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www.publish.csiro.au/journals/trj *The Rangeland Journal*, 2011, **33**, 209–220

Managing for rainfall variability: impacts of grazing strategies on perennial grass dynamics in a dry tropical savanna

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Abstract. Rainfall variability remains a major challenge to sustainable grazing management in northern Australia with perennial grasses the key to the stability of the resources that maintain a sustainable grazing industry. This paper describes the dynamics of five perennial grasses – *Bothriochloa ewartiana* (Domin) C.E. Hubb., *Chrysopogon fallax* S.T. Blake, *Aristida* spp., *Panicum effusum* R. Br. and *Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult. in relation to three grazing strategies – moderate stocking at long-term carrying capacity, heavy stocking and rotational wet season spelling. The research was conducted in permanent quadrats on the predominant land type in an extensive grazing study in an *Aristida-Bothriochloa* pasture in north Australia between 1998 and 2010. Summer rainfall was above average for two periods – 1998 – 2001 and 2008 – 2010 with drought and below-average rainfall from 2002 to 2007. Low rainfall affected the dynamics of all grasses by reducing survival and basal area through its effect on plant size; this impact was most noticeable for the shorter-lived *Aristida* spp., *P. effusum* and *H. contortus*. The impact of grazing was greatest on the long-lived *B. ewartiana* and *C. fallax*; this effect was accentuated by the 2002–07 drought. Heavy grazing during this period further reduced the survival and size of *B. ewartiana* in comparison with the moderate stocking and rotational spell treatments. In contrast, the survival of *C. fallax* was reduced in the moderate stocking and rotational spelling treatment during drought, relative to that under heavy grazing. The density of *B. ewartiana* declined even under moderate grazing and despite two sequences of above-average rainfall because seedling recruitment failed to offset mature plant death. Results from this study emphasised the importance of maintaining the existing populations of key long-lived species such as *B. ewartiana* through good management. These results also supported the overall findings from the grazing study indicating that stocking at the long-term carrying capacity is sustainable in managing for climate variability.

Additional keywords: *Bothriochloa ewartiana*, *Chrysopogon fallax*, grass dynamics, rainfall variability, stocking rate.

Introduction

Rainfall variability remains a major challenge to sustainable grazing management in northern Australia. Declining land condition throughout much of northern Australia has been recognised and described in terms of reduced ground cover and a decline in the occurrence of desirable perennial grasses (Tothill and Gillies 1992). Subsequently, the co-occurrence of heavy grazing pressure with drought has been identified as contributing to a series of eight major 'degradation episodes' throughout Australia including north-eastern Australia (McKeon *et al.* 2004).

In north-eastern Australia, studies of the impacts of grazing pressure on land condition are limited because earlier studies generally focussed on exotic grasses and/or legumes (Eyles *et al.* 1985). Nevertheless, McIvor and Gardener (1995) reported that perennial grasses dominated at moderate stocking rates but annual grasses and forbs increased with high stocking rates. More recently, Ash *et al.* (2011) demonstrated that lower pasture utilisation rates maintained and improved pasture condition whereas higher utilisation rates led to a substantial loss of productivity. Annual, early wet season spelling coupled with lower or moderate utilisation also improved pasture condition; significantly, spelling appeared to ameliorate the impacts of heavier (up to 50%) utilisation rates on pasture condition.

Although moderate stocking rates have been widely advocated as a key management tool for long-term sustainable management, there is little direct information on how different practices affect animal production and economic profitability. Mann (1993) advocated the use of moderate stocking rates to avoid overgrazing as the key pasture management tool for long-term sustainable management. In contrast, in central Queensland, Burrows *et al.* (2010) reported the highest economic return after

10.1071/RJ11032 1036-9872/11/020209

13 years of grazing was achieved at the highest stocking rate. However, this economic analysis failed to account for the unsustainable nature of this stocking rate as indicated by reduced pasture yields, declining pasture composition, accelerated soil erosion and reduced landscape function. In contrast, O'Reagain *et al*. (2009, 2011) reported interim results that showed animal production per unit area was greatest under heavy stocking, although individual liveweight gain was reduced leading to reduced carcass value. Furthermore, heavy stocking required substantial drought feeding and a reduction in stocking rate to survive low rainfall years and was not sustainable. These authors indicated that heavy stocking was neither profitable nor sustainable (O'Reagain *et al*. 2009, 2011).

Perennial grasses are the key to resource sustainability in northern Australia grazing communities because they are relatively reliable and are often the only source of forage in severe droughts. Perennial grasses also protect the soil surface and are important in maintaining soil health through increased soil carbon (Northup *et al*. 2005) and faunal activity (Gibb *et al*. 2008). In general, infiltration rates increase and runoff decreases as perennial grass density and soil health increase (Roth 2004). This is a key issue for those catchments where runoff from grazing lands is seen as a major threat to the health of the Great Barrier Reef Lagoon (Furnas 2003).

