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Patterns of change in the herbaceous layer of a mesic savanna, South Africa

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The basal cover and presence of savanna plant species of the herbaceous stratum were monitored seven times from 1975 to 1990. The two dominant grass species, *Eragrostis pallens* and *Digitaria eriantha* contributed 58.5% to the overall mean percentage basal cover. A significant decrease in mean basal cover between 1977 and 1980 and a significant increase between 1986 and 1990 were observed. However, there was no significant difference between the mean total basal cover for 1975 (5.46%) and 1990 (6.13%). Rainfall during the 21 months preceding sampling as well as fire may explain the trends in basal cover. The ordination trajectories of basal cover and species presence over time indicate that no clear monotonic trends were apparent; however, a cyclic pattern could be recognized.

Die basale bedekking en teenwoordigheid van savanne-plantspesies van die kruidstratum is vir die tydperk 1975 tot 1990 gemonitor. Die twee dominante grasspesies, *Eragrostis pallens* en *Digitaria eriantha*, het 58.5% tot die gemiddelde basale bedekking bygedra. 'n Betekenisvolle afname in die gemiddelde basale bedekking tussen 1977 en 1980, en 'n betekenisvolle toename tussen 1986 en 1990, is aangeteken. Daar het egter geen betekenisvolle verskil tussen die gemiddelde basale bedekking vir 1975 (5.46%) en 1990 (6.13%) voorgekom nie. Die tendense in basale bedekking kan moontlik deur die reënval van die voorafgaande 21 maande, asook deur vuur, verklaar word. Die verloop van basale bedekking en spesieteenwoordigheid oor tyd dui daarop dat geen duidelike monotone tendense na vore getree het nie, maar dat 'n sikliese patroon wel opgemerk kan word.

Keywords: Basal cover, monitoring, Nylsvley, ordination, savanna.

Introduction

Ecological monitoring is the purposeful and repeated examination of the state or condition of specifically defined biotic groups in relation to external stress, with emphasis on changes related to the living organisms (Hinds 1984). O'Connor (1985) stated that whatever conceptual models are generated to account for dynamics of the herbaceous layer of savanna grasslands, appropriate long-term data sets are required to corroborate these models. Consideration of climatic oscillations (Tyson 1986) suggests a minimum time scale of 20 years for monitoring of herbaceous vegetation in savanna (O'Connor 1985).

Much work has been done on grassland dynamics in South Africa (Tainton 1984), mostly concentrating on the influence of various management treatments. There is, however, a lack of published information on long-term vegetation changes in the savanna grasslands of South Africa (O'Connor 1985). Long-term monitoring has only recently commenced in wildlife areas (Joubert 1983), and Fourie *et al.* (1987) and Van Rooyen *et al.* (1990) have given accounts of the vegetation changes occurring in the southern Kalahari for periods of up to 16 years. Van Rooyen and Theron (1982) reported on the vegetation changes of the savanna herbaceous vegetation in the Nylsvley Nature Reserve over a six-year period (1975 – 1980).

This study originated as part of the Savanna Ecosystem Project (Anon. 1975) with the purpose of characterizing and quantifying the structural features of the vegetation. The aim of this paper is to describe the changes in species composition and basal cover of the herbaceous layer over a 16-year period, and to relate the changes to environmental factors, particularly rainfall and fire.

Study area

The study area is in the Nylsvley Nature Reserve which is situated between 24°36′ and 24°42′ S latitude and 28°40′ and 28°44′ E longitude, in the Transvaal province, South Africa. The average annual rainfall is 630 mm (Van Rooyen & Theron 1982), most of which falls during the summer months from October to March. The study site is dominated by relatively coarse sandy soils (Harmse 1977) and falls within the broad-leaved savanna vegetation classified as *Eragrostis pallens – Burkea* Tree Savanna (Coetzee *et al.* 1976). The area is lightly grazed by indigenous herbivores. A detailed description of the study area was given by an anonymous author (1975), Coetzee *et al.* (1976) and Theron *et al.* (1984).

Methods

Within the study area, Lubke *et al.* (1983) selected five relatively homogeneous areas (transects A – E) for studies on the structure of woody species. The same areas were used for the monitoring of the plant species of the herbaceous layer. These areas fell mainly within the *Eragrostis pallens – Dombeya rotundifolia* variation of the *Eragrostis pallens – Burkea* Tree Savanna (Coetzee *et al.* 1976).

