Ordination of the herbaceous stratum of savanna in the Nylsvley Nature Reserve, South Africa

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The purpose of the study was to determine the ecological status of representative herbaceous species with respect to environmental factors and subhabitats of which the spatial and temporal pattern could be elucidated.

The basal cover of the herbaceous vegetation was determined by means of the wheel-point method. Frequency data in each of 200 1 m² contiguous quadrats were ordinated by means of detrended correspondence analysis (DECORANA).

The distribution of the species along the first axis is a function of conditions representing an open habitat with full sunlight and somewhat drier conditions to the left and a denser and/or shrub habitat with more shade and wetter, more favourable conditions to the right. The gradient along the second axis is that of undisturbed conditions with more perennials at the lower end to disturbed conditions with more annuals at the upper end. From the scatter diagrams it can be concluded that the herbaceous layer is functionally homogeneous, that it represents a seral stage and that *Eragrostis pallens* and *Digitaria eriantha*, both with the highest basal cover in the study area, are representative of a seral stage rather than of the climax. The lack of pattern in the herbaceous layer can be attributed mainly to the large number of annual and perennial pioneer and disturbance-indicating species. In a similar study Whittaker *et al.* (in press) concluded that the woody vegetation dominates the pattern.

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Die doel van die studie was om die ekologiese posisie van verteenwoordigende kruidagtige spesies ten opsigte van omgewingsfaktore en subhabitatte te bepaal waardeur die ruimtelike en tydelike patroon dan verklaar kan word.

Die basale bedekking van kruidagtige spesies is deur middel van die wielpuntmetode bepaal. Frekwensiedata is verkry uit 200 1 m² aaneengeskakelde kwadrate wat deur middel van DECORANA georden is.

Die verspreiding van die spesies langs die eerste as van ordening verteenwoordig 'n droër oop habitat in volle sonlig links en 'n vogtiger, digter en struikhabitat met meer skaduwee regs. Die gradiënt langs die tweede as van ordening verteenwoordig minder versteuring met meerjarige plantsoorte onder en meer versteuring met meer eenjarige soorte bo. Daar kan uit die verstrooiingsdiagramme afgelei word dat die kruidstratum redelik homogeen is, en 'n serale stadium van plantsuksessie verteenwoordig en nie 'n klimaks nie. *Eragrostis pallens* en *Digitaria eriantha* het die hoogste basale bedekking in die studie-area gehad. Die gebrek aan patroon kan aan die groot getal eenjarige en meerjarige pionier- en versteuringspesies toegeskryf word. In 'n soortgelyke studie het Whittaker *et al.* (in pers) gevind dat die houtagtige plantsoorte die patroon domineer.

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Introduction

A cooperative savanna ecosystem project was initiated in 1974 on part of the Nylsvley Nature Reserve by the Terrestrial Biology Section of the South African National Programme for Environmental Sciences. As part of phase I of this project (description and quantification of structural features of the ecosystem), the research reported here was undertaken. It was broadly directed towards the study of pattern within the herbaceous component of the vegetation. Briefly, the purpose of the quantitative study was to determine the ecological status of representative herbaceous species with respect to environmental factors and subhabitats by means of which the spatial and temporal pattern could be elucidated. The response of herbaceous species to the two main subhabitats, namely, under-tree and open treeless areas, was of particular concern. In a parallel study Lubke *et al.* (1976) investigated the woody component.

R.H. Whittaker has successfully applied ordination techniques to strip transect data to study pattern (Whittaker *et al.* 1979, in press). In vegetation rich in species and with a marked two-phase character, ordination appears to be especially useful for the identification and quantification of overall species compositional pattern i.e. community, rather than the species-by-species relationships studied by Kershaw (1957) and Greig-Smith (1964). The savanna vegetation at Nylsvley is rich in species and its under-tree and open subhabitats are comparable with the discontinuous phase (shrub clumps) and open continuous phase (grassy matrix) described by Whittaker *et al.* (in press) in mesquite grassland in Texas. After inspection, however, the two-phase pattern is not as distinct within South African savanna as that described in Texas (Whittaker *et al.* 1979).

Study area

The Nylsvley Nature Reserve, 3 129 ha in extent, comprises the farm Nylsvley 560 KR, situated between 24°36′ and 24°42′S latitude and 28°40′ and 28°44′E longitude, 16 km south of Naboomspruit in the Northern Transvaal, South Africa. Most of the ecosystem research has been concentrated in a 745 ha study area within the reserve.

The reserve is situated in an extensive undulating to flat terrain between 1 080 m and 1 140 m altitude. The Nyl river runs across the reserve from south-west to north-east in a strip of flat, low lying land that divides the reserve into a number of gently sloping elevations. The study area itself lies on the south-eastern elevation on the southern side of the Nyl river and is situated on sandstone, grits and conglomerate bands of the

Waterberg System.

The climate, according to Köppen's system, is a hot dry steppe with a dry winter period, designated BShw (Schulze 1947). The absolute maximum temperature recorded is 38,9 °C, the absolute minimum is − 6,1 °C and the extreme grass minimum temperature is − 9,9 °C. The mean daily range is 17,1 °C with a mean daily maximum of 29,7 °C in the hottest month (January) and a mean daily minimum of 1,3 °C in the coldest month (July) (Huntley & Morris 1978). Ground frosts can be expected daily in June and July (Coetzee *et al.* 1976) and were recorded on 21 days in 1975 in the study area (Huntley & Morris 1978). The prevailing winds are east in summer and west in winter (Weather Bureau 1960). The average annual rainfall for the Nylsvley weather station over a period of 40 years is 630 mm (Weather Bureau 1965). The rainfall in the study area for the 1975/76 year totalled 672 mm falling on 74 days mainly during the months of October to March (Huntley & Morris 1978). The relative humidity of the air in the study area is consistently low in the early afternoon with the relative humidity at 08h00 ranging from 57% to 86% (Huntley & Morris 1978).

The soils of the reserve have been classified and mapped by Harmse (1977), with the dominant soil forms in the study area being Hutton, Clovelly and Mispah. Only one series, Mispah, was identified in the study area (Huntley & Morris 1978). The Mispah form profile comprises an orthic A-horizon (5 – 30 cm depth) over the parent rock.

The reserve lies within the veld type which Acocks (1975) called Mixed Bushveld. A detailed phytosociological survey of the whole reserve was carried out by Coetzee *et al.* (1976). The study area in which the present transects were located, falls within the broad-leaved savanna type of community defined as *Burkea* veld by Acocks (1975) and *Eragrostis pallens-Burkea* Tree Savanna by Coetzee *et al.* (1976). There are three major variations in this Tree Savanna, namely:

(a) the *Eragrostis pallens-Dombeya rotundifolia* variation,
(b) the *Eragrostis pallens-Setaria perennis* variation and
(c) the *Eragrostis pallens-Trachypogon spicatus* variation.

The study area is covered mainly by the *Eragrostis pallens-Dombeya rotundifolia* variation. The dominant trees in this variation are *Burkea africana, Terminalia sericea* and *Combretum molle* and the dominant shrubs are *Ochna pulchra* and *Grewia flavescens*. The field layer is dominated by the grasses *Eragrostis pallens* and *Digitaria eriantha* with *Setaria perennis* being very common on the lower slopes. On the higher sandstone areas the field layer is dominated by other grasses, namely, *Trachypogon spicatus* and *Schizachyrium sanguineum*, with *Elionurus muticus* being more common on the middle slopes. *Panicum maximum* is characteristic under large trees (Coetzee *et al.* 1976).

Methods

Within the study area, Lubke *et al.* (1976) selected five areas which represent the three variations of *Eragrostis pallens-Burkea* Tree Savanna for intensive sampling. The same areas (named A, B, C, D and E) were used in this study. Six 200-m transects, consisting of contiguous 1 m^2 quadrats were laid out within these areas. Two transects, B_1 and B_2, were laid out in area B, with B_2 being lower on the catena than B_1. One transect was located in each of the other four areas. Each quadrat was subdivided into 16 equal units and the rooted frequency recorded for each herbaceous and woody species up to 0,5 m tall in each quadrat. The presence or absence of tree cover was also noted in each quadrat.

