

Influence of pasture condition on plant selection patterns by cattle: its implications for vegetation change in a monsoon tallgrass rangeland

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Abstract

Diet selection patterns can have a strong influence on botanical composition in grasslands. This study examined responses in plant selectivity of a preferred (*Themeda triandra*) and non-preferred (*Chrysopogon fallax*) perennial grass to a change in pasture condition in a monsoon tallgrass community in northern Australia. Two contrasting pasture condition classes were defined: State I — dominated by palatable tussock perennial grasses; State II — dominated by less palatable tussock perennial grasses, annual grasses and forbs.

Themeda was selected actively by cattle in all seasons, except in the late dry. Pasture condition interacted with season of grazing to alter significantly the selectivity for *Themeda*. In the early and late wet seasons, selection for *Themeda* was significantly greater in State II than in State I. As the proportion of *Themeda* decreases (State I to State II), additional selection pressure is placed on the remaining plants, which is likely to hasten their loss from the system. Increasing the level of utilisation, in an effort to distribute the grazing pressure more evenly, had little effect on reducing the relative preference for *Themeda*. In State I, *Chrysopogon* was relatively avoided in all seasons, especially in the late wet and early dry. However, in State II, *Chrysopogon* was selected actively in all seasons except the late wet.

Grazing management strategies designed to increase the proportion of a palatable species in a pasture must take account of diet selection patterns. Simply reducing stocking rate to a

conservative level may not allow rapid recovery of *Themeda* populations because of continued preference for *Themeda*. Spelling of pasture over the wet season may offer the best means of manipulating pasture composition in monsoon grassland communities.

Introduction

Extensive grazing by cattle is the major land use in the perennial grasslands of tropical Australia. Stocking rates, which were historically low, increased dramatically in the 1960s and 1970s as a result of a collapse in world beef prices, the introduction of tick-resistant and drought-tolerant *Bos indicus* cattle, and increased use of mineral supplementation. High grazing pressure has been sustained through the 1980s and 1990s resulting in a significant loss of desirable perennial grasses over large areas of northern Australia, especially the tropical tallgrass and midgrass communities (Tohill and Gillies 1992). The monsoon tallgrass communities (Mott *et al.* 1985) are generally in better condition. These communities occupy infertile soils and their low productivity and nutritive value, together with limited property infrastructure and development, have resulted in comparatively low stocking rates. However, with increasing numbers of live cattle being shipped from ports adjacent to the monsoon grasslands (Stewart 1996), it is likely these pasture communities will come under increasing pressure.

Loss of perennial grasses in the monsoon grasslands occurs relatively easily as they are not resistant to grazing. Unlike the grasslands of America and Africa, northern Australian grasslands have not evolved under high grazing pressures (Freeland 1990). Consequently, plant morphological responses to grazing, such as prostrate tiller regrowth, are not well developed in many of the perennial grasses making these species susceptible to regrazing and defoliation-induced mortality. Also, some perennial grasses

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are particularly sensitive to defoliation at the onset of the monsoon-like wet season (Mott *et al.* 1992; Ash and McIvor 1998) because considerable plant resources are allocated at this time to a large flush of tillers. In addition to plant response to defoliation, diet selection patterns may exert a strong influence over plant community responses to grazing (Brown and Stuth 1993). A species such as *Themeda triandra*, which is sensitive to defoliation at the start of the wet season, may also be preferred by cattle (Andrew 1986a), placing it at even greater risk of loss due to grazing. Alternatively, species which are sensitive to defoliation and therefore apparently at risk may persist under grazing if they are not selected actively (Brown and Stuth 1993).

Knowledge of species preference and selectivity is central to improving our understanding of vegetation change and in developing management recommendations that maintain desirable perennial grasses in the pasture. This understanding is particularly important in the tropical and monsoon grassland ecosystems because loss of perennial grasses, which are essential for maintaining ecosystem function, can be rapid and irreversible (Mott 1987; Ash *et al.* 1994).

Most experiments dealing with selection patterns and their implications for vegetation change have focused on individual plants or plant communities in a particular state or condition. However, as shifts in botanical composition occur, species selection patterns will alter and this may have important feedback effects on rates of vegetation change and timing of management decisions. This study examined selectivity by cattle for a preferred (*Themeda triandra*) and non-preferred (*Chrysopogon fallax*) perennial grass in 2 pastures that contrasted in pasture condition and botanical composition, and included interactions with rate of stocking and season of grazing, in a monsoon tallgrass community in northern Australia.