An understanding of the dynamics of the major perennial grasses is therefore critical to the development of sustainable grazing strategies to manage for rainfall variability in northern Australia. Studies of the dynamics of a range of perennial grasses including *Astrebla* spp. (Orr 1998), *Heteropogon contortus* (Orr 2004; Orr *et al*. 2004*a*, 2010*a*; McIvor 2007; Jones *et al.* 2009), *Bothriochloa ewartiana* and *Chrysopogon fallax* (McIvor 2007; Jones *et al*. 2009) provide an overall understanding of sustainable grazing management in some important pasture communities in northern Australia.

This paper reports the impact of three grazing strategies – moderate stocking, heavy stocking and rotational wet season spelling – on the dynamics of five perennial grass species in a long-term grazing study described by O'Reagain *et al*. (2009). In particular, this paper concentrates on the persistence of these grasses in relation to grazing management in this highly variable rainfall environment.

Materials and methods

Site description

A large grazing study was established in 1997 in open *Eucalyptus* savanna at Wambiana (20°34′S, 146°07′E), 70 km south-west of Charters Towers north Queensland, Australia, to assess the impacts of five grazing strategies on animal production, profitability and resource condition. Long-term (98-year) mean annual precipitation for the nearest Bureau of Meteorology rainfall station (17 km north-west of the study site) is 636 mm with a coefficient of variation of 40%. Rainfall is generally highly seasonal with 70% falling between December and March and a long dry season in intervening months (Clewett *et al*. 2003). Soils are derived from tertiary sediments and are relatively infertile Kandosols, Sodosols, Chromosols and Vertosols (Isbell 1996). The vegetation is within the *Aristida-Bothriochloa* pasture community (Tothill and Gillies 1992) and is described as open savanna dominated by *Eucalyptus*, and to a lesser extent, *Acacia* woodland species overlying C_4 tropical grasses.

A detailed soil and vegetation survey was conducted during 1997 and was used to plan the study layout to ensure that experimental paddocks contained similar proportions of the three main soil-vegetation associations. There are 10 paddocks ranging in size from 93 to 117 ha, laid out in a randomised block design with two blocks of five treatments (see below). Further details are provided in O'Reagain *et al*. (2009).

The research reported in this paper was conducted within the *Eucalyptus brownii* community, which occupies 55% of the study area and typically occurs on brown Sodosols and Chromosols. These soils are relatively shallow (30–40 cm) of moderate fertility and are commonly dominated by a *B. ewartiana–C. fallax* pasture layer.

Treatments

Five grazing strategies, replicated twice, were tested in the main grazing study (O'Reagain *et al*. 2009). However, available resources restricted this population dynamics study to only three of these five grazing strategies: (i) moderate stocking rate (MSR): paddocks stocked at the long-term carrying capacity to achieve the recommended safe average utilisation rate of 20–25% of pasture growth that could be expected to be produced in most (~70%) years. This treatment was set stocked at ~10 ha per animal equivalent (AE: defined as a 450 kg steer) between 1997 and 1998 and 2000 and 2001 and at ~8 ha/AE thereafter. (ii) Heavy stocking rate (HSR): paddocks stocked at twice the long-term carrying capacity to achieve 40–50% utilisation of the pasture growth that could be expected in most years. The HSR treatment was set stocked at ~5 ha/AE between 1997 and 1998 and 2000 and 2001 and at 4 ha/AE thereafter. From May 2005 to May 2009, the stocking rate was cut to ~6 ha/AE because of the inability of the HSR treatment to sustain the original stock numbers. The stocking rate was returned to its former level of 4 ha/AE in June 2009.

(iii) Rotational spelling (R/spell): wet season, rotational spelling applied in a simulated three-paddock system: the treatment paddock in each replicate divided into three similar-sized sections with a different section spelled annually for the full wet season (usually November–June). All sections are grazed during the dry season. This R/spell treatment was initially set stocked at ~7.5 ha/AE i.e. half way between the MSR and HSR, based on the assumption that spelling would buffer the impacts of the slightly increased stocking rate (Ash *et al*. 2011). Note that in the wet season, non-spelled sections are effectively stocked at ~1/3 above the nominal stocking rate because of the reduced area available for grazing.

Fire management

The entire study site was burnt on 11 October 1999 to remove moribund grass and control woody species. It was then spelled until 12 January 2000 to allow pasture recovery. In the R/spell treatment it was also felt that the sections to be spelled could be burnt to suppress woody species; it was assumed that the consequent spell would allow recovery in all but the very worst seasons. This occurred successfully in 1999 and 2000, but not in November 2001, with drought conditions resulting in very poor post-fire recovery. Consequently, this burnt section had to be spelled for the next three wet seasons; this disrupted the planned spelling sequence with the sections studied (see below) enduring 3 successive years of heavy wet season grazing. These factors ultimately necessitated reducing the overall stocking rate in the R/spell treatment to ~9/AE in November 2003. Overall, the area where the present data was collected was spelled four times in 13 years.

Measurements

Species selected for study were *B. ewartiana* (desert bluegrass), *C. fallax* (golden beard grass), *Aristida* spp. (wiregrasses), *P. effusum* (Hairy panic) and *H. contortus* (black speargrass). *B. ewartiana* is the 'key' species in these pastures while the other species are important perennial grass species in the *Aristida-Bothriochloa* pastures in the region of this grazing study (Rolfe *et al*. 1997).

