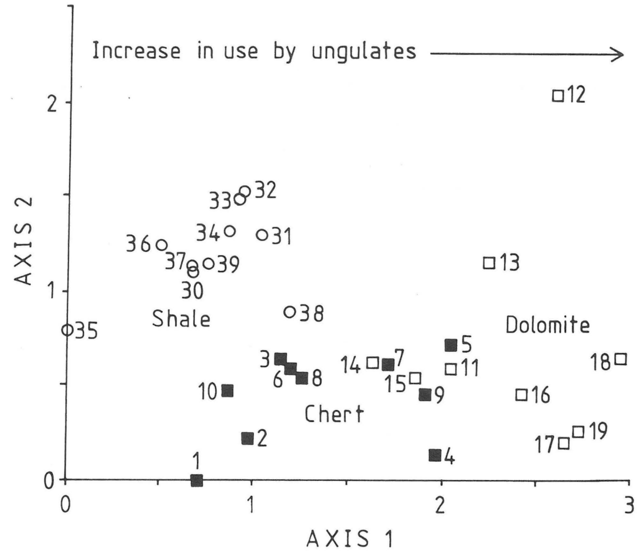

Figure 3 DECORANA ordination of samples in the three subclimax grassland communities. Eigenvalues for the first and second axes are 0.441 and 0.195 respectively and sample numbers are as follows: 1 to 10 = chert community, 11 to 19 = dolomite community and 30 to 39 = shale community.

apparent was from the plant species common to the under-utilized shale community on the left of the first axis to the plant species common to the over-utilized/disturbed areas on the right of the first axis (Scogings 1988).

The exclusion of the old land samples (20–29) from the detrended correspondence analysis resulted in the most interpretable gradients in both sample and species ordinations. The geological and ungulate utilization gradients were repeated, while two additional gradients were revealed (Figures 3 & 4). Both the geological and utilization gradients were aligned with the first axis; from less-used shale on the left, through chert-rich dolomite, to more-used, chert-poor dolomite on the right (Figures 3 & 4). The second axis of the sample ordination represented a gradient across the dolomitic end of axis one, from sites with less outcrop at the lower end, to sites with more outcrop (samples 12, 13 and 18) at the upper end (Figure 3). The third axis of the sample ordination reflected a gradient across the shale community from the relatively xeric, north-facing sample sites at the lower end to the relatively mesic, south-facing sample 39 at the upper end (Figure 4).

The ungulate utilization gradient was also well represented by the diagonal axis from upper left (under-utilization) to lower right (over-utilization) of the species ordination of the three subclimax communities (Scogings 1988). The end of the gradient representing under-utilization by ungulates was characterized by plant species generally common or unique to the shale community, including Increaser I grasses (Foran *et al.* 1978) and shrubs, while the end of the gradient representing over-utilization by ungulates was characterized by plant species generally common or unique to the dolomite community, including Increaser II grasses (*ibid.*) and herbs.

The TWINSPAN classifications of all the samples (Figure 2) and all the samples excluding the old land samples revealed the dissimilar nature of the four grassland communities. The order of the samples across Figure 2 also

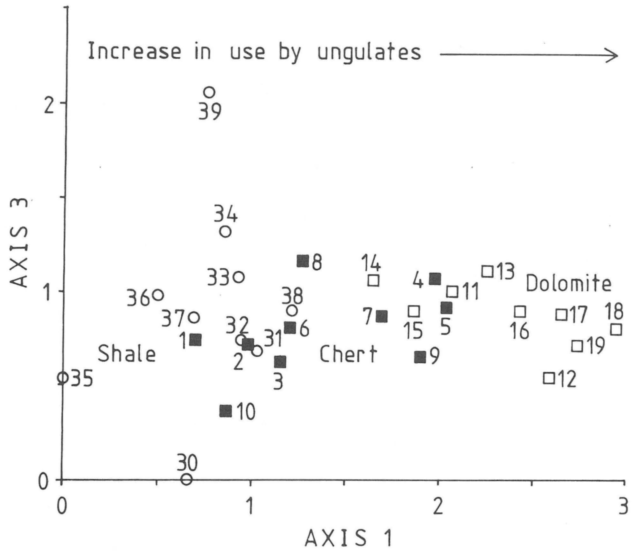

Figure 4 DECORANA ordination of samples in the three subclimax grassland communities. Eigenvalues for the first and third axes are 0.441 and 0.145 respectively and sample numbers are as follows: 1 to 10 = chert community, 11 to 19 = dolomite community and 30 to 39 = shale community.

reflected the geological gradient of vegetation on chert-poor dolomite to vegetation on shale.