During February and March of 1975, 1977, 1980, 1982, 1984, 1986 and 1990, a 2000-point basal cover (Tidmarsh & Havenga 1955) and/or nearest herbaceous individual surveys were conducted in each of the five sampling areas (transects A – E). At every point a strike (basal or rooted part of living plant) or, in case of a miss, the closest plant to the point, was recorded. Seedlings of woody species as well as dwarf shrubs were also recorded. The total basal cover of the herbaceous layer and of the different plant species, including the calculation of significant differences, was determined according to Tidmarsh and Havenga (1955). The percentage presence (comparable to frequency) of a plant species was calculated as the number of times the species was the nearest to the point, expressed as a percentage of the total number of points. Sampling was done by the same team of researchers throughout the study period, thereby avoiding differences in approach and interpretation of methodology. All plant names follow those of Gibbs-Russell (1985, 1987).

Austin (1977) and Austin *et al.* (1981) stated that multivariate techniques can provide a clear partitioning of types of dynamic behaviour present in grassland communities and should be used to study succession. Therefore, Detrended Correspondence Analysis (DECORANA, Hill 1979) was applied to the basal cover and presence values data sets of all plant species of each of the five transects A – E separately and the mean values for the study area. DECORANA has the advantage of producing axes that correspond to actual ecological distances, as defined by the abundance of species, and are not forced to be equal in length (Whisenant & Wagstaff 1991). The positions of points produced by DECORANA on the scatter diagram for each site over time should indicate vegetation change trajectories through time in the floristic space defined by the ordination axes. These trajectories were examined for patterns of behaviour between sites and over time.

Three data sets were subjected to Redundancy Analysis (RDA), a (multivariate) direct gradient analysis technique, using the CANOCO program package of Ter Braak (1986, 1987, 1988, 1990a, 1990b). This package allows both the dissection and expression of external effects and the testing of their significance (Gibson & Brown 1992; O'Connor & Pickett 1992). This analysis was done to test the significance of the environmental variables in explaining the changes in floristic composition and basal cover over the period of 16 years. The one data set consisted of the mean basal-cover values of the 20 dominant plant species for the seven sampling dates, and the second data set of the total basal cover values of each sampling date for the five different transects. The third data set consisted of the following environmental variables: the total rainfall of the calendar year (January to December) preceding the sampling date; the total rainfall for the 9 and 21 months preceding the sampling date; and the occurrence of fire. The 9 months preceding the sampling date cover one rainy season, whereas the 21 months cover two rainy seasons. The occurrence of fire between sampling dates was arbitrarily weighted as follows: if no fire had occurred in between sampling dates in a transect, a value of 1 was allocated, for a possible total of 5 (five transects) per sampling date; if a fire had occurred more than a year before sampling, a value of 2 per transect for a possible total of 10 was allocated; and if a fire had occurred within the preceding year of sampling, a value of 4 per transect was allocated for a possible total of 20 per sampling date. The Monte Carlo permutation test (Ter Braak 1990b) was performed on the data to test for significance of the first canonical axis.

Results and Discussion

Trends in basal cover and presence

The mean basal cover for all the transects varied between 4.07 and 6.13%, with an overall mean of 5.06% (Table 1).

Table 1 Percentage basal cover of the species of the herbaceous layer in the Nylsvley Nature Reserve

Species	Mean of transects A – E for sampling years							Overall mean
	1975	1977	1980	1982	1984	1986	1990	
Eragrostis pallens	1.59	1.63	0.98	1.54	1.97	1.48	1.49	1.526
Digitaria eriantha	1.46	1.64	1.01	0.55	1.06	1.44	2.88	1.434
Diheteropogon amplectens	0.40	0.59	0.27	0.30	0.14	0.22	0.26	0.311
Andropogon schirensis	0.23	0.24	0.18	0.12	0.13	O.18	0.30	0.197
Setaria sphacelata	0.18	0.16	0.10	0.09	0.15	0.12	0.14	0.134
Perotis patens	0.20	0.16	0.14	0.20	0.01	0.06	0.12	0.128
Aristida mollissima	0.19	0.10	0.12	0.13	0.10	0.08	0.16	0.126
Justicia minima	0.01	0.13	0.23	0.12	0.13	0.10	0.01	0.104
Trachypogon spicatus	0.06	0.11	0.15	0.11	0.14	0.08	0.04	0.099
Elionurus muticus	0.16	0.12	0.03	0.13	0.13	0.04	0.03	0.091
Melinis repens villosum	0.24	0.07	0.02	0.04	0.02	0.12	0.01	0.074
Cyperus margaritaceus	0.00	0.06	0.09	0.10	0.02	0.14	0.10	0.073
Fimbristylis hispidula	0.10	0.08	0.06	0.07	0.03	0.10	0.06	0.071
Panicum maximum	0.11	0.10	0.06	0.00	0.05	0.08	0.07	0.067
Cymbopogon plurinodis	0.07	0.05	0.05	0.03	0.03	0.09	0.11	0.061
Urelytrum agropyroides	0.10	0.12	0.07	0.01	0.01	0.02	0.07	0.057
Schizachyrium sanguineum	0.06	0.09	0.03	0.09	0.06	0.02	0.01	0.051
Heteropogon contortus	0.04	0.02	0.09	0.07	0.03	0.03	0.02	0.043
Aristida congesta	0.06	0.05	0.05	0.04	0.04	0.04	0.01	0.041
Schizachyrium jeffreysii	0.03	0.08	0.02	0.06	0.06	0.02	0.01	0.040
Other 47 species	0.17	0.36	0.53	0.27	0.29	0.45	0.23	0.329
	5.46	5.96	4.28	4.07	4.60	4.91	6.13	5.06