In 1998, 20 permanent quadrats, each 50 × 50 cm, were located in four nests each of 5 quadrats in the MSR, HSR and R/spell treatments. Within each nest, quadrats were selected to contain either 4, 3, 2, 1 or 0 *B. ewartiana* plants together with a variable number of *C. fallax*, *Aristida* spp., *P. effusum* and *H. contortus* plants. Quadrats were stratified on *B. ewartiana* density to cover the range of plant densities and sizes. In 1998, the position of individual grass tussocks in each quadrat was located by dividing each quadrat into four grid units, each 25 × 25 cm, and charting the position of each tussock within each grid cell. The diameter of each tussock was measured. Where tussocks were not circular, the width was measured first along the widest diameter and second along the diameter perpendicular to the first diameter. Between 1999 and 2010, further recordings were made annually at the end of the wet season, usually in May, of the survival and size of these existing tussocks together with any new seedling plants that had been recruited during the previous year (Orr *et al*. 2004*a*, 2010*a*).

Basal area of individual species was calculated on an individual quadrat basis as the area occupied by all individual tussocks of each species in the quadrat by assuming plants to be circular. Perennial grass tussocks fragment with age and, where this occurred, we identified each segment making up individual tussocks. When the plant or segment was not circular, the diameter was assumed to be the mean of the two diameters measured for that plant. Individual plant size, for both original plants and annual cohorts of each species, was determined as the area covered by each plant of that cohort and was calculated by dividing the total basal area of that cohort per quadrat by the number of individual plants (incorporating the number of segments making up each of these tussocks) in that quadrat (Orr *et al*. 2004*a*, 2010*a*). Plant turnover was calculated as 1 minus the fraction of the population not turning over during the period of study, expressed as a percentage (after O'Connor 1994). Life spans for the original plants were estimated from the survival of the original plants throughout the period of the study (after Sarukhan and Harper 1973). (The distribution of *H. contortus* was irregular and was recorded in three paddocks only – one replicate for each treatment so that results for *H. contortus* presented in this paper are limited).

Soil seed banks

The soil seed banks of the five perennial grasses were measured in 1999 and 2007 to assess differences in seedling recruitment. Soil cores were collected in October (spring) and the soil seed bank determined by germinating seed contained in these soil cores. Four soil cores, each 5 cm diameter and 5 cm deep, collected from the area surrounding the permanent quadrats, were bulked to produce each sample. There were 20 samples (i.e. 80 cores; five samples from each of four nests) from each paddock. In the summers of 2000 and 2008, when perennial grass dormancy had been overcome, each sample was spread as a 2-cm-thick layer over compacted sand in a 15-cm-diameter drained plastic pot. Seed in these samples was germinated by watering with an overhead sprinkler for 30 min daily for 6–8 weeks (Orr *et al*. 1996). Seedlings of *B. ewartiana*, *C. fallax*, *Aristida* spp., *Panicum* spp. and *H. contortus* were identified and counted and only one wetting cycle was conducted on each set of cores (Orr 1999).

Statistical analysis

In evaluating the effects of the grazing treatments on plant density and basal area for each species across time, both overall trends and seasonal effects were considered using REML. First, splines (Orchard *et al*. 2000) were used to assess seasonal impacts while fitting the full fixed (treatment × time) model. The significance of the splines was evaluated by a Chi-square test on the change in deviance. Second, the fixed effects were assessed for overall trends. Data on recruitment and plant size for each species were analysed separately for each year in GENSTAT (2002). Plant survival was analysed using a proportional hazards survival model (Cox 1972).

Results

Rainfall

Rainfall varied widely between 1998 and 2010 with distinct periods of above- and below-average rainfall during both summer and winter. Rainfall for three consecutive summers, 1998–99 to 2000–01, was above the 513-mm mean but was followed by 5 consecutive years of below-average summer rainfall. Annual rainfall for these 5 years was among the lowest 20–30% of rainfall years on record (Clewett *et al*. 2003). Rainfall for the 2007–08 to 2009–10 summers was again above average (Fig. 1*a*). Winter rainfall was also below average between 2001 and 2004 but was followed by 5 consecutive years of above-average winter rainfall from 2005 to 2009 (Fig. 1*b*).

Plant turnover

Between 1998 and 2010, a total of 536, 215, 787, 330 and 192 plants of *B. ewartiana*, *C. fallax*, *Aristida* spp., *P. effusum* and *H. contortus*, respectively, were encountered. Of these, 240, 138, 226, 42 and 8 were original plants while 296, 77, 561, 288 and 144 seedlings were recorded over the 13 years of this study. Plant turnover for *B. ewartiana* was higher ($P < 0.05$) in the HSR compared with the MSR and R/spell while turnover for *C. fallax* was higher ($P < 0.05$) in the MSR and R/spell compared with the HSR (Table 1). There was a complete population