Materials and methods

Vegetation, soils and climate

The experiment was conducted on Scott Creek Station (14.8°S, 131.8°E), approximately 80km south-west of Katherine in the Northern Territory, Australia. This area is representative of the monsoon tallgrass savanna; the tree layer is an open eucalypt woodland dominated by *Euca-*

lyptus tectifera and *Corymbia foelscheana* with an herbaceous layer dominated by the perennial, tussock grasses *Themeda triandra*, *Chrysopogon fallax*, *Sorghum plumosum* and *Sehima nervosum* (Mott *et al.* 1985). *Themeda* and *Chrysopogon* often comprise more than 50% of the herbaceous standing biomass. They have contrasting acceptability to cattle; *Themeda* is a highly preferred species, whereas *Chrysopogon* is a non-preferred species, which is generally avoided. The soil is an infertile loamy red earth (mesotrophic red kandosol, Isbell 1993) deficient in most nutrients. Rainfall in the region is distinctly seasonal with about 85% of the rain falling in the monsoon season between December and March. Average annual rainfall is 850mm.

Treatments

This study was part of a more extensive experiment examining the influence of land condition on pasture and animal production, described more fully by Ash *et al.* (1995). Briefly, areas of land on opposite sides of a paddock boundary were selected on the basis of differences in pasture standing biomass and botanical composition, which developed as a result of different grazing pressures (conservative *vs* moderate-heavy) in the previous decade. It was assumed that these differences in pasture condition across the fence-line were due to previous grazing management and not to inherent edaphic or vegetation differences. This assumption appeared valid on the basis of soil surveys and historical aerial photographs. The species and densities of shrubs and trees were similar on both sides of the fence-line.

The contrasting pasture condition classes were defined using a state-and-transition model (Westoby *et al.* 1989; Ash *et al.* 1994) as:

State I — dominated by palatable decreaser perennial tussock grasses (*Themeda triandra*, *Chrysopogon fallax*, *Sehima nervosum*, *Sorghum plumosum*);

State II — dominated by less palatable increaser perennial tussock grasses and annual grasses (*Chrysopogon fallax*, *Eriachne obtusa*, *Aristida browniana*, *Brachyachne convergens*).

About 500 ha of land were fenced for the experiment (200 ha State I, 300 ha State II). The State I and State II areas were subdivided into 2 large paddocks; 1 paddock was used in Year 1 and the other in Year 2. Each of the “year” paddocks was further subdivided into 2 replicate

blocks. These replicate blocks were divided into 4 separate areas to be grazed for discrete 8-week periods during the early wet, late wet, early dry and late dry seasons. Electric fencing was used to set up seasonal grazing areas just prior to use. Within each of these seasonal grazing areas, 3 stocking rates (low, medium and high) were imposed, using further subdivision with electric fencing, to achieve the desired level of utilisation (% of available herbage consumed). Stocking rates were set to achieve nominal utilisation rates of 15, 30 and 45% over the 8-week grazing period. Paddock sizes required to achieve these utilisation levels were calculated at the start of each grazing period on the basis of standing biomass, or expected standing biomass in the case of the early wet season when pastures were growing actively. Paddocks were grazed only for their

designated 8 weeks. A schematic representation of the paddock layout is shown in Figure 1.

Weaner Brahman or Brahman-Shorthorn steers (mean initial weights of 135 kg) were used to graze the treatment paddocks. Three animals per paddock were used for each of the grazing periods. At the end of each grazing period, cattle were allowed to graze in a "common" non-experimental paddock until the next grazing period, at which time they were assigned at random to new paddocks. The experiment commenced in December 1990 with the onset of the 1990–91 wet season and ended in November 1992.