In each of the five intensive sampling areas a 2 000-point basal cover survey was conducted. At every point a strike (rooted living plant) or, in the case of a miss, the closest plant to the point was recorded. The total basal cover of the field layer and of the different plant species was calculated according to Tidmarsh & Havenga (1955). Relative occurrence of a species was calculated as the number of times the species was nearest to a point, expressed as a percentage. Relative occurrence is comparable to frequency. Methods of sampling and assessing basal cover and relative occurrence of herbaceous species depend primarily on the objectives of the investigator. Different point methods described by Brown (1954) and Tidmarsh & Havenga (1955) were assessed by Walker (1970). Although Walker (1970) considered the wheel point method (Tidmarsh & Havenga 1955) as not the best method to determine basal cover, it is widely used in South Africa and is easy to apply. It was therefore used in this study.

Detrended correspondence analysis (DECORANA — Hill 1979), the ordination method used in this investigation, was applied to each of the six transects in turn; frequency of all species encountered in the field in each of 200 quadrats being the data used each time. DECORANA is a substantial improvement on reciprocal averaging (Hill 1973) and avoids its two main problems. These are the frequently encountered 'arch' caused by the quadratic dependence of the second and successive axes on the first axis, and the compression of axis ends. Like reciprocal averaging (see Noy-Meir & Whittaker 1978), DECORANA produces simultaneous ordinations of species and quadrats. In our application, two-dimensional plots of species scores were produced and, because sampling was done by means of transects consisting of contiguous quadrats, traces or profiles of DECORANA scores could be plotted (on the y-axis) against quadrat number running from 1 to 200 (x-axis).

Results and Discussion

Scatter diagrams representing the ecological positions of plant species in transects A, B_2, C, D and E, along the first and second axes of ordinations, are given in Figures 1, 3, 4, 5 & 6, and in transect B_1 along the second and third axes in Figure 2. The slight drop in eigenvalue between the first and second axes for transect B_1 resulted in a scatter diagram that was not easily interpretable and was therefore omitted from Figure 6. The first eigenvalue for the other transects was consistently higher than the second and the scatter diagrams were interpretable.

The distribution of the species along the first, or horizontal, axis is a function of conditions representing an open habitat with full sunlight and somewhat drier conditions to the left and a denser tree and/or shrub habitat with more shade and wetter conditions to the right. According to Bate (1979) the nutritional status under trees is better than in the open and the available water content under trees is higher (Bosch & van Wyk 1970); however, the basal cover of grass is lower underneath canopies than in the open at Nylsvley (Grunow *et al.* 1980). According to Moore (1980) there is no general difference in the water regime between the *Eragrostis pallens* and *Burkea africana* subhabitats. The evapotranspiration losses were, however, higher in the *B. africana* subhabitat than in the *E. pallens* subhabitat. The ecological gradient along the vertical, or second, axis is that of relatively undisturbed conditions (a condition indirectly inferred from the species composition based on past experience) with more perennials at the lower

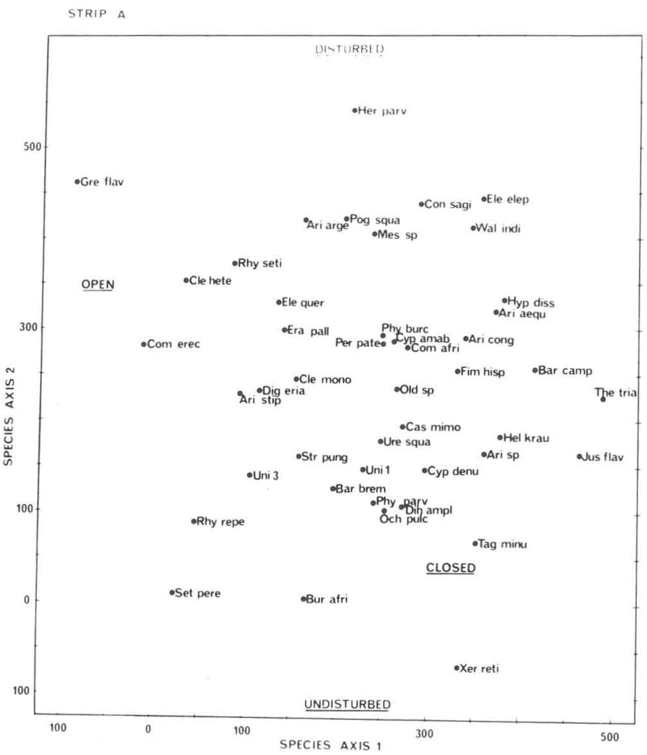

Figure 1 Scatter diagram of species participation in ordination of transect A.

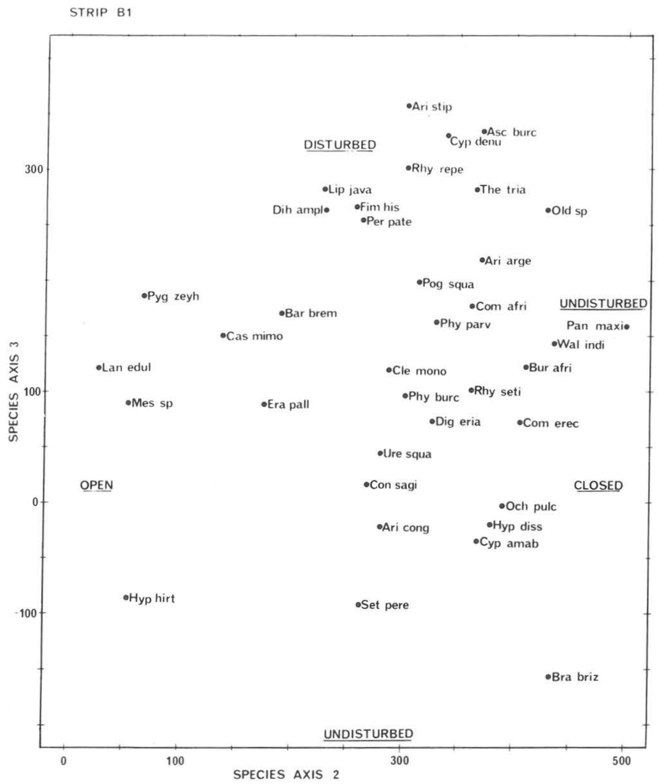

Figure 2 Scatter diagram of species participating in ordination of transect B_1.

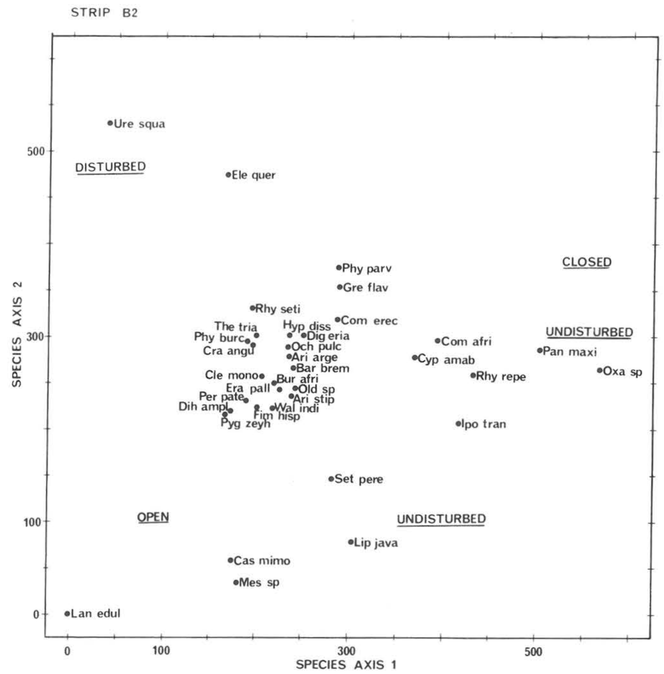

Figure 3 Scatter diagram of species participating in ordination of transect B_2.