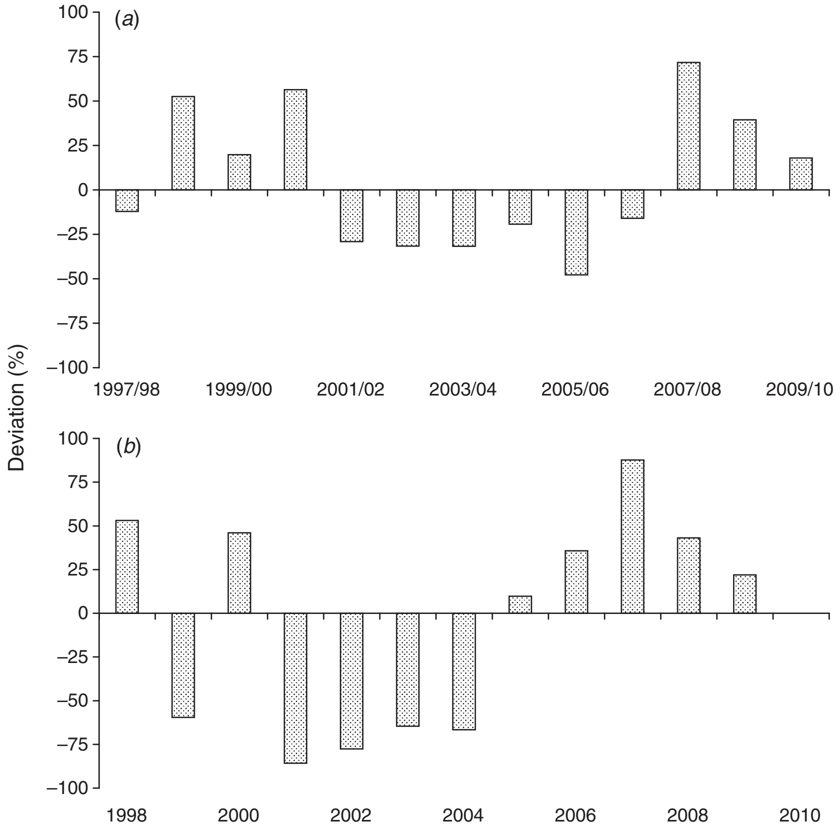

Fig. 1. Deviation (%) of (*a*) summer (October–March) and (*b*) winter (April–September) rainfall (mm) from historical long-term average between 1998 and 2010 at Wambiana.

Table 1. Plant turnover[A] of plant numbers for five perennial grasses in relation to three grazing strategies between 1998 and 2010 at Wambiana

Within columns (species) values followed by the same letters are not significantly different at $P = 0.05$

	Bothriochloa ewartiana	*Chrysopogon fallax*	*Aristida* spp.	*Panicum effusum*	*Heteropogon contortus*
Moderate	42.6a	62.2a	100	100	100
Rotational	42.5a	72.8a	100	100	100
Heavy	77.5b	36.8b	100	100	100

[A] Plant turnover for plant number was calculated as 1 minus the fraction of the population not turning over between 1998 and 2010 expressed as a percentage (after O'Connor 1994). The fraction not turning over was the number of individual plants present in 1998 and still present in 2010.

turnover for *Aristida* spp., *P. effusum* and *H. contortus* with no treatment differences apparent.

Density

The densities of both *B. ewartiana* and *C. fallax* generally declined throughout the study period; conversely the densities of *Aristida* spp., *P. effusum* and *H. contortus* varied between years. Spline analyses indicated different year × treatment interactions for *B. ewartiana* and *C. fallax* (Fig. 2*a, b*) with *B. ewartiana* density being reduced ($P < 0.05$) in the HSR compared with the MSR and R/spell. In contrast, *C. fallax* density was reduced ($P < 0.05$) in the MSR and R/spell compared with the HSR. For *Aristida* spp., density was consistently higher ($P < 0.05$) in the R/spell than in either of the other two treatments with the year effect also significant ($P < 0.05$). However, there was no interaction between treatment and year (Fig. 2*c*). Neither treatment, year nor their interaction was significant ($P > 0.05$) for *P. effusum* and *H. contortus* density (Fig. 2*d*).

Recruitment

Recruitment of all five species varied among years with no treatment differences apparent ($P > 0.05$) within each species (Fig. 3). For all five species, recruitment was generally less than 2 seedlings/m^2 although recruitment levels of 5, 3.5 and