Measurements

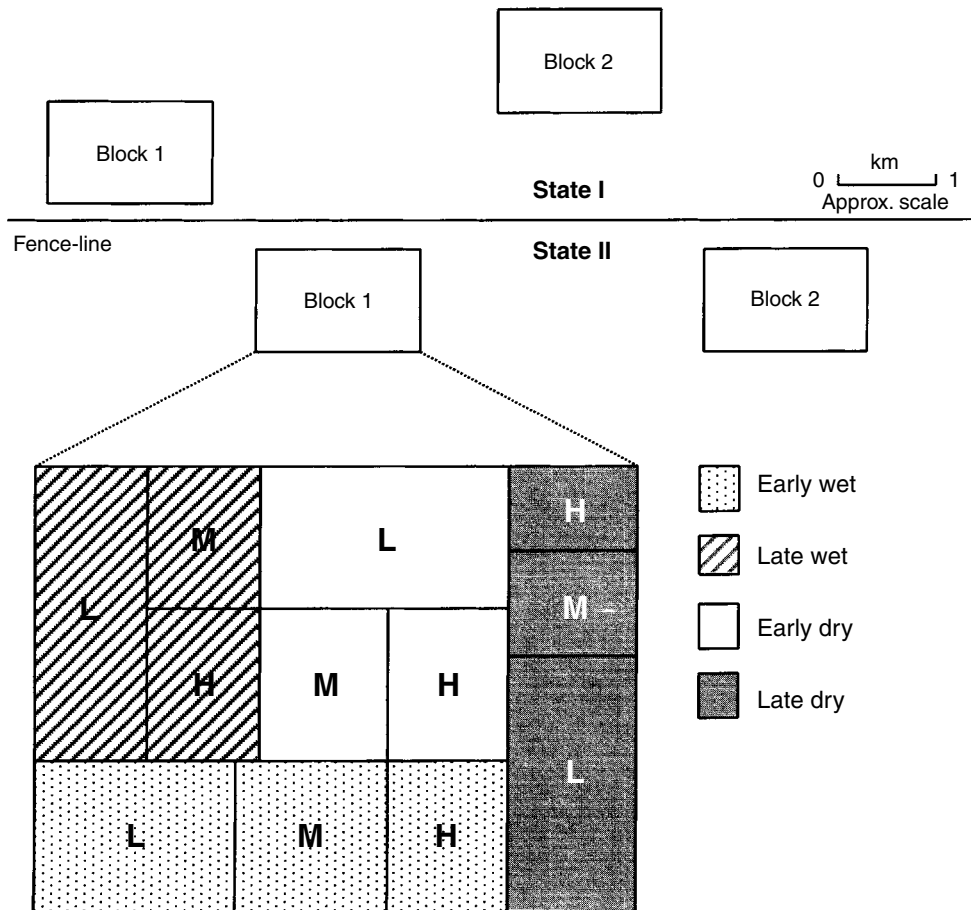


Figure 1. Schematic representation of experimental layout and example allocation of season and stocking rate grazing treatments within a block (L = low; M = medium; H = high stocking rate treatments).

Pasture standing biomass (kg/ha DM) and botanical composition were determined at the start and end of each grazing period in each paddock. Botanical composition and yield were estimated in 50, 60 and eighty 1 m² quadrats in the high, medium and low utilisation paddocks, respectively. The BOTANAL technique (Tothill *et al.* 1992) was used for estimating standing crop (double sampling technique) and composition (dry weight rank method). Forbs and native legume species were grouped. At the end of each grazing period, utilisation of individual species within quadrats was estimated using a 0–5 scale of utilisation where: 0 = no utilisation, 1 = trace utilisation (<5%), 2 = slightly utilised (5–25%), 3 = moderately utilised (26–50%), 4 = heavily utilised (51–75%) and 5 = extreme utilisation (76–100%). From these utilisation categories and frequency percentage of plants available in each paddock, a species selectivity index, based on the selectivity index of Ivlev (Ivlev 1961), was constructed using the procedures of Andrew (1986a). Only perennial grasses were included in the index because of the often low frequency of annual grasses and forbs in State I pasture and because defoliation is often difficult to recognise in these

more ephemeral plants. Thus, the selection index in this study represents relative preference for perennial grasses. Selection indices using Ivlev's procedure have the desirable feature that they are bound between –1 and +1 (Loehle and Rittenhouse 1982). A positive index represents relative preference for a species, whereas a negative index indicates relative avoidance (an index of –1 reflects complete avoidance).

Statistical analyses

The experiment was analysed as a split-split plot design (Steel and Torrie 1980) with pasture condition and year as main plots, seasonal grazing areas as sub-plots and stocking rates as sub-sub-plots.

Results and discussion

Themeda triandra comprised about 50% of the standing crop dry matter in State I but made up less than 10% of the standing crop in State II (Table 1). *Chrysopogon fallax* was the dominant grass in State II, but its standing crop biomass

Table 1. Effect of pasture condition, season of grazing and stocking rate on botanical composition and standing crop at the end of the 8-week grazing periods.

		Botanical composition (% of standing crop dry matter)					Standing crop (kg/ha DM)
		<i>Themeda triandra</i>	<i>Chrysop. fallax</i>	Other perennial grasses	Annual grasses	Forbs and native legumes	
State I							
Season	Early wet	41	37	9	1	12	620
	Late wet	44	41	11	1	3	1240
	Early dry	60	30	9	0	1	1250
	Late dry	63	30	7	0	0	1106
	SEM ¹	5.2* ²	4.8	0.8	0.4	1.8**	36**
Stocking rate	Low	54	33	9	0	4	1370
	Medium	53	36	8	0	3	1040
	High	49	34	9	1	7	760
	SEM	1.2*	1.9	1.9	0.4	1.8	31**
State II							
Season	Early wet	8	49	16	19	8	760
	Late wet	5	38	20	32	5	1150
	Early dry	7	44	20	27	2	1000
	Late dry	8	64	8	13	7	520
	SEM	2.3	5.7	2.8	5.5	2.9	83**
Stocking rate	Low	9	46	18	19	8	1060
	Medium	5	50	15	25	5	810
	High	7	50	15	24	4	700
	SEM	1.3	3.0	2.7	2.3	2.6	55**

¹SEM = Standard error of the mean.

²* = significant at P<0.05; ** = significant at P<0.01.

was no greater than in State I. Annual grasses made up more than 20% of the pasture in State II but contributed less than 1% to standing crop in State I. This pattern of botanical composition is consistent with the definition of vegetation states (pasture condition classes) used by Ash *et al.* (1994) in describing a generalised state-and-transition model for perennial grasslands in the tropics.