A significant ($P < 0.05$) decrease in basal cover between 1975 and 1982 and a significant increase between 1982 and 1990 were observed for the total area. However, there was no significant difference between the total basal-cover value of 1975 (5.46%) and 1990 (6.13%) (Table 1).

The basal cover of 67 of about 134 plant species encountered within the study area, was determined during the study period (Table 1). The two dominant grass species, *Eragrostis pallens* and *Digitaria eriantha* contributed 58.5%, and the 20 dominant species together contributed 93.3% to the total mean percentage basal cover. According to the results on percentage presence of all species (Table 2), *Melinis repens* subsp. *villosum* and *Aristida congesta* had relatively high presence values in 1975, but these declined during later years. According to Yeaton *et al.* (1988), these two species are favoured by annual burns. Species such as *Lophiocarpus tenuissimus, Limeum viscosum, Cleome maculata* and to a lesser extent also *Justicia minima* and *Perotis patens* attained maximum presence during 1980, when *Digitaria eriantha* had its lowest presence. In this period, a low total basal cover was also recorded which could be linked to low rainfall (Figures 1a & 1b). Since 1986, an increase in presence and/or basal cover in *Digitaria eriantha, Andropogon schirensis, Setaria sphacelata, Panicum maximum* and *Cymbopogon plurinodis* is evident. Yeaton *et al.* (1988) found that protection from annual burning increased the abundance of *Digitaria eriantha.*

The mean percentage basal cover of *Eragrostis pallens* in 1980 was significantly lower than for the other years. No significant difference could, however, be found for *Eragistis pallens* in percentage presence between the different years. The percentage basal cover and percentage presence of *Digitaria eriantha* was significantly higher ($P < 0.05$) in 1990 compared to the other years. When comparing the changes in the percentage basal cover of the 20 dominant plant species between 1975 and 1990, the basal cover of *Digitaria eriantha* increased, while significant decreases in basal cover were recorded for *Elionurus muticus* and *Melinis repens.*

Although *Eragrostis pallens* had a slightly higher overall mean percentage basal cover than *Digitaria eriantha* (Table 1), the latter species has a much higher percentage presence (Table 2). *Eragrostis pallens* is a relatively large-tufted bunch grass species, while *Digitaria eriantha* is a smaller tufted, stoloniferous grass species. *Digitaria eriantha* was therefore recorded more often than *Eragrostis pallens* as individuals nearest to the point.

It was noted that the accummulation of litter between grass tufts had a negative effect on the rooting of stolons of *Digitaria eriantha.* The removal of litter by means of fire could therefore eventually lead to an increase in the regeneration of *Digitaria eriantha* (Tables 1 & 2). At Nylsvley, Gandar (1982) also observed that grass species palatable to large herbivores, such as *Digitaria eriantha,* recovered more vigorously after a fire than unpalatable species, such as *Eragrostis pallens.* According to Yeaton *et al.* (1988), *Digitaria eriantha* and *Eragrostis pallens* may replace one another temporally by a successional process. The habit of *Digitaria eriantha* of reproducing vegetatively from stolons may aid this species in dispersing and successfully colonizing open microsites.