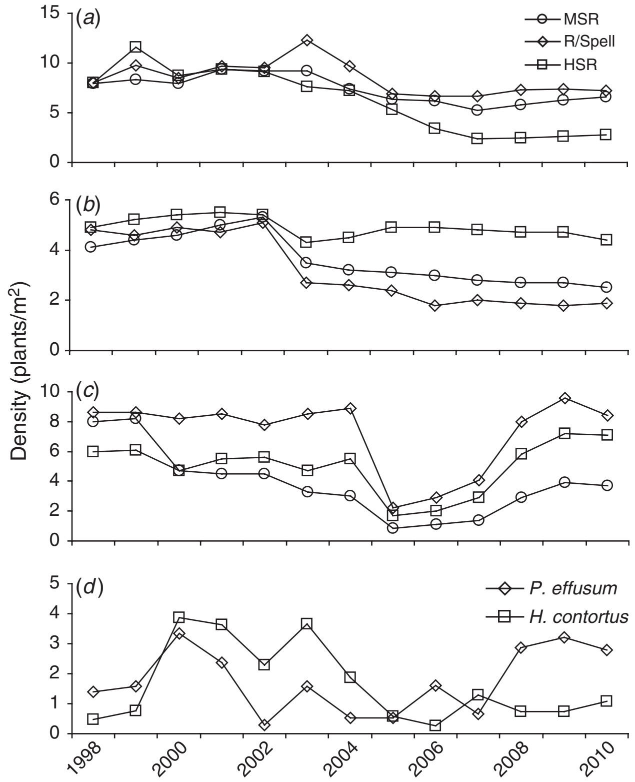

Fig. 2. Changes in the density (plants/m^2) of (*a*) *Bothriochloa ewartiana*, (*b*) *Chrysopogon fallax*, (*c*) *Aristida* spp. and (*d*) *Panicum effusum* and *Heteropogon contortus* (pooled across three grazing treatments) between 1998 and 2010 at Wambiana.

3 seedlings/m^2 were recorded for *Aristida* spp. in 2003, 2004 and 2008, respectively.

Survival

Although some original *B. ewartiana* and *C. fallax* plants survived the 13-year study period, overall survival of the original plants of all five species declined ($P < 0.05$) with time (Fig. 4). Plant death accelerated particularly for *B. ewartiana* and *C. fallax* during the drought and below-average rainfall years between 2002 and 2007. Survival of both *B. ewartiana* and *C. fallax* plants was clearly impacted by treatment with the survival of *B. ewartiana* lower ($P < 0.05$) in the HSR compared with the MSR and R/spell. In contrast, the survival of *C. fallax* was lower ($P < 0.05$) in both MSR and R/spell compared with HSR (Fig. 4*a, b*). *C. fallax* survival in both MSR and R/spell fell particularly sharply in 2003 following an 11-month period with virtually no rain. This decline was possibly compounded by the March 2003 outbreak of armyworm that was particularly damaging to *C. fallax* (P. O'Reagain, pers. obs.). Few seedlings of either *B. ewartiana* or *C. fallax* recruited during this study survived (data not presented). Estimated life spans for the original plants were 28, 30 and 16 years for *B. ewartiana* and 19, 17 and 50 years for *C. fallax* for the MSR, R/spell and HSR with no differences ($P > 0.05$) between treatments for either species.

Mortality in *Aristida* spp. was particularly high – only one original *Aristida* spp. plant survived until 2008 while all original *P. effusum* and *H. contortus* plants had died by 2005. The survival of all three of these species was unaffected ($P > 0.05$) by grazing (Fig. 4*c–e*). Survival of the original and some annual cohorts of *Aristida* spp. and *P. effusum* plants varied among years. Survival was clearly related to rainfall and was lower for the 2003 and 2004 cohorts compared with the 2008 and 2009 cohorts for both species. Survival of the 2000 and 2003 cohorts of *H. contortus* was similar.

Basal area

Basal area of all species increased with above-average rainfall between 1998 and 2001, but then declined sharply with the sudden change to drought conditions in 2002–03. Basal area of all species increased again only with above-average rainfall after 2007–08. In 2010, 88 and 73% of the total basal area of *B. ewartiana* and *C. fallax*, respectively, was still contributed by those plants originally present in 1998. This occurred because seedling recruitment was low for both these species and few of these seedling plants survived. Three years of above-average rainfall in 2008–10 failed to increase the basal area of either *B. ewartiana* or *C. fallax* to that measured in 2002 after the previous 3 years of above-average rainfall from 1998 to 2001.

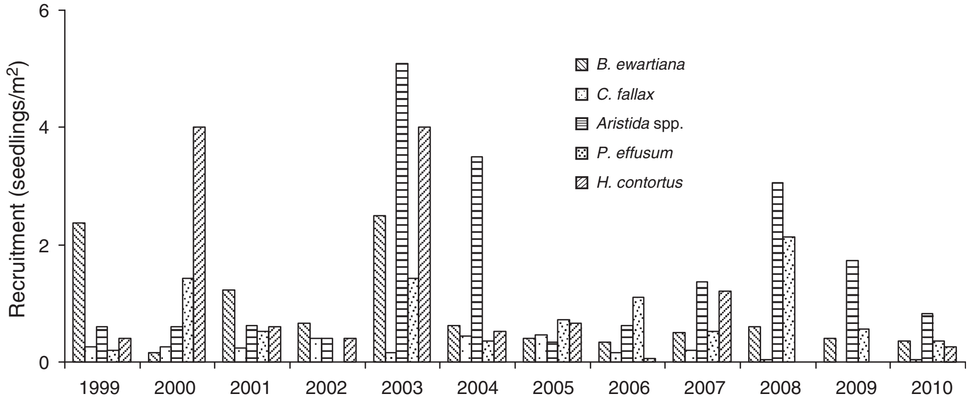

Fig. 3. Seedling recruitment (seedlings/m^2) of *Bothriochloa ewartiana*, *Chrysopogon fallax*, *Aristida* spp., *Panicum effusum* and *Heteropogon contortus* (pooled across three grazing treatments) between 1999 and 2010 at Wambiana.