Themeda in State I was the only species significantly affected by the stocking treatments (Table 1). Within State I paddocks, the percentage composition of *Themeda* was significantly lower ($P < 0.05$) in the early and late wet season grazing treatments and this effect was greatest at the highest stocking rate, *i.e.* there was a significant stocking rate \times season interaction (interaction not shown). Forbs and native legumes increased as *Themeda* declined, probably in response to available space, nutrients and moisture. This was most apparent at the highest stocking rate in the early wet season where the amount of *Themeda* was lowest; forbs and native legumes made up 25% of the standing biomass in this treatment.

There was no measurable effect of any treatment on botanical composition in State II. *Themeda* was a relatively minor component, making the impact of season of grazing or

stocking rate on this species, difficult to detect. As expected, standing crop was reduced significantly ($P < 0.01$) with increasing stocking rate (Table 1).

While treatment differences in botanical composition at the end of the grazing periods did not reflect selection patterns for different species in State II, selection indices clearly demonstrated large differences in selectivity between *Themeda* and *Chrysopogon* and these differences were modified by pasture condition, year, season of grazing and stocking rate. Cattle actively selected *Themeda* in all seasons except the late dry (Figure 2). This general preference for *Themeda* is consistent with that observed for similar grasslands in northern Australia (Andrew 1986a) and in studies in southern Africa (Danckwerts *et al.* 1983; O'Connor 1992). The apparent decline in preference for *Themeda* during the late dry period was associated with changes in relative palatability of species as the pasture "hayed off" and/or a general change in foraging behaviour. As the dry season advanced, the cattle tended to shift their focus from selectively grazing species at the bottom of the sward to grazing the tops of plants without apparently paying much attention to the species being grazed. Selection for *Themeda* over *Chrysopogon* was much stronger in Year 1 than in Year 2 ($P < 0.01$) (individual year

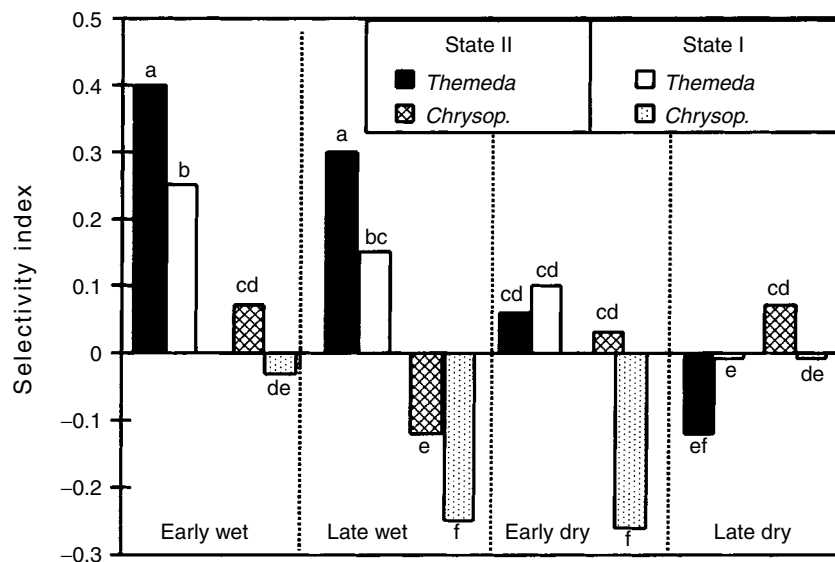


Figure 2. Influence of pasture condition and season of grazing on comparative selectivity of *Themeda* and *Chrysopogon* (+1 = complete preference; -1 = complete avoidance). Vertical bars labelled with different letters are significantly different ($P < 0.05$).

data not shown). Rainfall in Year 1 was just above the long-term average of 850 mm whereas Year 2 was quite dry with only 570 mm being recorded. There were extended dry spells during the active pasture growth period in Year 2 and animals appeared to decrease their selectivity between species in these dry periods.

Pasture condition interacted with season of grazing to affect significantly the selectivity for *Themeda*. In the early and late wet seasons, selection for *Themeda* was significantly greater ($P < 0.05$) in State II than in State I (Figure 2). At this time, *Themeda* is particularly sensitive to defoliation (Mott *et al.* 1992) and the effects of severe grazing, for just 8 weeks over a single wet season, can be detected up to 2 years after the grazing event (Ash and McIvor 1998). Thus, as *Themeda* decreases from being a major component in State I pasture to a minor component in State II pasture, additional selection pressure is placed on the remaining *Themeda* plants, which will increase intensity of defoliation and hasten their loss from the system. This rate of decline may be exacerbated by the presence of a less preferred species like *Chrysopogon* which, because it is less utilised, will have an advantage over *Themeda* in competition for resources (O'Connor 1991). Increasing the stocking rate, in an effort to "even out" grazing pressure on species, can

reduce the magnitude of the difference in selectivity between *Themeda* and *Chrysopogon* but not enough to overcome significant differences (Figure 3).