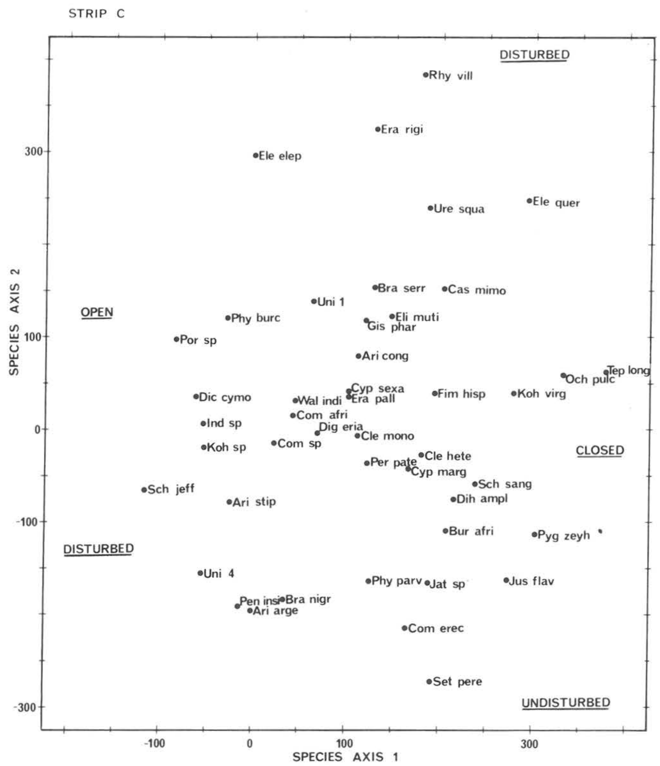

Figure 4 Scatter diagram of species participating in ordination of transect C.

end to disturbed conditions with more annuals at the upper end (Figures 1 – 5). On the scale of this study (within the *Burkea africana* Savanna) perennials and undisturbed conditions indicate xeric conditions. In Figure 6 (transect E) the open habitat is to the left in the middle of the diagram and the tree habitat is towards the upper right and the lower section of the diagram. In some cases, the original axes have been reversed and in others mirror images are given to facilitate comparison by having the same trends in the same directions along the same axes in all figures.

The species representing undisturbed conditions or a higher water and nutritional status at Nylsvley, including probably climax species, occur in the lower parts of the figures. The species representing disturbed conditions and a less favourable water and nutritional status or pioneer species are located in the upper parts of Figures 1 – 6. The interpretation of seral stages (succession) is based on a thorough study of a similar

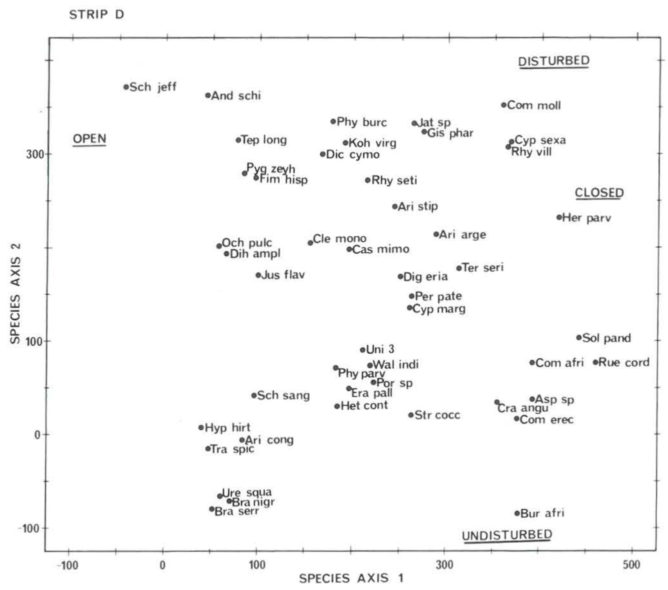

Figure 5 Scatter diagram of species participating in ordination of transect D.

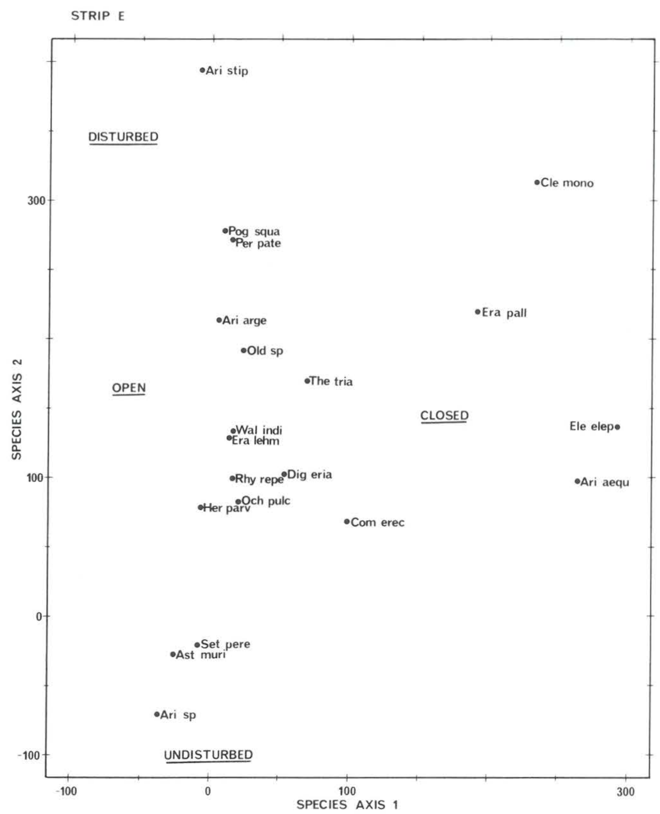

Figure 6 Scatter diagram of species participating in ordination of transect E.

Burkea africana Savanna within the Loskop Dam Nature Reserve some 110 km southeast of Nylsvley (Theron 1973). The species indicating disturbed conditions are more often associated with the pioneer or more xerophytic savanna species, than with the more mesophytic climax species of the *Burkea africana* Savanna. Those species with a wider distribution within the study area and probably representing species with a wider ecological tolerance occur most often to the centre of Figures 1 – 6.

The more mesophytic and probably climax species for the *Eragrostis pallens-Burkea africana* Tree Savanna are *Setaria perennis* and *Panicum maximum*; the latter is beneath trees. There is an increase of *Setaria perennis* in protected plots which supports the theory that *S. perennis* is one of the climax grass species in the *Burkea africana* Savanna (J.O. Grunow pers. com.). *Panicum maximum* has a high need for nitrogen which is available under trees (Bate 1979), but is also abundant in disturbed areas of the Lowveld (J.O. Grunow pers. com.). Disturbed and pioneer areas are often higher in available nitrogen than climax areas (Roux 1969) and this may explain the behaviour of *Panicum maximum*. The position of *Setaria perennis* in the middle or slightly to the left in Figures 1, 2, 3, 4 & 6 is indicative that *S. perennis* can grow underneath trees but it is more regularly associated with an open habitat. In the Loskop Dam Nature Reserve *S. perennis* frequently occurs on south facing slopes and under trees (Theron 1973). *Setaria perennis* is more or less uniformly distributed in transects A, B_1 and B_2, poorly represented in transects C and E and was not recorded in transect D (Table 2). This trend probably reflects a negative correlation with an increase in the woody component. Although *S. perennis* is represented throughout the study area, it has a low basal cover, reaching 0,55% in transect B_1 (Table 3). *Panicum maximum* occurs regularly in transect B_1 and locally in transect B_2 but was not recorded for the other transects (Table 2). Within the area of transect A, *P. maximum* was, however, recorded with a basal cover of 0,1% (Table 3). The highest basal cover recorded for *P. maximum* in the study was 0,45% (Table 3).

The position of *P. maximum* to the right in the middle of Figures 2 & 3 is indicative that *P. maximum* often occurs in the shade of trees. This is also confirmed by the pattern analysis of Whittaker *et al.* (in press). The more central position to the right in Figures 2 & 3 of *P. maximum* indicates that it is more restricted to the under canopy habitat than *S. perennis*.

Setaria perennis was not recorded in transect D (Figure 5) and is replaced by *Brachiaria serrata*, and to a lesser extent by *Eragrostis pallens* as the more mesophytic species of that area. In the basal cover study, *S. perennis* had a value of 0,1% (Table 3). The apparent absence of *Setaria perennis* can probably be related to the shallower soils and more disturbed conditions. More species were also recorded along transect D than along the other transects (Table 1), with a large number being pioneer or disturbance species. The lowest total basal cover for the herbaceous layer was also recorded for this area. It is therefore possible that transect D represents a lower seral stage in the succession than the other transects. Within transect D abundant pioneer microsites could have developed as a result of selective grazing.

Aristida argentea and *A. stipitata*, probably indicative of pioneer or disturbed conditions, have a preponderant position in the upper section, the middle or left in Figures 1 – 6. These species therefore do not only occur under more disturbed conditions, representing more xeric conditions, but more regularly in the open habitat.