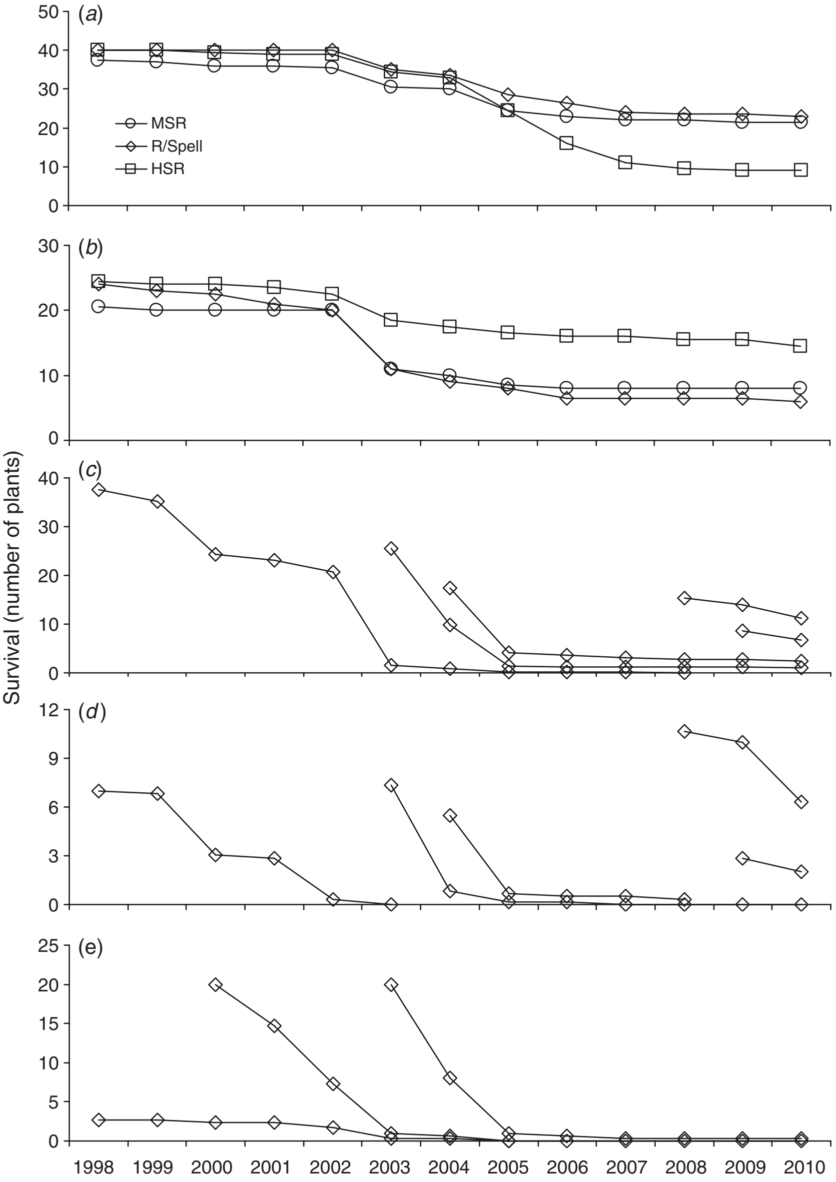

Fig. 4. Changes in the survival (number of plants) of original plants of (*a*) *Bothriochloa ewartiana*, (*b*) *Chrysopogon fallax* in relation to three grazing treatments and cohorts of (*c*) *Aristida* spp. (pooled across three grazing treatments), (*d*) *Panicum effusum* (pooled across three grazing treatments) and (*e*) *Heteropogon contortus* (pooled across three grazing treatments) between 1998 and 2010 at Wambiana.

Basal area of both *B. ewartiana* and *C. fallax* were both influenced by year × treatment interactions: *B. ewartiana* basal area was reduced ($P < 0.05$) in the HSR compared with MSR and R/spell. Conversely, *C. fallax* basal area was reduced ($P < 0.05$) in the MSR and R/spell compared with HSR (Fig. 5*a*, *b*).

Aristida spp. basal area was consistently higher ($P < 0.05$) in the R/spell compared with the other two treatments with the year effect also significant ($P < 0.05$); however, there was no year × treatment interaction ($P > 0.05$) (Fig. 5*c*). Neither treatment, year nor their interaction was significant ($P > 0.05$) for basal area of *P. effusum* and *H. contortus* basal area (Fig. 5*d*). In contrast to both *B. ewartiana* and *C. fallax*, by 2010, the total basal area of *Aristida* spp. and *P. effusum* was contributed solely by plants recruited and established since 2003 and 2008, respectively.