Discussion

The four grassland communities found in the study area and which were defined according to Coetzee's (1974) maps displayed unique features which made them identifiable units, with more or less overlap and definite ecological relationships. The primary dichotomy was the separation of the old lands community from the three subclimax communities. This dichotomy arose from the presence of the strongly differential *Hyparrhenia hirta* on the old lands. Less strongly differential old land species were *Sporobolus fimbriatus* and *Cymbopogon excavatus*.

The individual subclimax communities did not have strongly differential plant species associated with them, however, *Brachiaria serrata* was strongly affiliated to all three subclimax communities, followed by *Diheteropogon amplectens* and *Senecio venosus*. The chert community (on chert-rich dolomite), although geologically intermediate between the shale and dolomite communities (on shale and chert-poor dolomite respectively), was ecologically closer to the dolomite community. This relationship was illustrated by the differential species of more or less strength that typified the chert and dolomite communities. These species were, in decreasing order of differential capability, *Sporobolus pectinatus, Bulbostylis burchellii, Digitaria monodactyla, D. tricholaenoides, Parinari capensis* and *Tristachya rehmannii*. On the other hand, the weaker differential species *Rhynchelytrum repens, Urelytrum agropyroides* and, to a lesser extent, *Loudetia simplex* were indicative of shale and chert-rich dolomite. Furthermore, *Panicum natalense* associated the vegetation on shale with the vegetation on chert-poor dolomite.

Of the three subclimax communities, the chert community was more closely allied to the old lands than were either of the other two subclimax communities. This relationship was expressed by the presence in both the chert and old lands communities of *Eragrostis curvula, E. chloromelas, Heteropogon contortus* and *Aristida congesta* subsp. *congesta*, all of which were generally less common in the study area than species such as *Andropogon schirensis, Rhynchelytrum nerviglume, Schizachyrium sanguineum, Eragrostis racemosa* and *Themeda triandra*.

Within the old land succession there was a gradient of increasing abundance of *Cymbopogon excavatus, Eragrostis chloromelas* and *Paspalum scrobiculatum* and decreasing abundance of *Setaria sphacelata, Schizachyrium sanguineum, Andropogon schirensis* and *Kohautia amatymbica*. Other species characteristic of the old lands were the herbaceous exotics *Acanthospermum australe, Verbena bonariensis* and *Erigeron karvinskianus*, which occurred in the samples containing higher abundances of *Cymbopogon excavatus, Eragrostis chloromelas* and *Paspalum scrobiculatum*; these samples (20–24) were probably at earlier stages of secondary succession than were samples 25 to 29. More evenly distributed through the old lands, and representative thereof, were *Hyparrhenia hirta, Eragrostis curvula, Sporobolus fimbriatus, Heteropopon contortus, Cynodon dactylon, Themeda triandra* and *E. racemosa*.

The vegetation on chert-poor dolomite graded into the vegetation on chert-rich dolomite. The chert-poor areas coincided with extensive dolomite outcrop (25–50% of the land surface) and stone-free, deep soil, while the chert-rich areas tended to lack outcrop (< 5%) and had shallow, stony soil. This geological gradient was reflected in the change of floristics; areas of extreme chert paucity were represented by *Fingerhuthia sesleriiformis* and numerous uncommon non-grass species adapted to water stress, notably the succulent *Kalanchoe thyrsiflora* and *Euphorbia* sp. The geophytic *Hypoxis rigidula, Ledebouria revoluta* and *Anthericum fasciculatum* occurred in both the chert-poor areas and the areas of intermediate chert paucity.

With an increase in chert content there was a decrease in the abundance of *Triraphis andropogonoides, Stipagrostis zeyheri, Eragrostis curvula, E. chloromelas, Elionurus muticus* and *Setaria sphacelata*. There was a concomitant increase in *Digitaria brazzae, Tristachya rehmannii, Monocymbium ceresiiforme, Loudetia simplex, Rhynchelytrum repens, Urelytrum agropyroides, Schizachyrium sanguineum, Andropogon schirensis, R. nerviglume* and *Brachiaria serrata*, while *Panicum natalense* was most abundant in the middle of the gradient from chert-poor dolomite to chert-rich dolomite. The species common to both the dolomite and the chert communities were *Parinari capensis, Digitaria monodactyla, D. tricholaenoides, Bulbostylis burchellii, Sporobolus pectinatus, Bewsia biflora, Diheteropogon amplectens, Trachypogon spicatus, Senecio venosus, Eragrostis racemosa* and *Themeda triandra*.