Aristida argentea and *A. stipitata* are sometimes closely associated with *Eragrostis pallens* and *Digitaria eriantha* (e.g. Figure 1) and therefore do not always represent the most xeric conditions within the study area. In the Kalahari under semi-desert conditions *A. argentea* and *A. stipitata* occur in association with *Eragrostis pallens* under fairly undisturbed conditions. In Figures 1 – 6, *A. argentea* and *A. stipitata* usually occupy a more xeric disturbed position than *Eragrostis pallens* and may represent a lower stage in the succession.

Cleome spp., *Phyllanthus* spp., *Aristida* spp., *Rhynchelytrum repens, R. villosum, Pogonarthria squarrosa,*

Table 1 Frequency[a] of the plant species recorded in consecutive quadrats over six 200 m transects. a = frequency in ten composite samples

Plant name and abbreviation		Growth form	Transects					
			A	B_1	B_2	C	D	E
Andropogon schirensis Hochst.	And schi	Hsc					5	
Aristida aequiglumis Hack.	Ari aequ	Hsc	5					1
Aristida argentea Schweick.	Ari arge	Hsc	10	9	10	9	10	9
Aristida congesta Roem. et Schult.	Ari cong	Tsc/Hsc	6	4		10	7	
Aristida stipitata Hack.	Ari stip	Hsc	10	9	9	8	10	4
Aristida sp.	Ari sp.	Tsc/Hsc	3					1
Asclepias burchellii Schltr.	Asc burc	Pn		4				
Asparagus sp.	Asp sp.	Pn					4	
Felicia muricatus (Thunb.) Nees	Ast muri	Csf						1
Barleria bremekampii Oberm.	Bar brem	Csf	10	10	10			
Barleria sp.	Bar camp	Csf	4					
Brachiaria brizantha (Hochst.) Stapf	Bra briz	Hsc		4				
Brachiaria nigropedata (Munro) Stapf	Bra nigr	Hsc				3	6	
Brachiaria serrata (Spreng) Stapf	Bra serr	Hsc				4	4	
Burkea africana Hook	Bur afri	Pmi	4	8	7	6	6	
Cassia mimosoides L.	Cas mimo	Hsc	9	10	6	10	10	
Cleome sp.	Cle hete	Tsc	6			6		
Cleome monophylla L.	Cle mono	Tsc	5	10	8	10	9	3
Commelina africana L.	Com afri	Hsc	9	7	7	10	8	
Commelina erecta L.	Com erec	Tsc	3	3	5	6	6	3
Commelina sp.	Com sp.	Tsc				8		
Combretum molle R. Br. ex G. Don	Com moll	Pmi					1	
Convolvulus sagittatus Thunb.	Con sagi	Tsc	4	3				
Crabbea angustifolia Nees	Cra angu	Tsc			3		5	
Cyperus amabilis Vahl	Cyp amab	Hsc	9	4	4			
Cyperus denudatus L.f.	Cyp denu	Hsc	4	4				
Cyperus margaritaceus Vahl	Cyp marg	Hsc				10	10	
Cyperus sexangularis Nees	Cyp sexa	Hsc				7	5	
Dichapetalum cymosum (Hook.) Engl.	Dic cymo	Cg					10	
Deheteropogon amplectens (Nees) Clayton	Dih ampl	Hsc	9	4	4	10	10	
Digitaria eriantha Steud.	Dig eria	Hsc	10	10	10	10	10	10
Elephantorrhiza elephantina (Burch.) Skeels	Ele elep	Cg	3			4		2
Elephantorrhiza goetzei (Harms) Harms	Ele quer	Cg	5		2	6		
Elionurus muticus (Spreng.) Kunth	Eli muti	Hsc				10		
Eragrostis lehmanniana Nees	Era lehm	Hsc						4
Eragrostis pallens Hack.	Era pall	Hsc	10	10	10	10	10	6
Eragrostis rigidior Pilg.	Era rigi	Hsc				4		
Fimbristylis hispidula (Vahl) Kunth	Fim hisp	Hsc	8	8	6	10	10	
Giesekia pharnaceoides L.	Gis phar	Tsc				7	8	
Grewia flavescens Juss.	Gre flav	Pmi	3		3			
Helichrysum kraussii Sch. Bip.	Hel krau	Pn	4					
Hermannia parvula Burtt Davy	Her parv	Tsc	3				4	5
Heteropogon contortus (L.) Beauv.	Het cont	Hsc					9	
Hyparrhenia hirta (L.) Stapf	Hyp hirt	Hsc		3			6	
Hyperthelia dissoluta (Nees ex Steud.) Clayton	Hyp diss	Hsc	5	2	5			
Ipomoea transvaalensis A. Meeuse	Ipo tran	Tsc			3			
Jatropha sp.	Jat sp.	Gb				4	6	
Justicia flava (Vahl) Vahl	Jus flav	Tsc	1			10	10	
Kohautia virgata (Willd.) Brem.	Koh virg	Tsc				10	10	
Kohautia sp.	Koh sp.	Tsc				5		
Lannea edulis (Sond.) Engl.	Lan edul	Cg		5	2			
Lippia javanica (Burm. f.) Spreng.	Lip java	Pn		10	9			
Mesembryanthemum sp.	Mes sp.	Tsc	4	4	6			
Ochna pulchra Hook.	Och pulc	Pmi	10	10	10	10	10	3
Oldenlandia sp.	Old sp.	Tsc	7	9	6			3
Oxalis sp.	Oxa sp.	Gb			1			
Panicum maximum Jacq.	Pan maxi	Hsc		8	4			
Perotis patens Gand.	Per pate	Tsc	9	8	6	10	10	8
Phyllanthus burchellii Muell. Arg.	Phy burc	Tsc	9	9	6	33	5	
Phyllanthus parvulus Sond.	Phy parv	Tsc	7	7	7	10	9	

Pentarrhinum insipidum E. Mey.	Pen insi	Csc				5		
Pogonarthria squarrosa (Licht.) Pilg.	Pog squa	Tsc/Hsc	6	5				6
Portulaca sp.	Por sp.	Tsc					4	
Pygmaeothamnus zeyheri (Sond.) Robyns	Pyg zeyh	Cg		4	2	3	6	
Rhynchelytrum repens (Willd.) C.E. Hubb.	Rhy repe	Tsc/Hsc	8	8	7			4
Rhynchelytrum setifolium (Stapf.) Choiv.	Rhy seti	Hsc	9	6	5		10	
Rhynchelytrum villosum (Parl.) Choiv.	Rhy vill	Hsc				4	10	
Ruellia cordata Thunb.	Rue cord	Csf					2	
Schizachyrium jeffreysii (Hack.) Stapf.	Sch jeff	Hsc					6	
Schizachyrium sanguineum (Retz.) Alst.	Sch sang	Hsc				9	9	
Setaria perennis Hack.	Set pere	Hsc	10	10	9	4		2
Solanum panduraeforme E. Mey.	Sol pand	Csf					1	
Strychnos cocculoides Bak.	Str cocc	Pmi					9	
Strychnos pungens Soler.	Str pung	Pmi	6					
Tagetes minuta L.	Tag minu	Tsc	5					
Tephrosia longipes Meisn.	Tep long	Pn				6	7	
Terminalia sericea Burch. ex DC.	Ter seri	Pmi					5	
Themeda triandra Forsk.	The tria	Hsc	4	2	6			4
Trachypogon spicatus (L.f.) O. Kuntze	Tra spic	Hsc					5	
Urelytrum squarrosum Hack.	Ure squa	Hsc	8	1	3	5	7	
Waltheria indica L.	Wal indi	Hsc	6	5	6	6	9	8
Xerophyta retinervis Bak.	Xer reti	Pn	5					
Unidentified	Uni 1		2			10		
	Uni 2							10
	Uni 3		4					

P = phanerophyte; C = chamaephyte; H = hemicryptophyte; G = geophyte; T = therophyte; sc = suffrutescent; Cg = geoxylic suffrutices; n = nano-; mi = micro-. (Whittaker *et al.*, in press)

Table 2 Eigen values and summarized data for study areas. Biomass and leaf area indices (LAI) from Rutherford (1979)

Study area	Eigenvalue from DECORANA axis 1	axis 2	axis 3	Number of species in analysis	Biomass ($kg\ ha^{-1}$) Tree only	Total (tree & shrubs)	LAI	Basal cover %
A	0,388	0,287	0,183	45	17062	20022	10,094	6,65
B_1	0,660	0,538	0,273	37	14767	16335	7,200	5,80
B_2	0,807	0,424	0,263	35	14767	16335	7,200	5,80
C	0,298	0,214	0,146	45	11040	12647	5,715	5,10
D	0,355	0,200	0,176	47	14065	14800	6,933	4,70
E	0,685	0,474	0,277	20	15073	17555	9,187	5,20

Waltheria indica and a few other annual species are, in general, often associated with disturbed conditions within the *Burkea africana* Savanna. Some of these species occupy a less disturbed more mesic position in Figures 1 – 6 and hence have a wide ecological tolerance. These species are not restricted to either the more open or closed habitats and can be expected to occur under a wide range of disturbed conditions. They are either widely distributed through the study area (*Cleome monophylla* and *Phyllanthus* sp.) or occur locally (*Cleome heterophylla, Aristida congesta, Rhynchelytrum repens, Rhynchelytrum villosum* and *Pogonarthria squarrosa*) indicating local disturbed conditions or selective grazing (*cf.* Table 1; high value – wide distribution; low value – restricted or local distribution).