Plant size

The changes in basal area of all species were closely linked to changes in plant size among years. Plant size varied in line with rainfall with size increasing during years of above-average

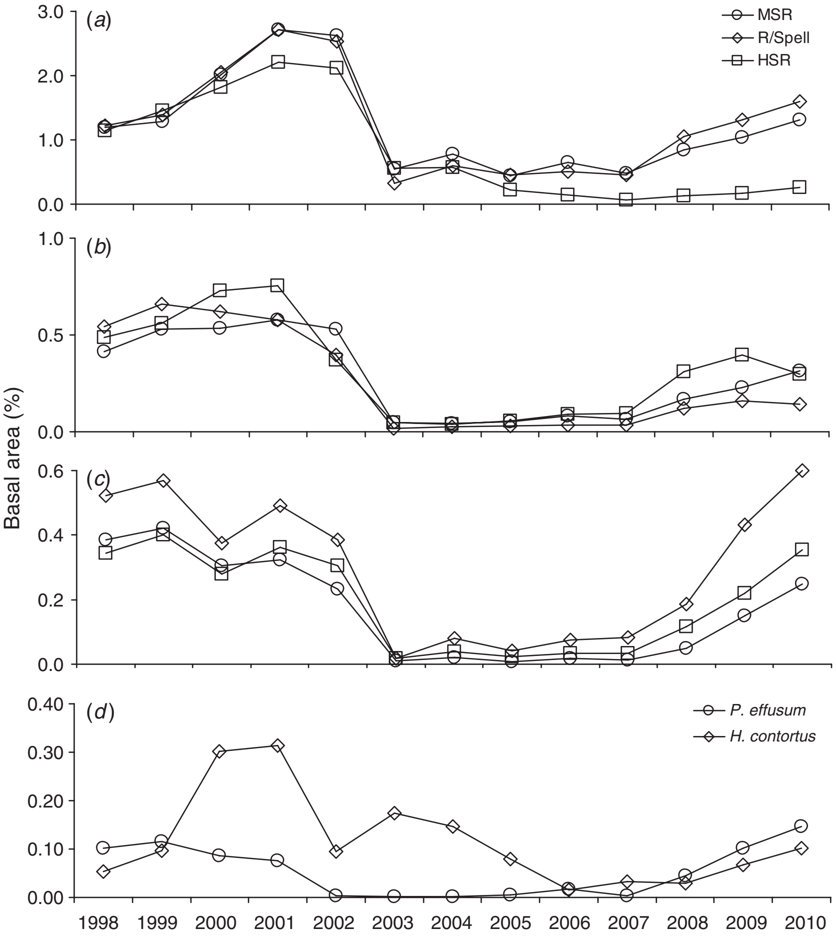

Fig. 5. Changes in the basal area (%) of (*a*) *Bothriochloa ewartiana*, (*b*) *Chrysopogon fallax*, (*c*) *Aristida* spp. in relation to three grazing treatments and (*d*) *Panicum effusum* and *Heteropogon contortus* (pooled across three grazing treatments) between 1998 and 2010 at Wambiana.

rainfall but declining in below-average rainfall years. For *B. ewartiana*, plant size was influenced ($P < 0.05$) by a year × treatment interaction and was reduced ($P < 0.05$) in the HSR compared with MSR and R/spell (Fig. 6*a*). *C. fallax* plant size was influenced ($P < 0.05$) by year but not by grazing treatment (Fig. 6*b*). Interestingly, as with basal area, 3 years of above-average rainfall between 2008 and 2010 failed to increase *B. ewartiana* or *C. fallax* plant size to the values achieved after the 3 years of above-average rainfall in 1998–2001.

The size of the original *Aristida* spp., *P. effusum* and *H. contortus* plants increased between 1998 and 2001 but fell sharply in response to the drought after 2001–02 (Fig. 6*c–e*). Plant size for annual cohorts of these three species varied among years and was related to seasonal rainfall. For example, increases in the size of the 2003 and 2004 cohorts of *Aristida* spp. and the 2003 cohort of *P. effusum* were limited by the relatively dry years between 2002 and 2007. In contrast, the 2008 and 2009 cohorts of these two species increased in size rapidly in response to above-average summer rainfall in 2008–09 and 2009–10.

Germinable soil seed banks

No germinable seed bank of either *B. ewartiana* or *C. fallax* was measured in either 1999 or 2007. Seed banks of 21, 7 and 2 seeds/m^2 were recorded for *P. effusum*, *H. contortus* and *Aristida* spp. in spring 1999 but none of these species were recorded in spring 2007.

Discussion

Rainfall variability interacted with grazing pressure to affect the occurrences of both the long-lived perennials *B. ewartiana* and *C. fallax* and the relatively short-lived perennials *Aristida* spp., *P. effusum* and *H. contortus*. Rainfall variability affected both plant survival and basal area largely via its impact on plant size, particularly for the three short-lived species. The effect of grazing pressure was greatest on *B. ewartiana* and *C. fallax* and this grazing impact was accentuated by severe drought. Results reported here are similar to those for *B. ewartiana* and *C. fallax* elsewhere in northern Australia (McIvor 2007; Jones *et al.* 2009) although the results for

