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Species associations in a grassland on a heavy cracking clay soil in north-west Queensland: their structure, soil associations and effects of flooding

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Abstract

Four plant associations were separated on the basis of relative abundance of species in an ungrazed area of open grassland on a heavy cracking clay soil in north-west Queensland. They were correlated with soil pH, exchangeable potassium, available phosphorus, moisture content and particle size. Two associations were characterized by Iseilema *spp.,* Astrebla *spp. and* Cyperus *spp. and two by* Eulalia fulva *and* Dichanthium fecundum.

Flooding caused a significant decline in the relative abundance of all major perennial grasses except Eulalia fulva, *an increase in* Cyperus *spp., a reduction in legumes, establishment of previously unrecorded forbs, and a reduction in the basal cover of all associations. Heavy grazing by cattle prior to flooding increased the proporton of particular forbs, almost eliminated* Astrebla squarrosa *and resulted in a basal cover of 1.8% compared with 4.4% in an adjacent exclosure.*

Introduction

In Australia there are extensive areas of cracking, heavy clay soils (vertisols) in a dry tropical environment and these are parallelled only in the Sudan and India (Dudal 1965). In north-west Queensland alone there are over 100 000 km^2 of cracking clay soils (Perry *et al.* 1964) supporting native pastures which are of prime importance to the cattle and sheep grazing industries. Little is known about the structure or composition of these grasslands, or their response to environmental stresses such as flooding.

This quantitative floristic study was carried out on the flat plains of the southern Gulf of Carpentaria region in the *Eulalia fulva–Dichanthium fecundum* grassland of the Balbirini land system (Perry *et al.* 1964). Here, cracking clay soils typically support sub-humid, tropical tallgrass grazing lands (Moore 1970), which are widespread throughout northern Australia.

The prime aim was to identify the plant species associations in an ungrazed grassland and investigate their correlation with readily measured soil characters. A site that had received no grazing by domestic stock was chosen because overgrazing leads to changes in botanical composition which are apparent around old watering points. Also, the effects of a flood on species occurrence in both ungrazed areas and a heavily grazed area of the grassland were examined.

Methods

The site

The study site was centred on a bore sunk in 1972 between Brown Creek and the Saxby River on Glenore Station, 90 km south of Normanton. The nearest watering point was over 12 km from the bore and there had been negligible cattle grazing throughout the area prior to establishing this watering facility.

A general description of the land system has been given by Perry *et al.* (1964) and Bishop (1973). The flat to gently sloping plains are typically treeless, except along watercourses, and support a grass dominated vegetation. Common species are *Dichanthium fecundum, D. tenuiculum, Eulalia fulva, Chrysopogon fallax, Aristida latifolia, Astrebla squarrosa, A. elymoides, Sorghum australiense* and *Iseilema* spp. (mainly *I. vaginiflorum*). Soils are of

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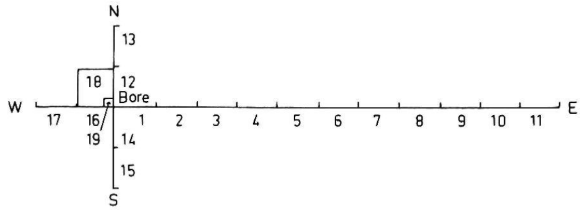

FIG. 1. Location of 500-point segments on the transects (1–17), heavily grazed paddock (18) and exclosure (19).

the Barkly association and are deep grey and brown alkaline cracking clays with no texture contrast, a uniform colour, a self-mulching uneven surface and carbonate and/or sulphate within a depth of 30 cm. Isbell, Webb & Murtha (1968) classified the soils as Ug 5.2 (Northcote 1971) and the chemical and physical properties of a profile in the land system have been reported by Sleeman (1963).

A 0.5 ha exclosure and an 80 ha paddock were erected near the bore to the north-west (Fig. 1). This paddock was grazed heavily in the latter half of the 1973 dry season when cattle were first introduced. The surrounding area was stocked at less than the accepted district rate of a beast to 11 ha. There were no stock in the area between February and July 1974.

Rainfall is strongly summer dominant. At Wondoola Station, 22 km south-west of the sampling area, mean annual rainfall over the last 60 y is 655 mm, with 92% falling between November and March. Rainfall for the 1972–73 wet season was 456 mm. The entire area was flooded to a depth of 1–1.5 m for about 7 days in late January–early February 1974.