In contrast to *Themeda*, *Chrysopogon* was largely avoided in State I, with a negative selection index recorded in every season (Figure 2). However, in State II, in the relative absence of the more preferred *Themeda*, *Chrysopogon* had a positive selection index in all seasons except the late wet season. *Chrysopogon* is known to be most unpalatable at this time (Andrew 1986a), so with a shift in botanical composition from *Themeda* to *Chrysopogon* dominance, greater cattle grazing pressure is placed on *Chrysopogon*. Relatively little is known of *Chrysopogon*'s response to defoliation but it appears to lack tolerance to defoliation, as its proportion also declines if moderate — heavy grazing persists over extended periods. Relative intolerance of *Chrysopogon* to grazing has been demonstrated in patch grazing studies (Mott 1987). Heavily grazed patches, where all grass tussocks were kept at about 5cm height, exhibited a large reduction in perennial grass basal area and, by the third grazing season, most individual tussocks had died. Within grazed patches, *Themeda* was the first species to disappear, and then for a short time (1–2 years), *Chrysopogon* was the main

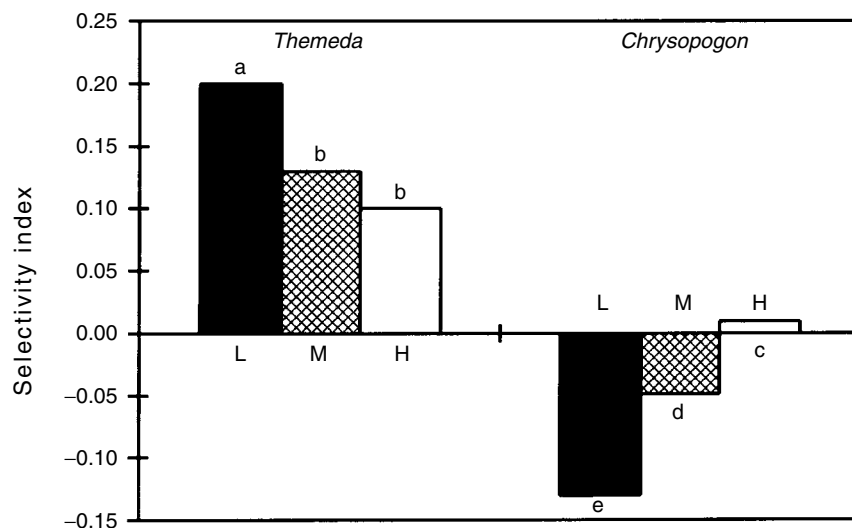


Figure 3. Effect of stocking rate (L = low; M = medium; H = high) on selectivity of *Themeda* and *Chrysopogon* (+1 = complete preference; -1 = complete avoidance). Vertical bars labelled with different letters are significantly different ($P < 0.05$).

species until it too was grazed out, except around the less utilised edges of patches, where it remained dominant (Mott *et al.* 1979). Similarly, in defoliation studies, *Chrysopogon* basal area was shown to decline rapidly when subjected to a fortnightly clipping regime during the wet season (Andrew 1988). It may be concluded that the increase in *Chrysopogon* dominance in State II (in terms of percentage composition) is therefore more a consequence of its escaping grazing

rather than any particular tolerance of defoliation.

There were no differences in the spatial distribution of utilisation due to pasture condition for either *Themeda* or *Chrysopogon*. This indicates that changes in botanical composition from State I to State II did not affect how cattle spatially grazed these 2 species. Season of grazing, however, had a strong influence on *Themeda* utilisation patterns with grazing in the early wet season