An increase in percentage presence was also recorded for

Table 2 Percentage presence of the herbaceous species in the Nylsvley Nature Reserve

Species	Mean of transects A – E 1975	1980	1986	1990	Overall mean
Digitaria eriantha	28.04	19.28	27.03	40.17	28.63
Eragrostis pallens	21.62	16.26	21.32	18.02	19.31
Diheteropogon amplectens	5.13	4.47	4.26	3.90	4.44
Andropogon schirensis	3.35	2.94	3.99	4.90	3.80
Perotis patens	4.22	5.30	3.26	2.27	3.76
Aristida mollissima	4.26	2.98	4.03	3.05	3.58
Ochna pulchra	1.88	3.28	3.38	3.64	3.05
Lophiocarpus tenuissimus	0.00	5.71	3.32	2.60	2.91
Limeum viscosum	0.00	5.76	2.68	1.46	2.48
Justicia minima	1.89	2.97	2.55	1.23	2.16
Cleome maculata	0.52	5.00	0.60	0.90	1.76
Fimbristylis hispidula	1.85	1.48	2.26	1.00	1.65
Melinis repens villosum	3.08	0.64	2.26	0.36	1.59
Panicum maximum	1.96	1.58	1.24	1.44	1.56
Aristida congesta	2.23	1.78	0.71	0.23	1.24
Cassia mimosoides	1.20	0.85	1.50	1.11	1.17
Trachypogon spicatus	1.54	1.56	1.13	0.43	1.17
Dichapetalum cymosum	0.90	1.48	0.81	1.39	1.15
Waltheria indica	0.78	1.35	1.57	0.61	1.08
Setaria sphacelata	1.08	0.60	0.69	1.23	0.90
Other 114 species	14.47	14.73	11.41	10.06	12.67
Total	100	100	100	100	100

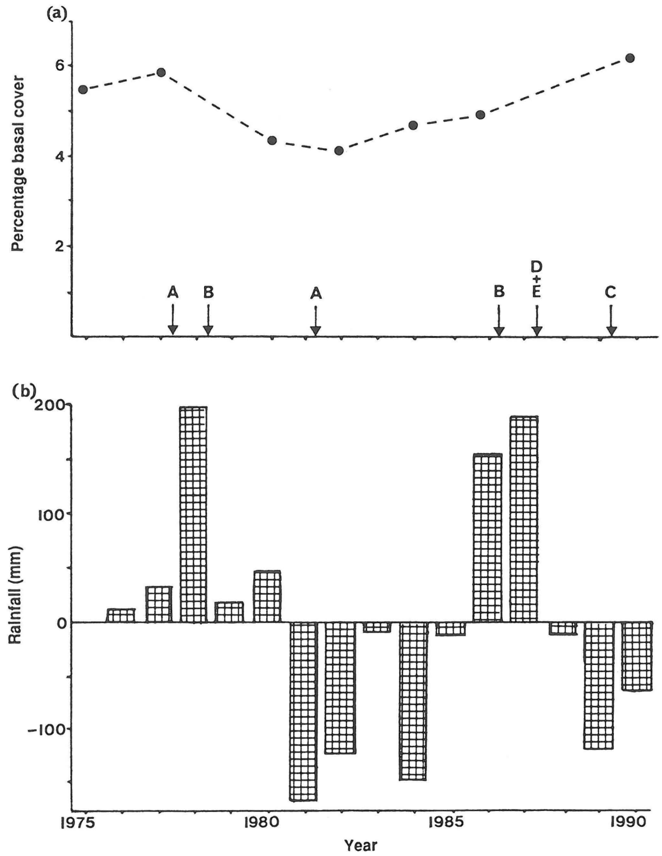

Figure 1 (a) Mean percentage basal cover of all species of transects A – E from 1975 to 1990 (the occurrence of fire in transects A – E is indicated by arrows); and (b) the annual rainfall (calendar year) above or below the average rainfall for the study period.

Ochna pulchra, but this increase was not reflected in the basal cover (Tables 1 & 2). Decreases in both percentage basal cover and percentage presence were recorded for *Aristida congesta* and *Schizachyrium sanguineum*.

According to Theron *et al.* (1984), the dominance of *Eragrostis pallens* and *Digitaria eriantha* indicates a seral stage and it can be expected that the importance of *Eragrostis pallens* will decline as succession proceeds towards a climax or late succession stage, while *Digitaria eriantha* will remain as a subdominant or an associated species in the climax community. Although *Digitaria eriantha* declined in abundance during the early eighties, possibly as a result of the drought (429 mm) during the 1978/79 season, an increase in basal cover and presence has occurred since. The possibility that the herbaceous layer could return to a stage dominated by *Panicum maximum* under trees and *Setaria sphacelata* in the open, was also speculated on by Theron *et al.* (1984). The present trends in the species abundance only partially support this hypothesis, as neither *Eragrostis pallens* nor *Panicum maximum* showed any specific overall trend since 1975, but *Setaria sphacelata* tended to have a higher presence value, but not basal cover, in 1990 (Tables 1 & 2).