Botanical composition

Botanical composition and basal cover of the ungrazed grassland were recorded in June 1973, using a wheel point apparatus (Tidmarsh & Havenga 1955) with two points per 3 m revolution. Recordings were along four transects radiating from the bore at directions of the cardinal compass points. There were 1000 points recorded along the north, south and west transects (1500 m long) and 5500 points along the east transect (8250 m long; Fig. 1). A compass was used to maintain direction.

Basal cover was determined from the number of strikes on living plant material at soil level and botanical composition was determined by the method used by Roberts (1972). Because the number of strikes on plants was low (less than 7%), there is a relatively small amount of species data recorded for basal cover. The species recorded are predominantly perennial tussock grasses and not the small forbs which are mainly annual inter-tussock species. Consequently, the plant nearest to the point was recorded when a strike did not occur. This method gives a measure of the relative number of plants of each species in the grassland. It is relative because the method is plotless and does not describe numbers per unit area. This measure is called relative abundance by Orr (1981). The measure does not take into account foliage cover or biomass. In this community where there are species with both a small and large basal cover, the method can give higher values for the small inter-tussock species. The distance from the point to the nearest plant in this study rarely exceeded 20 cm and was mostly less than 10 cm. One operator made all recordings to maintain a consistent definition of a basal strike. All species present along the transects including those that were never nearest the recording point were identified in 1973.

The transects were recorded again in July 1974, after the flood, using the same procedure. In addition, 500 points were recorded with the wheel point in both the exclosure and the fenced paddock.

Data analysis and preliminary examination

Data were recorded from a total of 18 000 points and there were 34 species present in 1973 and 45 species in 1974. For computation of basal cover and relative abundance the transects were divided into 17 segments, each consisting of 500 points. The exclosure and paddock were also included in the analyses in 1974, making a total of 19 segments of 500 points.

Pattern revealing programs were used to elucidate the structure of the plant 'associations'. These were drawn from the TAXON package (Dale *et al.* 1981) and were: agglomerative polythetic programs CENPERC (using an information statistic) and MULCLAS (using both Euclidean and Bray & Curtis (1957) distances); principal coordinate analysis program GOWER; and the data display program MIN-

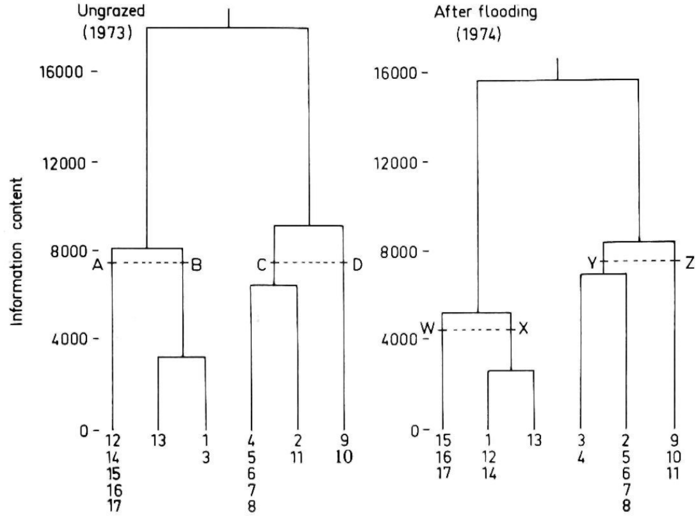

Fig. 2. Hierarchical classification (CENPERC) of species relative abundance (%) in 500-point segments (1–17) in 1973 and 1974: Letters A, B, C, D and W, X, Y, Z indicate segment grouping used to derive species 'associations'

SPAN. All analyses produced similar results. 'Associations' delimited by the ordination, for instance, were similar to those designated by the classifications discussed later (Figs. 2 and 3). Results from the CENPERC classification are discussed. In addition, analyses of variance were used to compare edaphic differences between some of the 'associations' identified.

Soil sampling

Surface soil samples (0–4 cm) were collected for pH analysis every 100 m along the transects, and bulked 0–10 cm samples were collected in the centre of each 500-point segment for detailed chemical and physical analyses. Available phosphorus was determined by both sulphuric acid extraction (Kerr & von Stieg-