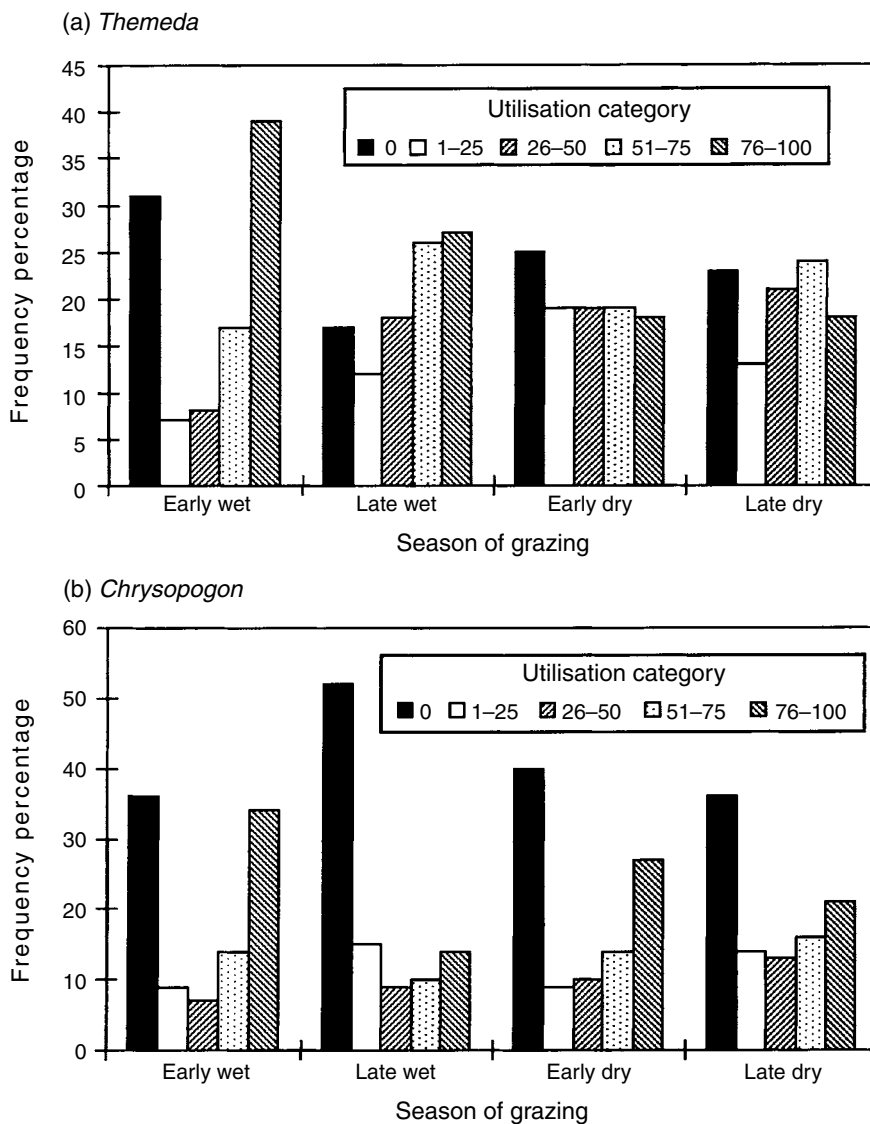


Figure 4. Effect of season of grazing on the pattern of utilisation of *Themeda* and *Chrysopogon* (0 = no utilisation; 1-25 = 1-25% of plant utilised; 26-50 = 26-50% of plant utilised; 51-75 = 51-75% of plant utilised; 76-100 = 76-100% of the plant utilised).

being much patchier than in other seasons (Figure 4). This was exhibited as a strong binomial distribution in utilisation categories in the early wet season with a high frequency of plants which were either unutilised or heavily utilised. Grazing in other seasons was marked by a more even distribution of utilisation categories. Patch grazing at the start of the wet season is common in this environment as cattle tend to regraze discrete patches while the bulk of the paddock

remains ungrazed and often grows rank and unpalatable. Such patch formation can improve diet quality and feed intake (Houliston *et al.* 1996) but is also responsible for accelerated degradation (Mott 1987) unless grazing distribution can be altered by management tools such as fire (Andrew 1986b). *Chrysopogon* was similarly grazed patchily in the early wet season and also in the early dry season.