The under-utilized, moribund, shale community which had not been burnt for seven to eight years, was characterized by the generally commoner species such as *Diheteropogon amplectens, Elionurus muticus, Trachypogon spicatus, Schizachyrium sanguineum, Andropogon schirensis, Themeda triandra, Rhynchelytrum nerviglume* and *Eragrostis racemosa* which were typically more abundant than in the other communities. Of the less common species, *Panicum* *natalense, Rhynchelytrum repens* and *Urelytrum agropyroides* were typical of the shale community. The shale community also had the lowest number (25) and the lowest percentage dry mass (2.6%) of non-grass species. A gradient from mesic to xeric conditions existed where the south-facing, relatively mesic sample 39 was characterized by the increased abundance of *Brachiaria serrata* and *Panicum natalense* and the singular occurrence of *Digitaria diagonalis.*

There were therefore two important ecological gradients across all four grassland communities. The first was from the undisturbed, natural, subclimax grasslands to the disturbed, subseral, old land succession. The second gradient of note was from the vegetation on shale (including the old lands) to the vegetation on chert-rich dolomite. These two gradients were reflected in the subclimax communities, but along one axis instead of two, where the geological gradient was accompanied by a gradient of ungulate utilization; the shale community was less utilized while the dolomite community was more utilized, even over-utilized in places.

The results presented in this paper support the findings of Coetzee (1974) and indicate the multipurpose potential for data obtained by low intensity, rapid sampling such as used for dry-weight-rank analysis. Such data can provide a broad classification and reveal ecological gradients for the vegetation of an area. They can also provide information on the species composition and the condition of the vegetation. It must be realized though that by using the results of dry-weight-ranking as data for further analysis by multivariate techniques, non-normal data are being used. The data should be transformed in order to be strictly suitable for TWINSPAN and DECORANA which assume normally distributed data.

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References

ACOCKS J.P.H 1975. Veld types of South Africa. *Mem. bot. Surv. S. Afr.* 40: 1–128.

BARNES, D.L., ODENDAAL, J.J. & BEUKES, B.H. 1982. Use of the dry-weight-rank method of botanical analysis in the eastern Transvaal highveld. *Proc. Grassld. Soc. sth. Afr.* 17: 79–82.

BEN-SHAHAR, R. 1988. Patterns of plant species associations on a Sour Bushveld nature reserve. *S. Afr. J. Bot.* 54: 504–506.

COETZEE, B.J. 1974. A phytosociological classification of the vegetation of the Jack Scott Nature Reserve. *Bothalia* 11: 329–347.

FORAN, B.D., TAINTON, N.M. & BOOYSEN, P. DE V. 1978. The development of a method for assessing veld condition in three grassveld types in Natal. *Proc. Grassld Soc. sth. Afr.* 13: 27–33.

GIBBS RUSSEL, G.E., REID, C., VAN ROOY, J. & SMOOK, L. 1985. List of species of southern African plants. 2nd edn, Part 1. *Mem. bot. Surv. S. Afr.* 51: 1–152.

GIBBS RUSSEL, G.E., WELMAN, W.G., RETIEF, E., IMMELMAN, K.L., GERMISHUIZEN, G., PIENAAR, B.J., VAN WYK, M. & NICHOLAS, A. 1987. List of species of southern African plants. 2nd edn, Part 2. *Mem. bot. Surv. S. Afr.* 56: 1–270.

HILL, M.O. 1979a. DECORANA — A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Cornell University, Ithaca, NY.

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

JONES, R.M. & HARGREAVES, J.N.G. 1979. Improvements to the dry-weight-rank method for measuring botanical composition. *Grass For. Sci.* 34: 181–189.

KELLY, R.D. & MCNEILL, L. 1980. Tests of two methods for determining herbaceous yield and botanical composition. *Proc. Grassld. Soc. sth. Afr.* 15: 167–171.

SCOGINGS, P.F. 1988. An ecological study of the grasslands of the Jack Scott Nature Reserve, Transvaal, with special reference to plant production and ungulate–habitat relationships. M.Sc. thesis, Univ. of Pretoria.

SCOTT, D. 1989. Description of vegetation using visual ranking of species. *N.Z. J. Ecol.* 12: 77–88.

't MANNETJE, L. & HAYDOCK, K.P. 1963. The dry-weight-rank method for the botanical analysis of pasture. *J. Br. Grassld. Soc.* 18: 268–275.

WALKER, B.H. 1970. An evaluation of botanical analysis on grasslands in Rhodesia. *J. Appl. Ecol.* 7: 403–417.

WERGER, M.J.A. & COETZEE, B.J. 1978. The Sudano–Zambezian Region. In: Biogeography and ecology of southern Africa, ed. Werger, M.J.A., Ch. 10, W. Junk, The Hague.