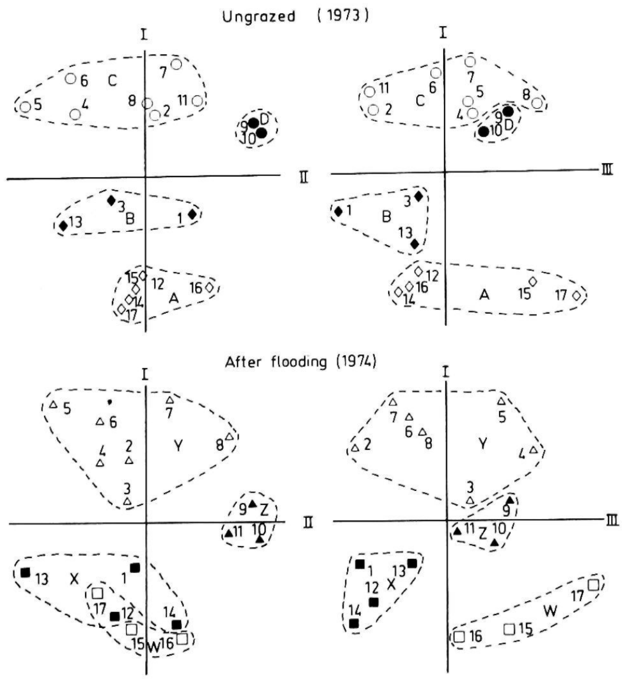

Fig. 3. Projections of four main 'associations' in 1973 and 1974 from classification analysis (CENPERC) of 500-point segments onto the plane of vectors I and II, and vectors I and III from principal co-ordinate analyses (GOWER).

litz 1938) and bicarbonate extraction (Colwell 1963) methods.

Topography

Topographic levels were measured along the north, south and west transects and along a straight road starting 800 m south of the bore and converging with the extremity of the east transect. There were variations up to 17 cm in relief within a 50 cm radius of some grass tussocks. This prevented free vehicle movement along most of the east transect. A linear function of topographic levels across each 500-point segment was calculated to give a measure of the overall slope across the segment.

Results

Species

Fifty-two species comprising 18 grasses, 7 legumes and 27 other forbs, were recorded as nearest the point along the transects in the two years. The species along the transect that were never nearest the recording point in 1973 are listed separately (Table 1). The area is richer in legumes, with ten genera present, than suggested by Perry *et al.* (1964); this may reflect a relatively short sampling period in the initial survey work, or a richer flora in this ungrazed area.

Botanical composition

The results of the CENPERC analysis of species relative abundance in both 1973 and 1974 (Fig. 2) show two distinct segment groups each with two sub-groups (labelled A, B, C, D and W, X, Y, Z respectively). Further subdivision was not ecologically meaningful. This arrangement of segments is supported by the ordination where the same four groupings are identified (Fig. 3). The most highly correlated species with the first three vectors from this analysis are shown in Table 2. These vectors combined account for 73.1% and 79.2% of the variance in 1973 and 1974 respectively.

TABLE 1. Species present in ungrazed 'associations' (1973) and after flooding (1974)

Common species 1973–1974	Species present only in 1973	Species present only in 1974	Species present 1973 but never nearest the recording point
Grasses	Grasses	Grasses	Grasses
Aristida latifolia	*Brachyachne convergens*	*Elytrophorous spicatus*	*Chloris pumilio*
Astrebla elymoides	*Chionachne hubbardiana*	grass (not ident. No.653)	*Echinochloa turnerana*
Astrebla squarrosa	*Schizachyrium fragile*		*Eragrostis tenellula*
Chrysopogon fallax		Legumes	*Leptochloa neesii*
Dichanthium fecundum	Legumes	*Aeschynomene indica*	*Ophiuros megaphyllus*
Dichanthium tenuiculum	*Galactia muelleri*	*Crotalaria* sp. (No.646)	
Eriochloa crebra	*Rhynchosia minima*		Legumes
Eulalia fulva	*Uraria lagopodioides*	Other Forbs	*Alysicarpus rugosus*
Iseilema spp.		*Alternanthera nodiflora*	*Flemingia pauciflora*
Panicum effusum	Other Forbs	*Ammannia multiflora*	*Indigofera trita*
Pennisetum basedowii	*Abelmoschus ficulneus*	*Bacopa floribunda*	*Sesbania brachycarpa*
Sorghum australiense	Euphorbia mitchelliana	*Bergia pedicellaris*	*Uraria picta*
Sporobolus australasicus	Gomphrena canescens	*Blumea* sp. (No.651)	
	Spermacoce sp. (No. 10)	*Euphorbia drummondii*	Other Forbs
Legumes	forb (not ident. No.51)	*Goodenia glauca*	*Abutilon oxycarpum*
Crotalaria dissitiflora		*Ipomoea aquatica*	*Bergia ammanioides*
Neptunia monosperma		*Ludwigia perennis*	*Hibiscus trionum*
		Marsilea hirsuta	*Ipomoea lonchophylla*
Other Forbs		*Phyllanthus maderaspatensis*	*Phyllanthus virgatus*
Corchorus olitorius		*Phyllanthus rhytidospermus*	*Spermacoce brachystema*
Cyperus spp.		*Polymeria marginata*	
Justicia procumbens		*Sphaeranthus indicus*	
Marsilea sp. (No. 8)			
Morgania glabra			
Operculina turpethum			
Sida spinosa			