The poisonous geoxylic *Dichapetalum cymosum* is frequently associated with xeric and/or disturbed conditions (Figure 5) and is more abundant in disturbed areas within *Burkea africana* Savanna that is burned.

Eragrostis pallens, a strong bunch or tuft grass, and *Digitaria eriantha*, a stoloniferous creeping grass, which have the highest basal covers of all herbaceous species (Table 3) occur regularly throughout the study area (Table 2). With the exception of transect D, both these species occupy a central position in Figures 1, 2, 3, 4 & 6 with *E. pallens* often occurring slightly more towards the open disturbed side and *D. eriantha* towards a more central, less disturbed position. It is also known that *E. pallens* occurs under semi-desert conditions while *D. eriantha* is confined to the higher rainfall areas of South Africa (Kok 1978) or occurs in the drier areas under more favourable conditions, for example, in the rocky koppies of the false Upper Karoo (Acocks 1975). Apparently *E. pallens* and *D. eriantha* represent a seral stage for the study area with *E. pallens* in a lower position in the sere than *D. eriantha*. It can be expected that the importance of *E. pallens* will decline as succession proceeds towards the climax while *D. eriantha* will remain as a subdominant or an associated species in the climax community.

Urelytrum squarrosum, Schizachyrium sanguineum, Schizachyrium jeffreysii, Hyparrhenia hirta, Hyperthelia dissoluta, Diheteropogon amplectens, Andropogon schirensis and *Trachypogon spicatus* are an interesting group of hard, coarse grasses in the study area with localized to wide distribution and represented in small numbers and with a basal cover

Table 3 Species basal cover per cent (b) and relative presence (p) in each study area

	Study area									
	A		B		C		D		E	
	b	p	b	p	b	p	b	p	b	p
Eragrostis pallens	2,45	36,8	1,7	29,6	1,25	24,5	0,85	18,3	1,7	32,7
Digitaria eriantha	1,4	21,1	1,35	23,5	2,3	45,1	1,3	28,0	0,95	18,3
Diheteropogon amplectens	0,25	3,7	0,05	0,9	0,55	10,8	0,4	8,6	0,75	14,4
Rhynchelytrum villosum	0,4	6,0	0,25	4,3	0,05	1,0	0,2	4,3	0,3	5,7
Andropogon schirensis	0,1	1,5			0,3	5,9	0,65	14,0	0,1	1,9
Perotis patens	0,1	1,5	0,3	5,2	0,1	1,9	0,1	2,2	0,4	7,7
Aristida argentea	0,2	3,0	0,15	2,6	0,15	2,9	0,15	3,2	0,3	5,7
Setaria perennis	0,25	3,7	0,55	9,6			0,1	2,2	0,05	1,0
Elionurus muticus	0,5	7,5	0,25	4,3						
Panicum maximum	0,1	1,5	0,45	7,8						
Urelytrum squarrosum	0,05	0,8	0,3	5,2	0,05	1,0	0,1	2,2		
Fimbristylis hispidula			0,1	1,8	0,1	1,9	0,2	4,3	0,1	1,9
Cymbopogon marginatus					0,05	1,0	0,25	5,3	0,05	1,0
Themeda triandra	0,35	5,3								
Trachypogon spicatus	0,15	2,3					0,1	2,2	0,05	1,0
Aristida congesta	0,15	2,3	0,15	2,6						
Schizachyrium sanguineum					0,05	1,0	0,15	3,2	0,1	1,9
Heteropogon contortus	0,1	1,5	0,1	1,8						
Schizachyrium jeffreysii					0,05	1,0			0,1	1,9
Selaginella dregei									0,15	2,8
Brachiaria serrata	0,1	1,5								
Aristida aequiglumis									0,05	1,0
Pogonarthria squarrosa									0,05	1,0
Rhynchelytrum setifolium							0,05	1,0		
Commelina africana							0,05	1,0		
Cassia mimosoides			0,05	0,9						
Justicia spp.					0,05	1,0				
Xerophyta retinervis					0,05	1,0				
Total	6,65		5,80		5,10		4,70		5,20	

of up to 0,75% (Tables 2 & 3). These species occur, in general, in the open habitat under both mesic and xeric conditions. They are probably disseminates from the neighbouring Sourish Mixed Bushveld (Acocks 1975) on shallow rocky soils with, e.g., *Urelytrum squarrosum, Diheteropogon amplectens* and *Trachypogon spicatus* in a seral position under prevailing conditions in the *Burkea africana* Savanna (Theron 1973). Even in the climax stage these species will be present in small numbers.

From the scatter diagrams it is clear that *Panicum maximum* is mostly associated with a dense or closed canopy habitat, with species such as *Commelina africana* and *C. erecta* being found more often in the shade beneath trees but not restricted to this habitat (Figures 1 – 6). In general, there are only a small number of species in the study area which are specifically associated with the under-tree habitat. As previously mentioned, the majority of species associated with conditions of disturbance, for example *Rhynchelytrum villosum*, have a wide range of tolerance and occur more frequently under trees than in the open. Most trees are umbrella shaped and do not project a very dense shade with the result that on clear days nearly all under-tree areas receive sunshine for a period of time. The presence of specific species under trees is therefore probably more often a result of local moisture or nutritional conditions than of shade (Havenga 1970).

Themeda triandra, a grass with a very wide distribution in South Africa and usually one of the subclimax or climax species, is only represented by a relatively small number of plants within the study area. Based on the ordination diagrams, *T. triandra* appears to be associated with more disturbed or pioneer conditions in the study area (Figure 2).

The ecological position of the woody species in the scatter diagrams e.g. *Burkea africana, Ochna pulchra, Grewia flavescens, Combretum molle* and *Strychnos cocculoides*, is unclear but usually represents the denser tree habitats. Only woody individuals, shorter than 0,5 m high, were recorded in the survey. Preliminary work indicates that seedlings of most woody species more often occur in the under-tree habitat than in the open. As a result the position of many woody species is more often inclined towards the closed habitat to the right in the scatter diagrams (Figures 1 – 6). The position of *Ochna pulchra* to the left in Figure 5 can be attributed to the presence of scattered individuals of young *O. pulchra* plants in the open subhabitat. According to these results the seedlings of many woody species probably prefer the more favourable water and nutritional conditions under the tree canopies than those in the open. The young woody individuals are, however, not confined to the under-tree subhabitat and this explains the sometimes more central position of woody species in e.g. Figure 3. The tree component was obviously under-sampled in this survey and the position of tree species within the ordinations must be evaluated with reservation.

The geoxylic suffrutices *Pygmaeothamnus zeyheri* and *Lannea edulis* are often conspicuous in the open burnt veld. Both these species occur in Figures 2 & 3 towards the lower left-hand corner which indicates a less disturbed, probably somewhat wetter open habitat for these species. In the study area these two species are more common in the open, lower lying areas closer to the marsh.

Although soil depth does not figure clearly in the scatter diagrams, the horizontal axis in Figure 1 is also an expression of soil depth with deep sandy soils to the left and shallower sandy soils to the right. *Xerophyta retinervis* and *Aristida aequiglumis* are characteristic of shallow rocky soils in this area.

Although the relative ecological positions of all species in the five transects differ, it is mainly the positions of the species associated with disturbed conditions that differ greatly from those of species such as *Setaria perennis, Eragrostis pallens* and *Digitaria eriantha*. This is an indication of the adaptability of the disturbance indicators which can occur under a wide range of conditions and are able to exploit conditions less favourable to perennials.