Multivariate analysis

The mean basal-cover values (Figure 2a) and mean species presence values (Figure 2b) of the plant species in all five transects for each of the different sampling dates (years), were ordinated to indicate the trajectories through time in the floristic space defined by the ordination axes. The trajectories over time of basal cover and species presence indicate that no clear linear trends were apparent (Figures 2a & 2b), but rather that a cyclic pattern could be distinguished. This was also evident from all the ordinations of each of the five transects separately (Figures 3 & 4), based on basal cover and species presence.

The RDA on the basal cover data set of the five transects for the different sampling dates, showed that the rainfall of the preceding 21 months accounted for 25% of the variance, fire added 12%, while the variance explained by all variables was 89% (Figure 5). The eigenvalues of the first two axes were 0.483 and 0.293, respectively, indicating that these two axes account for 77.6% of the variation in the data. The Monte Carlo permutation test, however, showed that the first canonical axis was not significant at the 5% level.

The RDA on the mean basal-cover values of the 20 dominant species for the different sampling dates, showed fire accounted for 36% of the variance, while the interaction of rainfall/fire (rainfall of the past 21 months), added another 12%. The eigenvalues of the first two axes were 0.793 and 0.126, respectively, indicating that these two axes accounted for 91.9% of the variation in the data. However, also in this case the Monte Carlo permutation test showed that the first canonical axis and the overall test were not significant at the 5% level. Fire seems to be related to negative basal-cover changes in *Setaria sphacelata* and *Eragrostis pallens* (Figure 6). Apparently, *Digitaria eriantha* seems not to be influenced by fire. *Heteropogon contortus*, *Perotis patens* and *Justicia minima* are positively correlated with fire. The rainfall of the preceding 21 months also negatively influenced *Setaria sphacelata*.

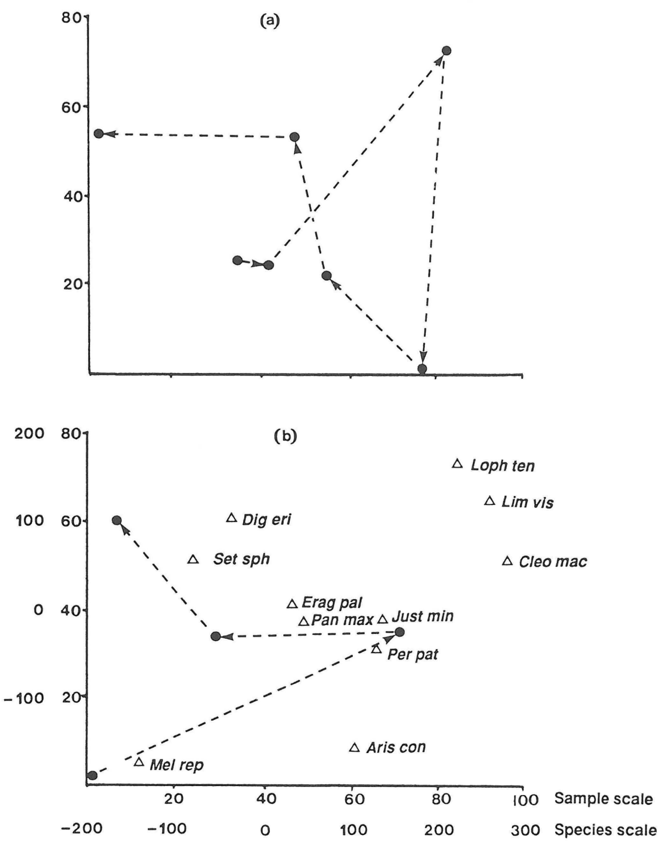

Figure 2 DECORANA scatter diagrams of sampling dates based on (a) mean percentage basal cover of all species (eigenvalue axis 1: 0.081; axis 2: 0.037); and (b) sampling dates and selected plant species based on percentage presence of all species, over the study period 1975 to 1990 (eigenvalue axis 1: 0.091; axis 2: 0.017). *Aris con, Aristida congesta; Cleo mac, Cleome maculata; Dig eri, Digitaria eriantha; Erag pal, Eragrostis pallens; Just min, Justicia minima; Lim vis, Limeum viscosum; Loph ten, Lophiocarpus tenuissimus; Mel rep, Melinis repens; Pan max, Panicum maximum; Per pat, Perotis patens; Set sph, Setaria sphacelata.*