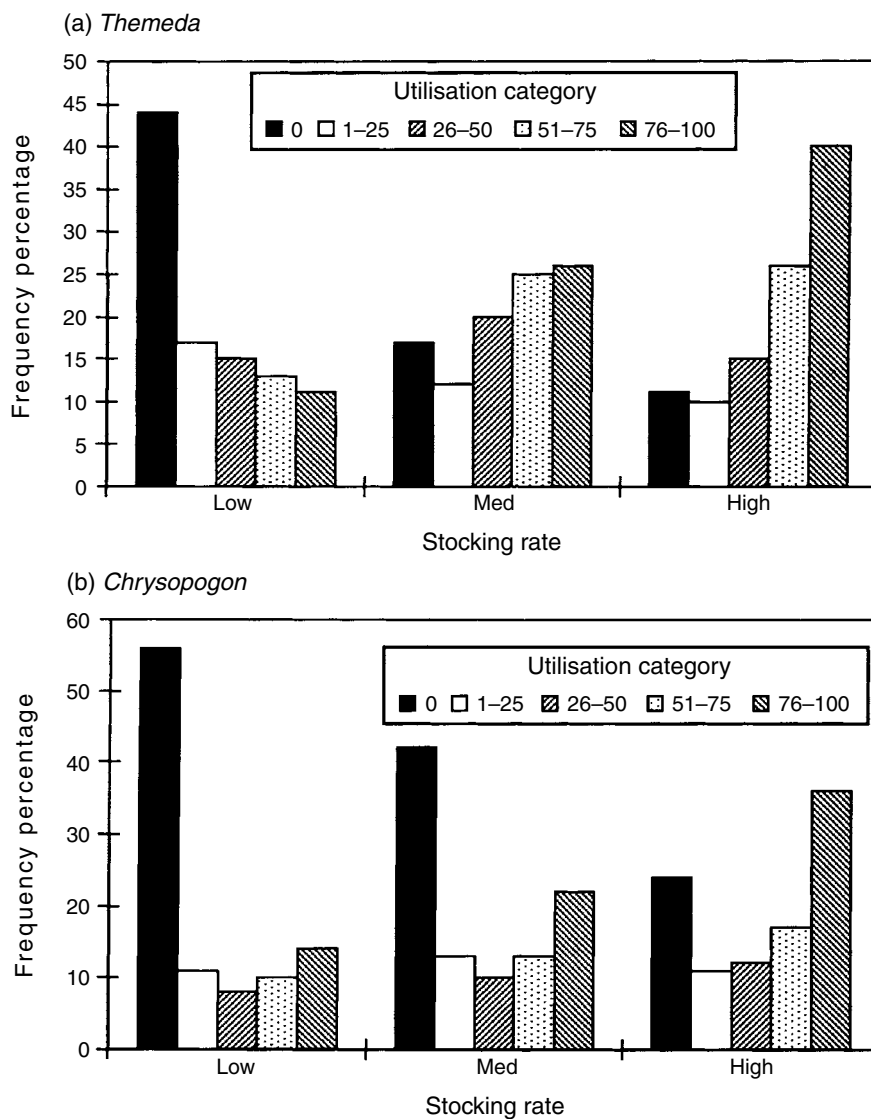


Figure 5. Effect of stocking rate on the pattern of utilisation of *Themeda* and *Chrysopogon* (0 = no utilisation; 1-25 = 1-25% of plant utilised; 26-50 = 26-50% of plant utilised; 51-75 = 51-75% of plant utilised; 76-100 = 76-100% of the plant utilised).

Stocking rate also strongly influenced defoliation patterns in this study and interacted with species being grazed (Figure 5). At the high stocking rate, few *Themeda* plants were left unutilised while the majority were heavily utilised. In contrast, *Chrysopogon* was still patchily grazed at the high stocking rate, with a high frequency of both unutilised and heavily utilised plants. Extreme stocking rates for an extended period would be necessary to achieve a majority of the utilisation in the most severe category (>75% utilisation). This highlights the difficulty in using intensive grazing methods to maintain even utilisation of species in a community where there are large differences in preference between the major grass species.

Conclusions

Diet selection patterns of cattle in this grassland, observed as large differences in preferences between species and distinct patch grazing, may be the overriding influence on species composition change. Selectivity for the palatable species *Themeda* increases as it becomes rarer, placing it under even greater threat of local extinction. Grazing management strategies designed to increase the proportion of a palatable species in a pasture must, therefore, take account of these selection patterns. For example, simply reducing stocking rate to a conservative level may not allow recovery of *Themeda* populations that have been reduced as a consequence of moderate or heavy stocking. Because of the strong selection pressure exerted on *Themeda*, stocking rates with continuous grazing would have to be unrealistically low, by commercial standards, to permit a recovery.

Grazing methods, such as short-duration or time-controlled grazing, may appear to offer a means of overcoming some of these selection patterns by forcing animals to eat all species using high intensity grazing. However, in our study, high stocking rates still did not overcome the relative preference for *Themeda*. Similarly, work in South Africa has shown that preferred plants tend to be regrazed before less preferred species are consumed (O'Reagain and Grau 1995). Spelling during the wet season may provide a more practical alternative in improving pasture composition where palatable species have been reduced by overutilisation. *Themeda* is not

sensitive to grazing once it has set seed and senesced (Ash and McIvor 1998). Moderate stocking rates could be imposed after the rest period, for the remaining 8 months of the year. This could allow the same total number of grazing days in the year as a continuous conservative stocking rate but with the advantage of improving pasture composition. Regardless of the exact method used, grazing strategies must take into account plant response to defoliation as well as herbivore selection patterns if they are to be successful in manipulating pasture composition.