The arrangement of segment groups in 1973 is shown by the minimum spanning tree (Fig. 4) where most of the variation is taken out in the major axis. The larger inter-element distances, which might be regarded as discontinuities, have been marked with dotted arrows. The segment groups (A, B, C and D) correspond to those derived by the CENPERC analysis. The species 'associations' present in these four zones are shown in Table 3.

Starting at the left of the minimum spanning tree there is an area containing 25 species, 'association' A, which is dominated by *Iseilema* spp. (28%), *Cyperus* spp. (predominantly *Cyperus bifax*) (26%) and *Astrebla* spp. (19%) (*A. squarrosa* 11% and *A. elymoides* 8%). *Neptunia monosperma* (5%) is the most frequent legume. 'Association' B differs primarily in degree; the same species are dominant but to a lesser extent. Other species including *D. fecundum, Galactia meulleri* and *Rhynchosia minima* are present, and some species very rare in 'association' A (e.g. *Crotalaria dissitiflora)* are better represented. 'Association' C has *E. fulva* (19%) and *D. fecundum* (16%) co-dominant and *Astrebla* spp. and *Cyperus* spp. assuming lesser significance. Legumes also are less important; *N. monosperma* is prominent (4%), but *G. muelleri* and *R. minima* are absent. Finally, there is the relatively species-poor 'association' D, dominated by *Cyperus* spp., *D. fecundum* and *E. fulva*. Only in this 'association' is *A. elymoides* more frequent than *A. squarrosa*. *Neptunia monosperma* is the only legume present in this perennial grass dominated 'association'.

The botanical composition changed markedly after flooding (Table 3) and the main axis of the minimum spanning tree accounts for virtually all of the variation (Fig. 4). *Cyperus* spp. increased greatly, several new species appeared (e.g. *Ludwigia perennis, Ammannia multiflora, Elytrophorus spicatus*), and most grass species declined significantly in relative abundance, although *E. fulva* was not affected (Table 4). Composition of the legume flora also changed markedly; *C. dissitiflora* and *N. monosperma* persisted, but at a reduced relative abundance, *G. muelleri, R. minima* and *Uraria lagopodioides* disappeared and *Aeschynomene indica* and a *Crotalaria* species appeared.

TABLE 2. Most highly correlated species (correlation coefficient >0.5) with the first three vectors from the principal co-ordinate analysis (GOWER) of 500-point segments in 1973 and 1974

Ungrazed (1973)				After flooding (1974)			
Vector	Variance explained (%)	Species	Correlation coefficient	Vector	Variance explained (%)	Species	Correlation coefficient
I	53.4	*Dichanthium fecundum*	0.94	I	52.8	*Eulalia fulva*	0.91
		Eulalia fulva	0.92			*Dichanthium fecundum*	0.78
		Brachachne convergens	0.66			*Marsilea hirsuta*	0.74
		Marsilea sp. (No.8)	0.58			*Elytrophorus spicatus*	0.60
		Polymeria longifolia	0.56			*Blumea* sp. (No.651)	0.53
		Pennisetum basedowii	−0.52			*Chrysopogon fallax*	0.53
		Corchorus olitorius	−0.53			*Eriochloa crebra*	−0.51
		Euphorbia mitchelliana	−0.57			*Justicia procumbens*	−0.53
		Sida spinosa	−0.60			*Astrebla elymoides*	−0.59
		Justicia procumbens	−0.71			*Cyperus* spp.	−0.95
		Abelmoschus ficulneus	−0.72				
		Cyperus spp.	−0.73	II	16.3	*Phyllanthus maderaspatensis*	0.70
		Iseilema spp.	−0.83			*Sida spinosa*	0.63
						Marsilea hirsuta	0.58
II	11.3	*Morgania glabra*	0.67			*Corchorus olitorius*	0.52
		Astrebla elymoides	0.59			*Neptunia monosperma*	−0.54
		Polymeria longifolia	−0.50			*Sporobolus australasicus*	−0.56
		Neptunia monosperma	−0.54			*Aristida latifolia*	−0.59
		Sorghum australiense	−0.62			*Ludwigia perennis*	−0.90
III	8.4	*Astrebla squarrosa*	−0.86	III	10.1	*Bergia pedicellaris*	0.71
		forb (not ident. No.51)	−0.50			*Panicum effusum*	0.53
						Crotalaria dissitiflora	0.52
						Astrebla elymoides	0.51
						Astrebla squarrosa	−0.72