The composition and production of grassland may change rapidly when it is subjected to disturbance conditions such as high grazing pressure and incorrect fire management (Tainton 1984). Fire tends to exaggerate the instability of herbaceous trends resulting from rainfall variability (O'Connor 1985). The significant decrease in basal cover between 1977 and 1980 could be attributed to fires that occurred in transects A and B in 1978 and 1979, respectively, combined with the below-average rainfall of 429 mm for the 1978/79 season (Table 1 and Figure 1). According to the RDA analysis, the basal-cover changes in transects A and B over the study period seem to be positively correlated with fire, while changes in transects D and E were influenced more by rainfall (Figure 6).

Conclusions

Tracing ordination trajectories over time highlighted general patterns of floristic change. It is concluded that the herbaceous vegetation on the sandy soils of this mesic savanna is relatively stable and shows cyclic patterns of floristic and basal-cover changes due to fluctuations in rainfall and in reaction to fire. Management strategies should therefore not be based on short-term trends in the herbaceous layer of savanna vegetation.

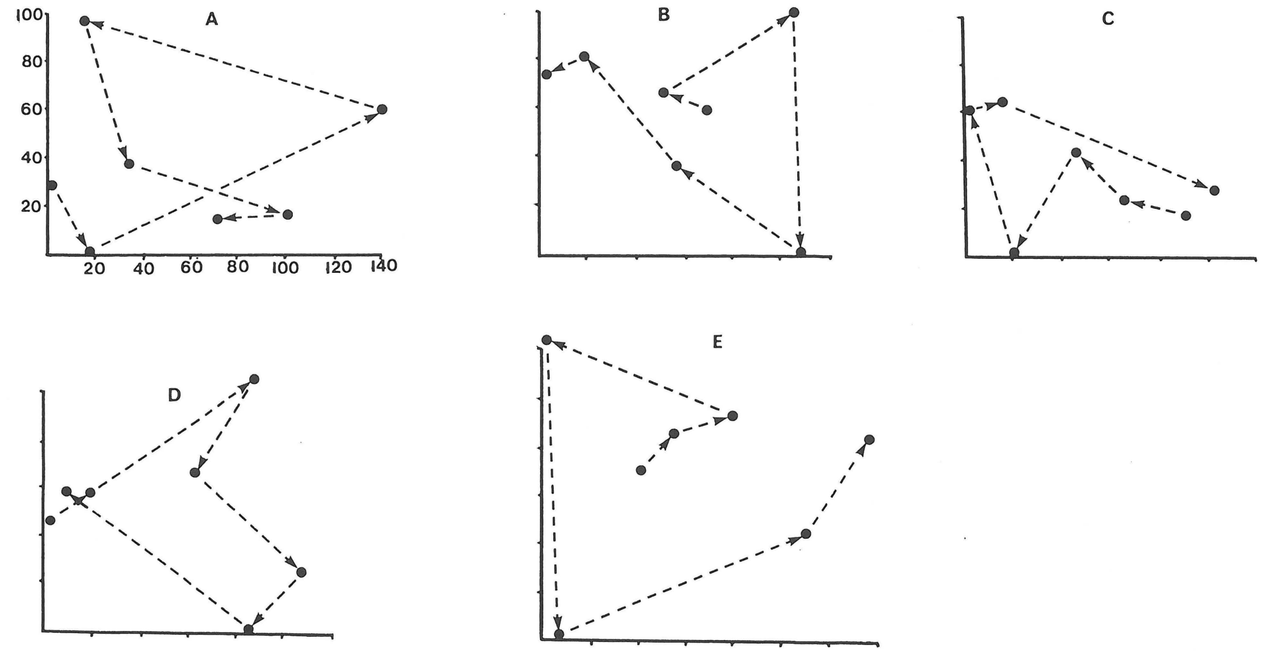

Figure 3 DECORANA scatter diagrams of sampling dates (1975, 1977, 1980, 1982, 1984, 1986, 1990), based on percentage basal cover of all species of each of the five transects A – E. Eigenvalues for axis 1 and axis 2, respectively: A: 0.229 and 0.07; B: 0.167 and 0.107; C: 0.133 and 0.012; D: 0.151 and 0.112; E: 0.19 and 0.058. The units for all axes are the same as for A.