Fewer species were recorded for transect E (Table 1) with fewer pioneer or disturbance species occurring than in the other transects (Table 2 & Figure 6). Nevertheless, the total herbaceous cover corresponds favourably with that of the other areas (Tables 1 & 3). On the other hand, the greatest number of species were recorded in transect D with the lowest total basal cover (Table 1). The low basal cover can probably be attributed to the large number of pioneer species or disturbance indicators with small basal covers which occur in this area.

Although the biomass and leaf area index for the woody species (Rutherford 1979) in transect C (Table 2) are smaller than those in the other transects, the ecological position of the more important grass species and forbs within this transect do

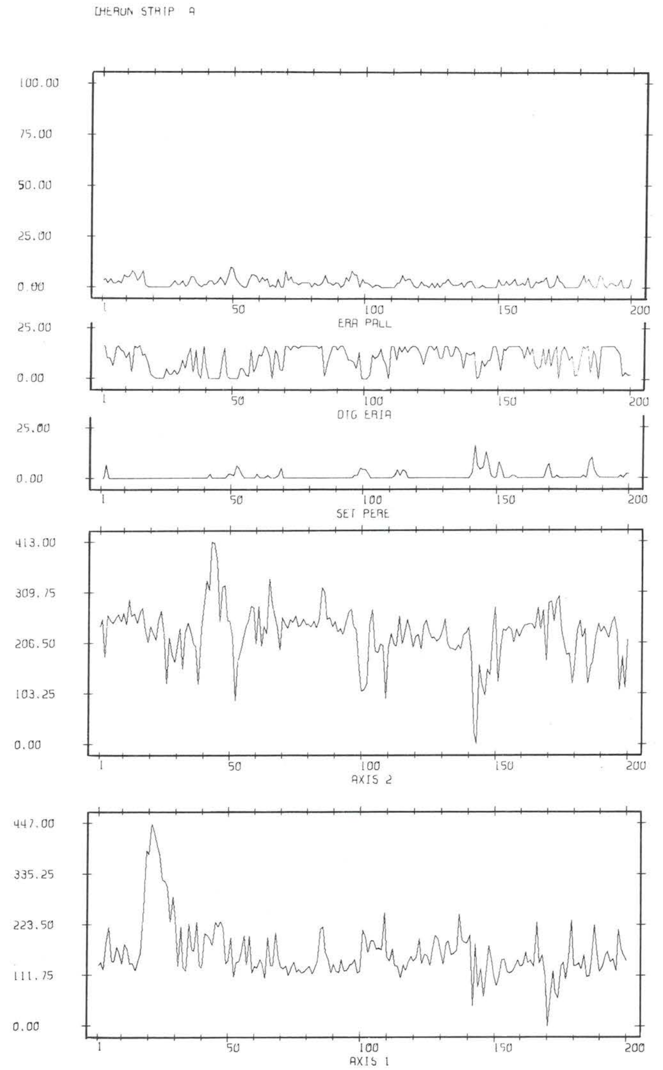

Figure 7 Traces of ordination and species scores along the field sequence of 200, 1 m^2 quadrats of transect A. Axes 1 and 2 — quadrat scores on the first and second DCA axes. Species frequency for species in quadrats as recorded in the field.

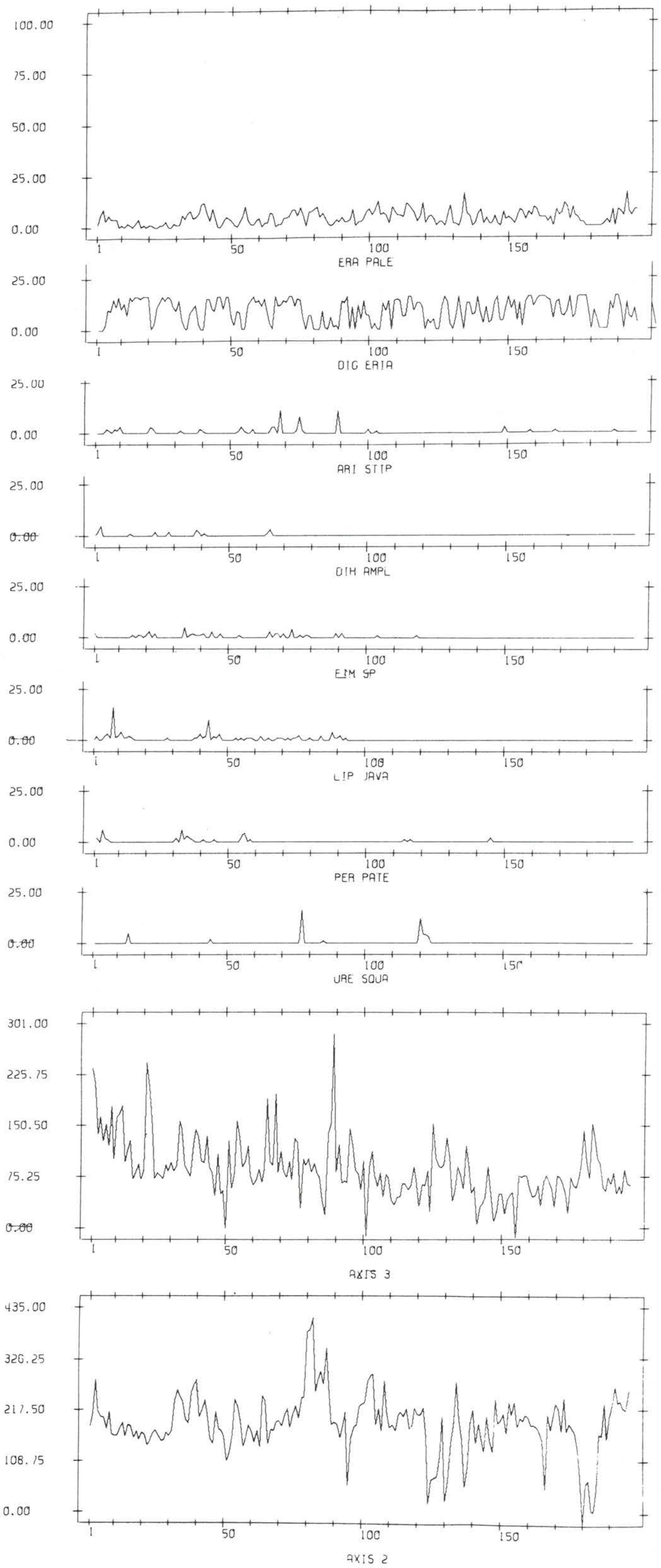

Figure 8 Traces of ordination and species scores along the field sequence of 200, 1 m^2 quadrats of transect B_1. Axes 2 and 3 — quadrat scores on the second and third DCA axes. Species — frequency for species in quadrats as recorded in the field.

not differ from those found in the other transects. It is therefore clear that the species composition, species distribution and basal cover differ in the different transects (Table 3 & Figures 1 – 6). The species composition under trees and in the open and the ecological position and relation of the species to each other in the different transects are, however, not significantly influenced by the tree stratum. The herbaceous layer in the *Eragrostis pallens-Burkea africana* Tree Savanna can therefore be considered to be ecologically relatively homogeneous. The possibility that the herbaceous layer represents a synusium independent of the other strata can thus not be ignored.

The quadrat scores (frequency) for the first two axes (Figures 7, 9, 10, 11 & 12) and the second and third axes (Figure 8) present a clear pattern. By comparing the frequency values of several species in the quadrats with the corresponding quadrat scores (Figures 7 – 12), it becomes clear that the species of general occurrence, e.g. *Eragrostis pallens* and *Digitaria eriantha*, do not elucidate the high and low scores. On the other hand, several of the more xerophytic or disturbance (pioneer) species with a more restricted distribution e.g. *Aristida stipitata, Perotis patens, Cassia mimosoides, Cleome monophylla* and *Lippia javanica* reflect some of the high and low quadrat scores (Figures 8, 10 & 12). Several of the coarse grass species, disseminates from neighbouring veld types or communities and representing seral stages with more specific habitat preferences, e.g. *Diheteropogon amplectens, Schizachyrium jeffreysii* and *Urelytrum squarrosum* support the obtained patterns to a greater or lesser extent.