TABLE 3. Botanical composition (relative abundance %) of the four main 'associations' in the ungrazed grassland (A, B, C, D) and after flooding (W, X, Y, Z) derived from classification* (CENPERC) of 500-point segments

	Ungrazed				After flooding			
Species	A	B	C	D	W	X	Y	Z
Abelmoschus ficulneus	0.56	0.47						
Aeschynomene indica								0.07
Alternanthera nodiflora						0.05		
Ammannia multiflora					7.00	5.40	4.77	3.87
Aristida latifolia	5.80	6.60	5.31	6.30		0.70	0.37	
Astrebla elymoides	8.28	6.40	2.91	11.60	6.53	2.75	2.09	3.33
Astrebla squarrosa	10.64	12.80	9.88	7.60	0.60	5.15	3.71	0.40
Bacopa floribunda					2.53	2.25	3.54	1.33
Bergia pedicellaris					7.47	1.50	2.80	1.00
Blumea sp. (No.651)					0.07	0.30	0.57	0.27
Brachyachne convergens	2.76	5.27	9.23	5.10				
Chionachne hubbardiana	0.64	0.73	0.34	0.20				
Chrysopogon fallax			0.02				0.60	
Corchorus olitorius	0.52	0.40	0.05			0.10		0.20
Crotalaria sp. (No.646)					2.93	1.75	1.43	4.53
Crotalaria dissitiflora	0.44	2.47	0.34				0.03	
Cyperus spp.	25.52	19.33	10.89	17.90	58.07	59.60	21.94	48.80
Dichanthium fecundum		5.87	16.02	14.80		1.50	8.57	3.73
Dichanthium tenuiculum	0.88	1.13	1.57	0.10		0.35	0.17	
Elytrophorus spicatus					0.93	2.85	6.77	3.73
Eriochloa crebra	0.04				0.13			
Eulalia fulva		2.80	18.69	14.30	0.07	0.70	18.57	11.07
Euphorbia drummondii					0.07			
Euphorbia mitchelliana	2.40	0.13						
Galactia muelleri		0.40						
Gomphrena canescens	0.04	0.27						
Goodenia glauca						0.05	0.23	0.07
Ipomoea aquatica					2.40		0.03	0.73
Iseilema spp.	27.60	15.67	9.03	6.80	0.13			0.07
Justicia procumbens	3.28	3.07	0.80	1.50	1.67	0.45	0.23	1.20
Ludwigia perennis					5.87	11.95	10.80	1.00
Marsilea sp. (No.8)			0.71	1.80				
Marsilea hirsuta					.47	0.65	9.29	10.27
Morgania glabra			0.26	4.70	.40	0.55	1.29	2.60
Neptunia monosperma	4.52	4.87	3.80	2.00	1.60	0.70	1.57	0.33
Operculina turpethum	0.04	0.13	0.11					0.07
Panicum effusum	0.20	0.13	0.29	0.40	0.40	0.15	0.14	0.27
Pennisetum basedowii	0.12	0.07			0.27		0.03	
Phyllanthus maderaspatensis					0.07			0.33
Phyllanthus rhytidospermus					0.13			0.07
Polymeria longifolia	0.20		2.57					
Polymeria marginata							.03	
Rhynchosia minima		0.07						
Schizachyrium fragile		0.33						
Sida spinosa	0.72	0.07	0.09		0.07			0.40
Sorghum australiense	2.96	4.07	3.31	3.50		0.15	0.09	
Spermacoce sp. (No. 10)	0.76	0.67	0.85	1.30				
Sphaeranthus indicus								0.07
Sporobolus australasicus	1.04	4.87	2.86		0.13	0.40	0.23	0.20
Uraria lagopodioides	0.04							
Unidentified (Forb No.51)		0.03	0.03	0.10				
Unidentified (Grass No.653)							0.11	

*'Associations' correspond to hierarchical classification Fig. 2.