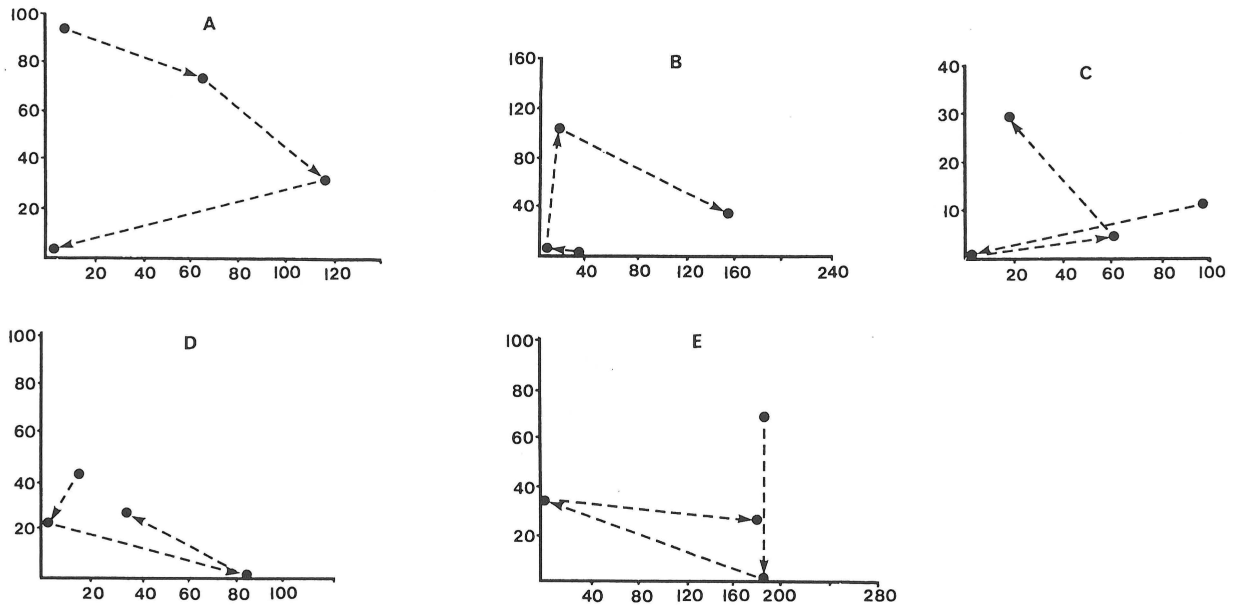

Figure 4 DECORANA scatter diagrams of sampling dates (1975, 1980, 1986, 1990), based on percentage presence of all species of each of the five transects A – E. Eigenvalues for axis 1 and axis 2, respectively: A: 0.232 and 0.072; B: 0.351 and 0.084; C: 0.161 and 0.0; D: 0.115 and 0.0; E: 0.497 and 0.051.

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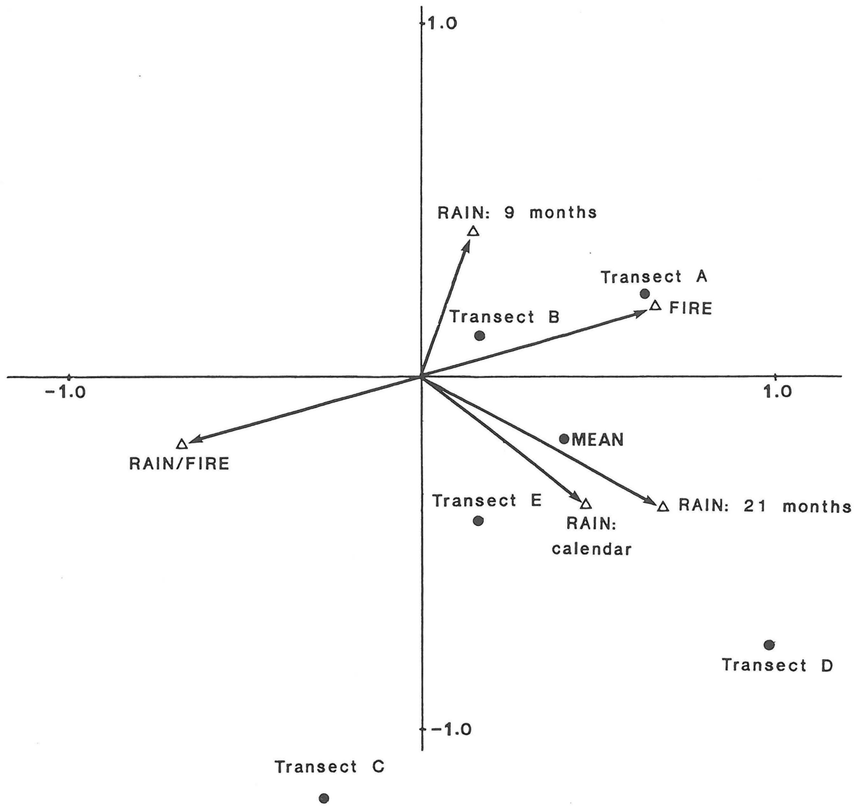