In transect A the frequency values of *Setaria perennis*, one of the probable climax grasses in the study area, reflect only to a lesser extent the quadrat scores for the second axis (Figure 7). This suggests that the ecological environment within the transect is not of such an amplitude that it becomes limiting for the possible climax species.

With the exclusion of exceptionally high or low quadrat scores, the other high and low scores along the axes can be attributed to the combined influence of several species rather

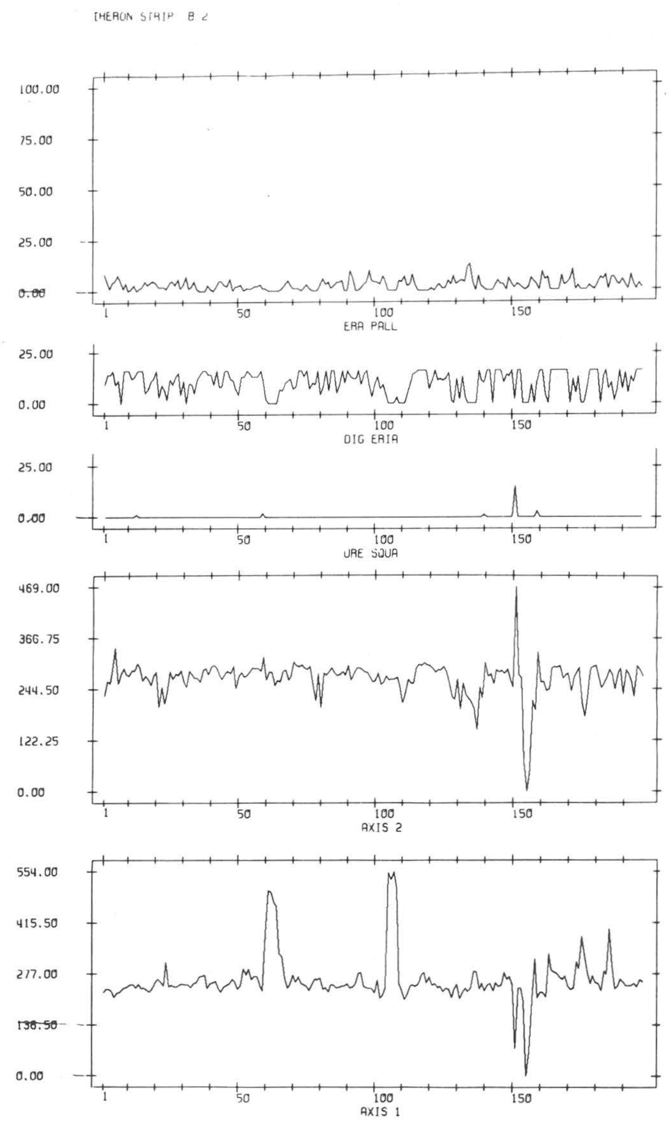

Figure 9 Traces of ordination and species scores along the field sequence of 200, 1 m^2 quadrats of transect B_2. Axes 1 and 2 — quadrat scores on the first and second DCA axes. Species frequency for species in quadrats as recorded in the field.

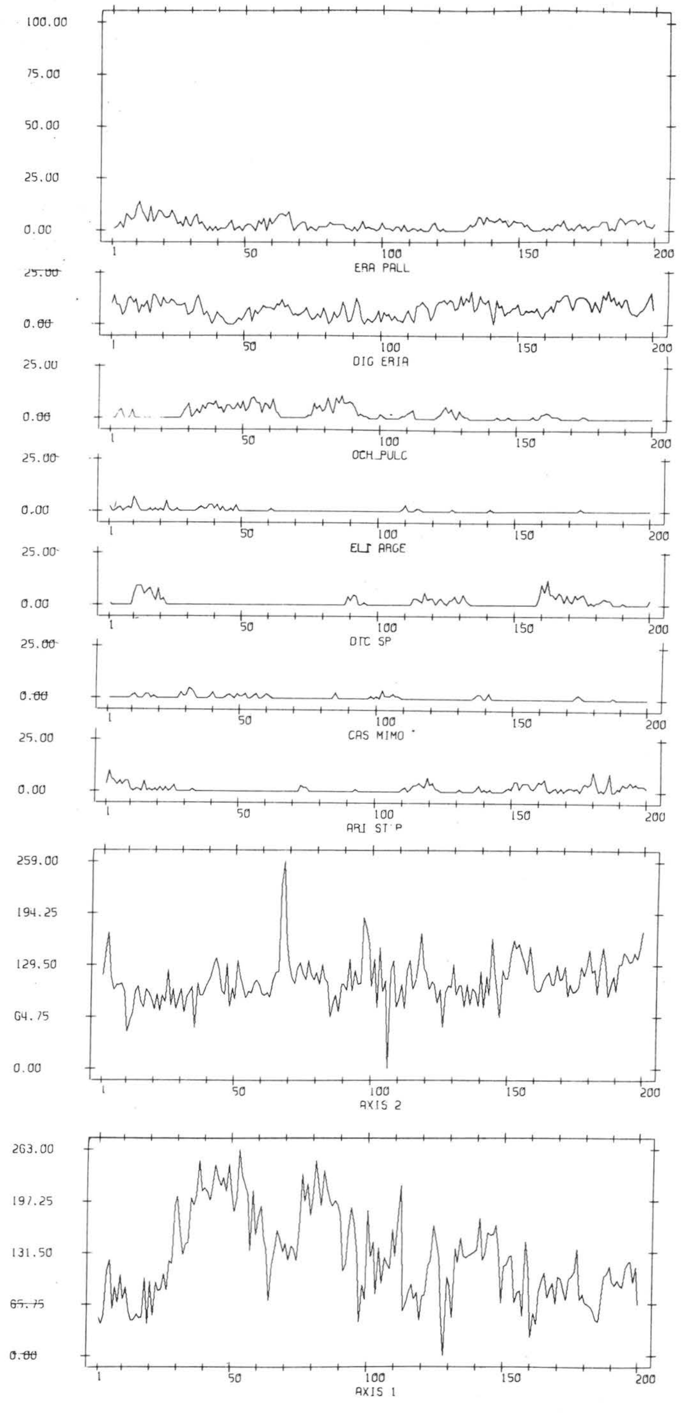

Figure 10 Traces of ordination and species scores along the field sequence of 200, 1 m^2 quadrats of transect C. Axes 1 and 2 — quadrat scores on the first and second DCA axes. Species frequency for species in quadrats as recorded in the field.

than to that of individual species. The exceptionally high and low quadrat scores can be attributed to certain species, with a restricted distribution or specific distribution pattern, which occur at regular intervals. The high peak to the left along the first axis in Figure 7 is a result of *Themeda triandra* occupying an extreme position (to the far right) on the horizontal axis in Figure 1. The low peak to the left along the first axis in Figure 7 is the function of the high frequency values for *Grewia flavescens* in the corresponding quadrats. The precise ecological positions of *Themeda triandra* and *Grewia flavescens* are, however, not clearly defined. Generally, the species with a polar position along the horizontal and vertical axes in Figures 1 – 6 are, respectively, responsible for the extreme high and low quadrat scores represented in Figures 7 – 12.

As the frequency values of the herbaceous species in the consecutive quadrats do not generally correspond with the different quadrat scores, it can be concluded that the herbaceous species cannot be considered to be critical indicator species of gradients in prevailing ecological environmental factors. In other words, as there are few species at the ends of axes in Figures 1 – 6, there are many indeterminate species in the area. These results also confirm the suggestion that the herbaceous layer is representative of a seral stage, characterized by many pioneer and disturbance species with wide ecological amplitudes.