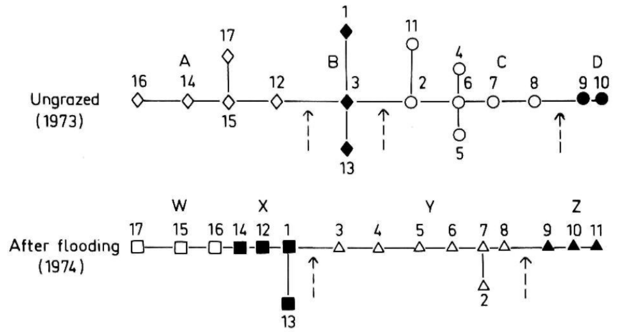

FIG. 4. Segment arrangement produced by the MINSPAN program in 1973 and 1974. Main discontinuities are shown by arrows and letters correspond to groups identified by classification (CENPERC) analysis.

The relative abundance of *A. squarrosa* was 0.6% in the heavily grazed paddock and 7.0% in the adjacent exclosure after flooding. The composition of these two areas is shown in Table 5.

Basal cover

The basal cover between the four ungrazed 'associations' ranged from 4.4% to 6.4% in 1973. The combined *Eulalia* and *Dichanthium*-dominated 'associations' (C plus D) had a significantly higher ($P<0.05$) basal cover (6.3%) than the combined *Iseilema, Astrebla* and *Cyperus* 'associations' (A + B) (5.0%). Basal cover in all segments was reduced by flooding and this depression was particularly severe (> 50%) in 'associations' A and D. The *Eulalia-Dichanthium* 'associations' (4.2%) still had a significantly higher ($P<0.01$) basal cover than combined *Iseilema-Astrebla-Cyperus* 'associations' (2.9%). Perennial grasses were the major component of basal cover in both years.

Grazing

Following heavy grazing and flooding, the basal cover of the paddock was 1.8% compared with 4.4% in the exclosure. When the relative abundance of these areas was included in the CENPERC classification, both were placed with adjacent segments dominated by *Cyperus* spp. and *L. perennis* ('association' B) which are all close to the bore.

Soil properties, topography and plant associations

The land surface sloped gradually from south to north (90 cm fall in 3000 m) and from the bore to the east (net fall of 44 cm in 8250 m). There was a 17 cm depression across the length of the transect to the west of the bore. It is not surprising that no clear correlations were found between plant associations and slope.

There were, however, significant differences in soil chemical and physical properties along the transects based on both the 1973 (Table 6) and 1974 segment groupings derived by classificiation analysis. Exchangeable potassium and available phosphorus, which are both known to affect grass/legume combinations (Hall 1978) varied between 'associations' as did the surface (0–4 cm) pH, moisture content at a water potential of −1500 kPa and soil particle size. The *Iseilema-Astrebla* 'associations' had 57% clay compared to 47% clay in the *Eulalia-Dichanthium* 'associations'. Unfortunately, little or nothing is known of the effect of the soil properties on the growth or persistence of the species involved.

After flooding, the two *Cyperus-Astrebla* 'associations' had significantly higher exchangeable potassium, available phosphorus, moisture content at a water potential of −1500 kPa, clay and silt contents and a significantly lower surface (0–4 cm) pH than the *Eulalia-Dichanthium* associations.

Discussion

Ungrazed 'associations' based on *Eulalia-Dichanthium* and *Iseilema-Astrebla-Cyperus* were identified from the 500-point segment analyses. Most of the more abundant species were not exclusive to any one segment group, which indicates a merging of the 'associations'. Some species (e.g. *A. latifolia* and *N. monosperma*) occurred in all associations at a similar relative abundance, while

TABLE 4. Mean relative abundance (%) of all species (combined 'associations') before and after flooding and significant changes in the more abundant species