Figure 5 Ordination diagram (transect and environmental coordinates for a *t*-value biplot), based on Redundancy Analysis (RDA) of the 20 dominant species' mean percentage basal cover for all transects at different sampling dates, with respect to environmental variables rainfall and fire. The transect/environment correlations of the first two axes are 0.995 and 0.977, respectively. (Eigenvalues of the first and second axes are 0.793 and 0.126, respectively; scaling = 2.)

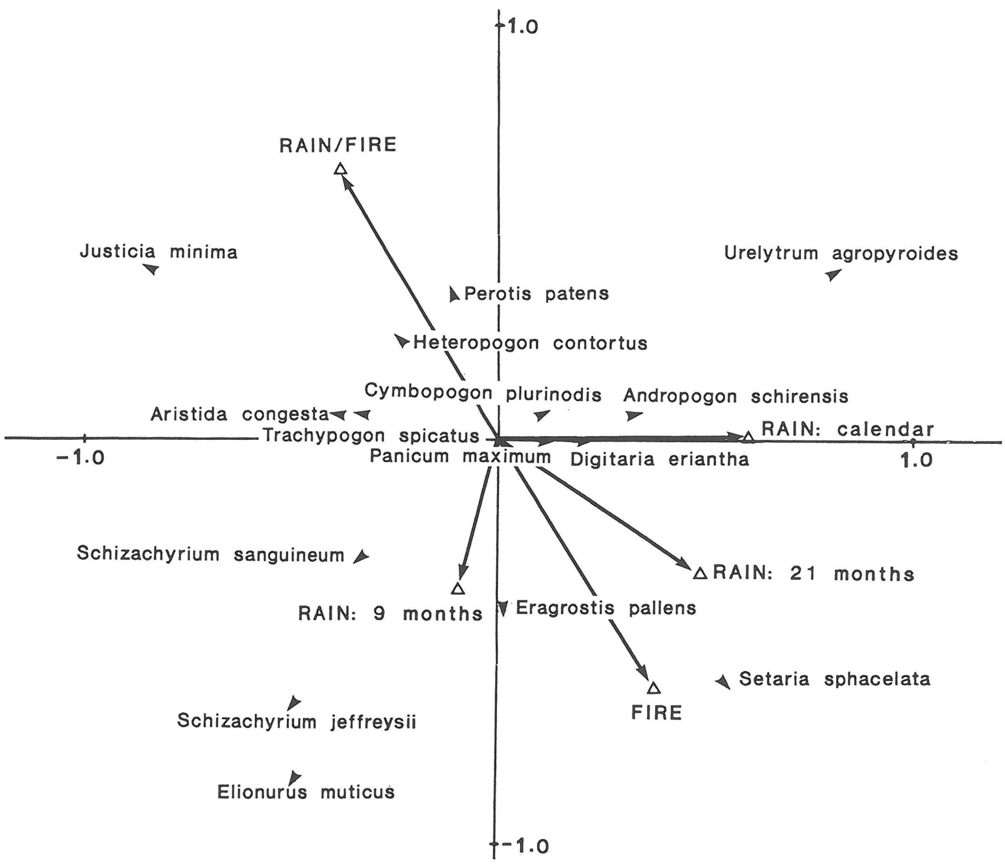

Figure 6 Ordination diagram (transect and environmental coordinates for a *t*-value biplot), based on Redundancy Analysis (RDA) of each transect's total percentage basal cover at different sampling dates, with respect to environmental variables rainfall and fire. The transect/environment correlations of the first two axes are 0.998 and 0.891, respectively. (Eigenvalues of the first and second axes are 0.483 and 0.293, respectively; scaling = 2.)

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