In a relatively undisturbed *Burkea africana* Savanna within the Loskop Dam Nature Reserve, which is protected from overgrazing, the importance value of *Setaria perennis* can be as high as 53,5% in comparison with the 15,5% of *Digitaria eriantha* (= *D. smutsii*). At the same time *Eragrostis pallens*

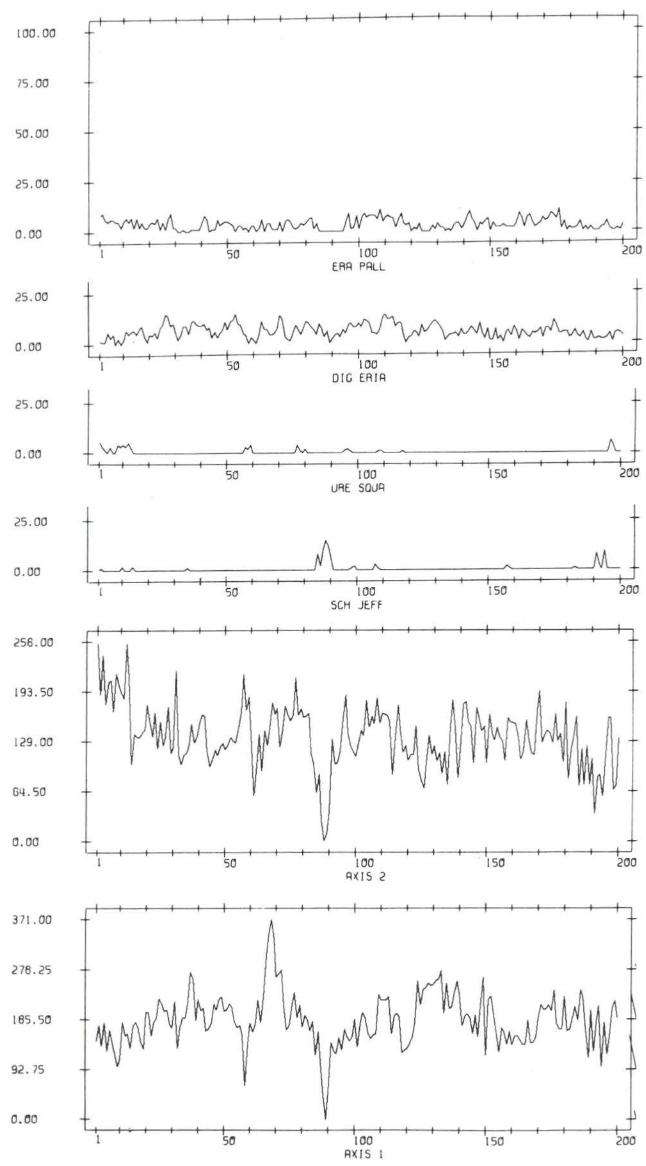

Figure 11 Traces of ordination and species scores along the field sequence of 200, 1 m² quadrats of transect D. Axes 1 and 2 — quadrat scores on the first and second DCA axes. Species frequency for species in quadrats as recorded in the field.

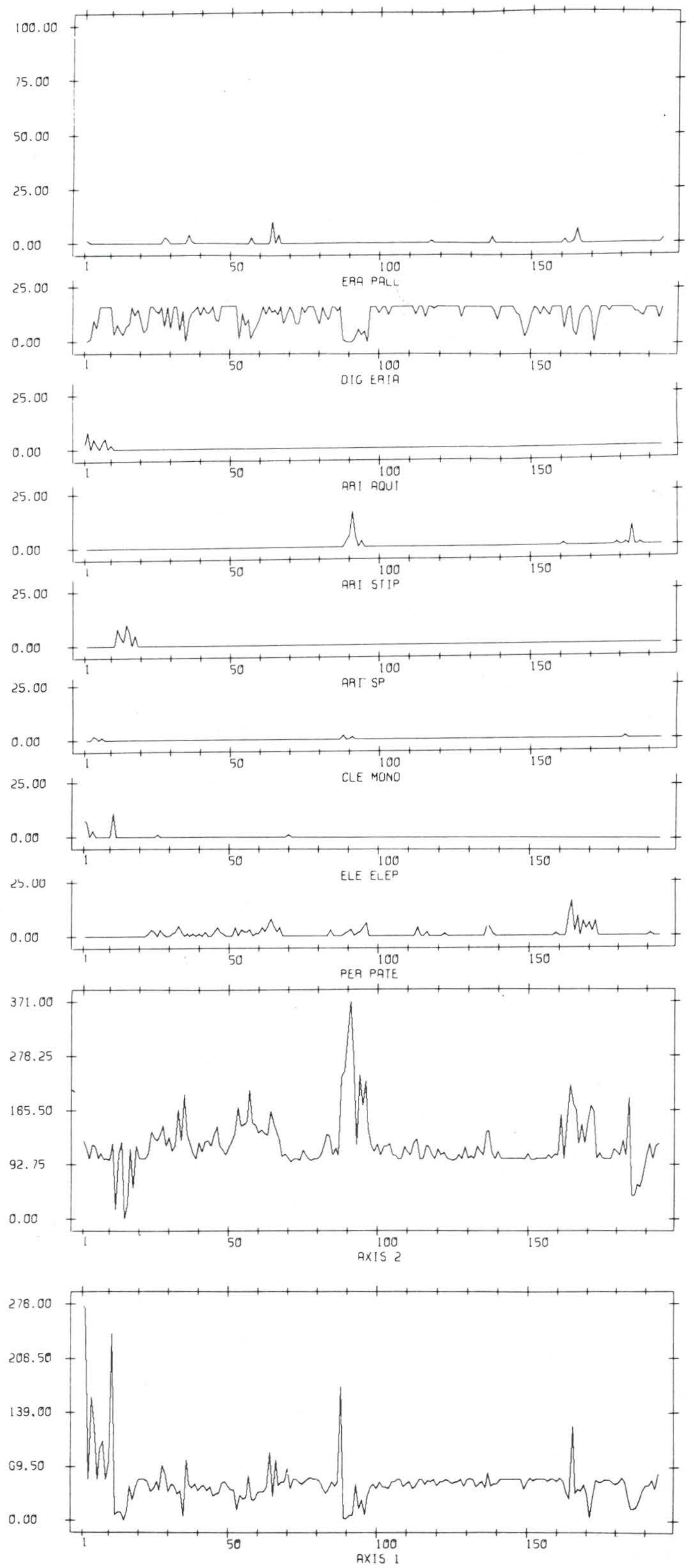

Figure 12 Traces of ordination and species scores along the field sequence of 200, 1 m² quadrats of transect E. Axes 1 and 2 — quadrat scores on the first and second DCA axes. Species frequency for species in quadrats as recorded in the field.

is only represented by scattered individuals (Theron 1973). On 15-year-old cultivated lands within the same *Burkea africana* Savanna the basal cover of *S. perennis* was 15,4%, that of *D. eriantha* was 5,8%, while *E. pallens* was represented by scattered individuals. In both areas *Panicum maximum* was restricted to under canopies with a fairly low basal cover (Theron 1973). There is therefore a possibility that the basal cover and important values of species, as well as the species composition for the climax *Burkea africana* Savanna, as found in the Loskop Dam Nature Reserve, represent the optimum community. It can therefore be concluded that the two grass species with the highest basal cover, *Eragrostis pallens* and *Digitaria eriantha* (Table 3), have wide ecological tolerances and do not represent the climax species for the *Eragrostis pallens-Burkea africana* Tree Savanna. The possibility remains that with a scientifically based management regime (or natural conditions) the herbaceous layer could return to a stage dominated by *Panicum maximum* under the trees and *Setaria perennis* in the open.

Conclusion

The different scatter diagrams (Figures 1 – 6) represent approximately the same ecological distribution for the different species and therefore reflect the same ecological function. It can therefore be concluded that the herbaceous layer in the *Eragrostis pallens-Burkea africana* Tree Savanna, irrespective of local differences in distribution of herbaceous species, species composition and herbaceous species cover-abundance values, is functionally homogeneous. It is also clear that the herbaceous layer, especially species composition under trees in comparison with the open habitat, is not greatly influenced by the tree layer. The herbaceous layer furthermore represents a seral stage. *Eragrostis pallens* and *Digitaria eriantha*, both with the highest basal cover in the study area, are representative of a seral stage rather than of the climax vegetation. The lack of pattern in the herbaceous layer can mainly be attributed to the large number of annual and perennial pioneer and disturbance species. In a similar study using the same quadrat size Whittaker *et al.* (in press) were able to detect pattern. However, they included a detailed survey of the woody vegetation that dominated the pattern. On the other hand, the possible climax species *Setaria perennis* and *Panicum maximum*, represented by small numbers and with local distribution, do not represent a specific pattern at this seral stage. According to the results of Theron (1973), under correct management this Veld Type should develop to a stage where *Setaria perennis* is the dominant grass in the open and *Panicum maximum* is dominant under the trees, with *Digitaria eriantha* and *Themeda triandra* as subdominants and with the coarse grasses, *Diheteropogon amplectens, Trachypogon spicatus, Hyparrhenia* spp. and *Eragrostis pallens*, represented in small numbers.

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