Species	Flooding Before	Flooding After	Flooding effect*
Abelmoschus ficulneus	0.25		
Aeschynomene indica		0.01	
Alternanthera nodiflora		0.01	
Ammannia multiflora		5.15	+
Aristida latifolia	5.80	0.32	−
Astrebla elymoides	6.12	3.25	−
Astrebla squarrosa	10.35	2.92	−
Bacopa floribunda		2.67	+
Bergia pedicellaris		3.00	+
Blumea sp. (No.651)		0.36	
Brachyachne convergens	6.14		−
Chionachne hubbardiana	0.48		
Corchorus olitorius	0.25	0.05	
Chrysopogon Fallax	0.01	0.25	
Crotalaria sp. (No. 646)		2.32	+
Crotalaria dissitiflora	0.71	0.01	
Cyperus spp.	17.51	41.92	+
Dichanthium fecundum	9.38	4.54	−
Dichanthium tenuiculum	1.12	0.15	−
Elytrophorus spicatus		4.28	+
Eriochloa crebra	0.01	0.02	
Eulalia fulva	9.87	9.78	0
Euphorbia drummondii		0.01	
Euphorbia mitchelliana	0.73		
Galactia muelleri	0.07		
Gomphrena canescens	0.05		
Goodenia glauca		0.12	
Ipomoea aquatica		0.56	
Iseilema spp.	15.40	0.04	−
Justicia procumbens	2.01	0.71	−
Ludwigia perennis		8.47	+
Marsilea sp. (No. 8)	0.51		
Marsilea hirsuta		5.87	+
Morgania glabra	0.66	1.19	
Neptunia monosperma	3.99	1.15	−
Operculina turpethum	0.08	0.01	
Panicum effusum	0.25	0.21	
Pennisetum basedowii	0.05	0.06	
Phyllanthus maderaspatensis		0.07	
Phyllanthus rhytidospermus		0.04	
Polymeria longifolia	1.12		
Polymeria marginata		0.01	
Rhynchosia minima	0.01		
Schizachyrium fragile	0.06		
Sida spinosa	0.26	0.08	
Sorghum australiense	3.36	0.07	−
Spermacoce sp. (No. 10)	0.85		
Sphaeranthus indicus		0.01	
Sporobolus australasicus	2.34	0.25	−
Uraria lagopodioides	0.01		
Unidentified (Forb No. 51)	0.19		
Unidentified (Grass No. 653)		0.05	

*Significant flooding effect ($P<0.01$): − reduced, + increased, 0 no change.

others were associated with either the *Eulalia-Dichanthium* associations (e.g. *Brachyachne convergens*) or the *Iseilema-Astrebla* 'associations' (e.g. *Justicia procumbens*).

Cyperus spp. are characteristic of wet areas and were increased in relative abundance by flooding. *Eulalia fulva* is also characteristic of relatively wet sites, such as river banks and flood plains (Lazarides 1970) or gilgai depressions (Everist 1935) and is associated with *A. squarrosa* on low lying country in southern inland Queensland (Francis 1935). It was the most flood tolerant perennial grass, maintaining its relative abundance, while that of *A. squarrosa* declined. Differences in the flood tolerance of grasses and legumes have been reported from other areas (Rhodes 1964; Anderson 1973; Cameron 1973). McManmon & Crawford (1971) suggest tolerance is related to certain areas of plant metabolism and to specific enzyme systems. The root

TABLE 5. Botanical composition (relative abundance %) of the exclosure and heavily grazed paddock following flooding (1974)

Species	Relative abundance (%) Exclosure	Holding paddock
Grasses		
Astrebla elymoides	4.6	4.4
Astrebla squarrosa	7.0	0.6
Elytrophorus spicatus	2.0	3.8
Panicum effusum	0.2	0.2
Sporobolus australasicus	0.2	0.4
Aristida latifolia	0.4	0
Dichanthium tenuiculum	1.0	0
Eriochloa crebra	0.2	0
Iseilema spp.	1.0	0
Sorghum australiense	2.6	0
Forbs		
Ammannia multiflora	2.8	13.6
Crotalaria sp. (No.646)	2.4	3.0
Cyperus spp.	63.2	53.2
Ipomoea aquatica	0.6	0.2
Justicia procumbens	1.8	1.2
Ludwigia perennis	3.2	8.6
Neptunia monosperma	2.4	0.2
Bacopa floribunda	2.2	6.0
Blumea sp. (No.651)	0.2	0
Marsilea hirsuta	0.6	0
Sida spinosa	1.0	0
Bergia pedicellaris	0.4	3.0
Goodenia glauca	0	0.2
Morgania glabra	0	1.4

TABLE 6. Surface soil (0–10 cm) chemical and physical properties and pH of 0–4 cm samples in the four main 'associations' (CENPERC) in the ungrazed grassland (1973)