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References

- ANDREW, M.H. (1986a) Selection of plant species by cattle grazing native monsoon tallgrass pasture at Katherine, N.T. *Tropical Grasslands*, **20**, 120–127.
- ANDREW, M.H. (1986b) Use of fire for spelling monsoon tallgrass pasture grazed by cattle. *Tropical Grasslands*, **20**, 69–78.
- ANDREW, M.H. (1988) Rangelands ecology and research in tropical north-west Australia in relation to the intensifying management of the beef industry. In: Singh, P., Shankar, V. and Srivastava, A.K. (eds) *Proceedings of the Third International Rangeland Congress*. pp. 688–690. (Range Management Society of India: Jhansi, India).
- ASH, A.J., BELLAMY, J.A. and STOCKWELL, T.G.H. (1994) State and transition models for rangelands. 4. Application of state and transition models to rangelands in northern Australia. *Tropical Grasslands* **28**, 223–228.
- ASH, A.J., MCVIVOR, G.G., CORFIELD, J.P. and WINTER, W.H. (1995) How land condition alters plant-animal relationships in Australia's tropical rangelands. *Agriculture, Ecosystems and Environment*, **56**, 77–92.
- ASH, A.J. and MCVIVOR, J.G. (1998) How season of grazing and herbivore selectivity influences herbaceous composition and growth in monsoon tallgrass communities of northern Australia. *Journal of Vegetation Science*, **9**, 123–132.
- BROWN, J.R. and STUTH, J.W. (1993) How herbivory affects grazing tolerant and sensitive grasses in a central Texas grassland — integrating plant response across hierarchical levels. *Oikos*, **67**, 291–298.
- DANCKWERTS, J.E., AUCAMP, A.J. and BARNARD, H.J. (1983) Herbaceous species preference by cattle in the False Thornveld of the eastern Cape. *Proceedings of the Grassland Society of Southern Africa*, **18**, 89–94.
- FREELAND, W.J. (1990) Large herbivorous mammals: exotic species in northern Australia. *Journal of Biogeography*, **17**, 445–449.
- HOULISTON, F.J., ASH, A.J. and MOTT, J.J. (1996) The influence of patches on the intake and grazing behaviour of

- cattle in tropical rangelands. In: Hunt, L.P. and Sinclair, R. (eds) *Proceedings of the 9th Biennial Australian Rangeland Conference*. pp. 95–96. (Australian Rangeland Society: Port Augusta).
- ISBELL, R.F. (1993) A classification system for Australian soils. *CSIRO Division of Soils Technical Report 2/1993*. CSIRO, Australia.
- IVLEV, V.S. (1961) *Experimental Ecology of the Feeding of Fishes*. (Yale University Press: New Haven).
- LOEHLE, C. and RITTENHOUSE, L.R. (1982) An analysis of forage preference indices. *Journal of Range Management*, **35**, 316–319.
- MOTT, J.J. (1987) Patch grazing and degradation in native pastures of the tropical savannas in northern Australia. In: Horn, F.P., Hodgson, J., Mott, J.J. and Brougham, R.W. (eds) *Grazing-lands Research at the Plant-animal Interface*. pp. 153–161. (Winrock International: Arkansas, USA).
- MOTT, J.J., BRIDGE, B.J. and ARNDT, W. (1979) Soil seals in tropical tall grass pastures of northern Australia. *Australian Journal of Soil Research*, **30**, 483–494.
- MOTT, J.J., WILLIAMS, J., ANDREW, M.H. and GILLISON, A.N. (1985) Australian savanna ecosystems. In: Tothill, J.C. and Mott, J.J. (eds) *Ecology and Management of the World's Savannas*. pp. 56–82. (Australian Academy of Science: Canberra, Australia).
- MOTT, J.J., LUDLOW, M.M., RICHARDS, J.H. and PARSONS, A.D. (1992) Effects of moisture supply in the dry season and subsequent defoliation on persistence of the savanna grasses *Themeda triandra*, *Heteropogon contortus* and *Panicum maximum*. *Australian Journal of Agricultural Research*, **43**, 241–260.
- O'CONNOR, T.G. (1991) Local extinction in perennial grasslands: a life history approach. *American Naturalist*, **137**, 753–773.
- O'CONNOR, T.G. (1992) Patterns of plant selection by grazing cattle in two savanna grasslands: a plant's eye view. *Journal of the Grassland Society of Southern Africa*, **9**, 97–104.
- O'REAGAN, P.J. and GRAU, E.A. (1995) Sequence of species selection by cattle and sheep on South African sourveld. *Journal of Range Management*, **48**, 314–321.
- STEEL, R.G.D. and TORRIE, J.H. (1980) *Principles and Procedures of Statistics*. (McGraw-Hill: New York).
- STEWART, J.W. (1996) Savanna users and their perspectives: grazing industry. In: Ash, A.J. (ed.) *The Future of Tropical Savannas: An Australian Perspective*. pp. 47–53. (CSIRO Publishing: Australia).
- TOTHILL, J.C., HARGREAVES, J.N.G., JONES, R.M. and McDONALD, C.K. (1992) BOTANAL — A comprehensive sampling and computing procedure for estimating pasture yield and composition. 1. Field sampling. *Tropical Agronomy Technical Memorandum No. 78*. CSIRO Division of Tropical Crops and Pastures, Brisbane.
- TOTHILL, J.C. and GILLIES, C.G. (1992) The pasture lands of northern Australia. Their condition, productivity and sustainability. *Tropical Grassland Society of Australia, Occasional Publication No. 5*. Brisbane.
- WESTOBY, M., WALKER, B. and NOY-MEIR, I. (1989) Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, **42**, 266–274.

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