Seg-ment group	pH 0–10 (cm)	pH 0–4	Available P Acid (ppm)	Bicarb. (ppm)	Exchange K (m.equi. %)	Total N (%)	Elect. con-duct. (mScm−1)	Cl⁻ (ppm)	Moisture content at 1500 kPa air dry (g/g %)		Dispersion ratio R1	Dispersion ratio R2	Clay (%)	Silt (%)	Sand (%)	Organic C (%)
A	7.3	6.6^{c}	6.4	4.0	0.41^{a}	0.03	0.03	19	14.4^{a}	3.9	0.4	0.3	57^{a}	15^{a}	28^{b}	0.40
B	7.2	6.7^{bc}	5.0	2.3	0.35^{ab}	0.03	0.04	18	14.0^{a}	3.8	0.5	0.4	58^{a}	8^{b}	34^{bc}	0.39
C	7.3	7.1^{b}	4.4	2.7	0.24^{c}	0.03	0.03	16	11.6^{b}	3.0	0.14	0.3	47^{b}	9^{b}	44^{a}	0.44
D	7.4	7.5^{a}	5.0	2.7	0.27^{bc}	0.04	0.04	19	13.5^{ab}	3.5	0.3	0.2	48^{b}	9^{b}	44^{a}	0.37
(A+B)	7.25	6.6	5.9	3.5	0.39**	0.03	0.03	19	14.3**	3.9	0.5	0.3	57**	13*	30	0.40
(C+D)	7.31	7.2**	4.6	2.8	0.25	0.03	0.03	16	12.0	3.2	0.4	0.3	47	9	44**	0.42

'a' group means with different superscripts are significantly different ($P<0.05$). Significant difference between means of combined groups (A + B) (C + D): * $P<0.05$ ** $P<0.01$.

physiology of most grasses present at this site has not been reported. Plants were in an active growth phase when flooded and this period is when mortality is most likely from flooding (Williamson & Kriz 1970). In addition, grasses are less tolerant of deep flooding as occurred here, than of shallow flooding for the same duration (Rhodes 1964).

The basal cover in the grazed paddock after flooding was lower than in the adjacent exclosure. Similarly, Anderson (1973) showed that introduced tropical grasses were more intolerant of flooding following recent defoliation.

Soil particle size and fertility influenced species occurrence. The *Iseilema-Astrebla* 'associations' favour areas of relatively higher clay and silt deposition. These soils have significantly higher potassium, lower surface (0–4 cm) pH and slightly higher moisture content at a water potential of −1500 kPa than the soils with a higher sand content supporting the *Eulalia-Dichanthium* 'associations'. Differences in soil nitrogen and phosphorus between the *Iseilema-Astrebla* and *Eulalia-Dichanthium* 'associations' were not significant in 1973. The increase in plant nitrogen content following addition of nitrogen fertilizer is less for *E. fulva* and *D. fecundum* however, than for either *Astrebla* spp. or *Iseilema* spp. (Bishop 1977); this may indicate their better adaptation to lower fertility. *Astrebla* spp. and *Iseilema* spp. are the dominant grasses on the more fertile clay soils of the Mitchell grass downs in the lower rainfall zone south of this land system; and during the dry season, *E. fulva* and *D. fecundum* have lower nitrogen and phosphorus concentrations than the two *Astrebla* species in this grassland (Hall 1981).

The 'associations', particularly along the west-east transects, could be influenced by old infilled channels which have surface soils with a higher clay and silt content. To the south of the sampling area, the Saxby River and Brown Creek-Norman River drainage systems are close together and flow in a northerly direction. In above average floods, these streams could deposit silt in lower areas, such as across the west transect. The streams across this plain are known to carry silt during floods (Simpson & Doutch 1977). They considered the channel system was formed under conditions of greater runoff than exist today, so areas of higher clay and silt deposition would occur throughout the plain.

Forbs that were not present in the ungrazed 'associations' but made a significant contribution after flooding, may have been introduced as seed by flood waters or their seed could remain dormant in the soil until favourable germination conditions occur. These conditions may include a reduction in competition from perennial grasses which occurs if the pasture is overgrazed. *Ludwigia perennis, Ammannia multiflora, Elytrophorus spicatus, Bergia pedicellaris, Bacopa floribunda* and a *Crotalaria* sp. established after flooding and have the short growing cycle and prolific seeding ability characteristic of pioneer species. These plants may become particularly abundant if the grassland is overgrazed. The unpalatable, annual grass *Pennisetum basedowii* is abundant in some wet and heavily grazed areas on these plains.

The basal cover in the *Astrebla* 'associations' in this grassland was higher than the 3.0% reported by Hall & Lee (1980) in a lightly grazed *Astrebla lappacea-A. squarrosa* community in north-west Queensland. Also, it was higher than the mean of 3.7% Roberts, Graham & Orr (1976) found in *A. lappacea* dominant grasslands on clay soils in lower rainfall areas of southwestern Queensland.

A more complete analysis of the effects of grazing and flooding will require data on seasonal and long-term changes in the relative abundance of perennial grasses, annuals and legumes; perennial grasses provide pasture stability and legumes are normally of relative high quality and are often grazed selectively.

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