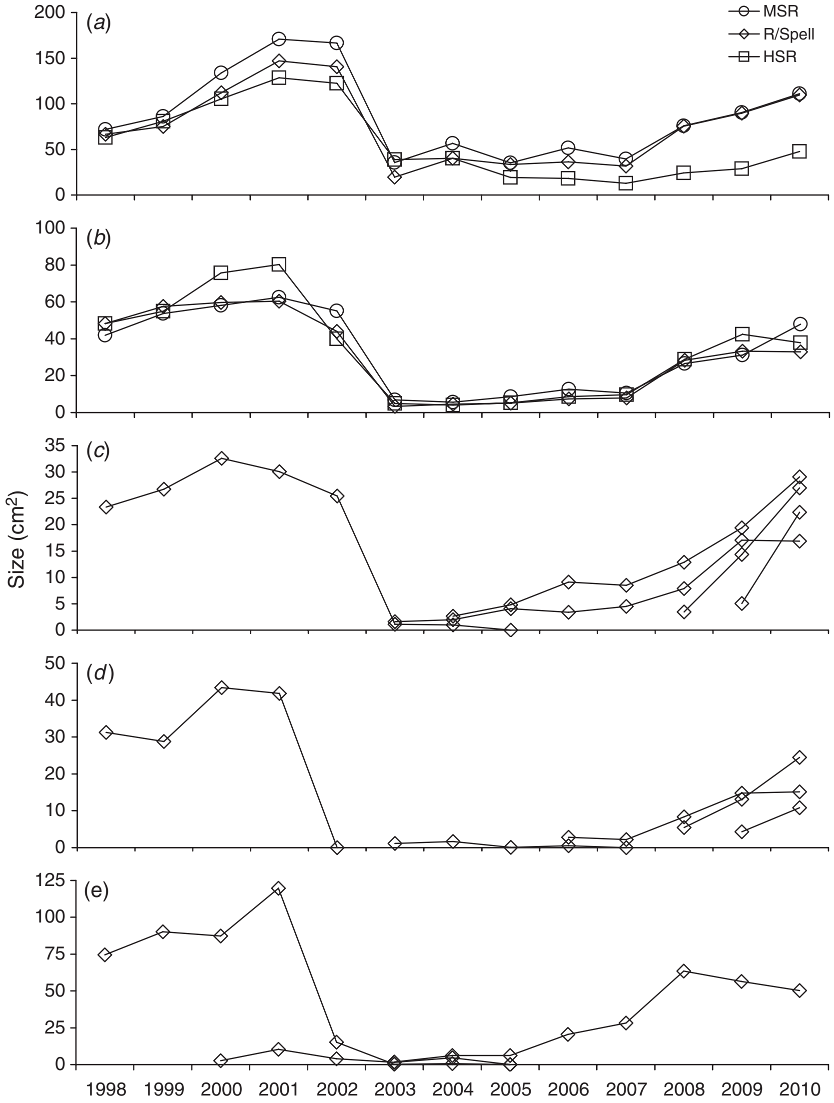

Fig. 6. Changes in the plant size (cm^2/plant) of original (*a*) *Bothriochloa ewartiana*, (*b*) *Chrysopogon fallax* in relation to three grazing treatments and original and annual cohorts of (*c*) *Aristida* spp. (pooled across three grazing treatments), (*d*) *Panicum effusum* (pooled across three grazing treatments) and (*e*) *Heteropogon contortus* (pooled across three grazing treatments) plants between 1994 and 2000 at Wambiana.

H. contortus differ markedly from those in other geographical regions (Orr *et al*. 2004*a*, 2010*a*; Jones *et al*. 2009).

Plant turnover

B. ewartiana and *C. fallax* both had relatively small fluctuations in density because of low levels of recruitment and death. This is in direct contrast with the shorter-lived *Aristida* spp., *P. effusum* and *H. contortus*, which all had highly variable recruitment and death leading to relatively large fluctuations in density. Heavy grazing increased *B. ewartiana* turnover while both moderate grazing and rotational spelling increased *C. fallax* turnover. This increased *B. ewartiana* turnover under heavy grazing is consistent with similar results for *B. ewartiana* under heavy grazing in central Queensland (Jones *et al*. 2009). However, increased *C. fallax* turnover in the present study contrasts with no grazing impact on this species in central Queensland (Jones *et al*. 2009). This difference probably reflects the longer time span of our study (13 years) compared with that (6 years) for the central Queensland study. This suggestion is further supported by higher mean plant turnover of 54 and 55% for *B. ewartiana* and *C. fallax* compared with 34 and 33% in central Queensland.

Complete turnover of *Aristida* spp., *P. effusum* and *H. contortus* populations in the present study reflects their short life spans relative to the length of this study. In comparison, Jones *et al*. (2009) recorded a turnover for *H. contortus* of 67% over 6 years with no grazing pressure impact while a longer, 13-year study (Orr *et al*. 2010*a*) recorded a turnover of 95% also with no effect of grazing pressure. These differences again reflect different study durations relative to the life span of *H. contortus*.

Plant density

Densities of both *B. ewartiana* and *C. fallax* declined gradually throughout this study due to low rates of both seedling recruitment and low mature plant death. For *B. ewartiana* this decline was greater under heavy grazing, particularly during the severe 2002–03 drought and the dry years that followed. Conversely, for *C. fallax* the decline was greater in the MSR and R/spell treatments. Reduced *B. ewartiana* density with heavy grazing is consistent with this species being palatable to cattle (Rolfe *et al*. 1997). Although *C. fallax* is palatable to cattle (McIvor 2007; Hendricksen *et al*. 2010), the higher density of this species with heavy grazing possibly results from its higher tolerance to defoliation that is conferred by its underground rhizome structure (Rolfe *et al*. 1997) and possibly also from reduced competition from *B. ewartiana*. Densities of both *B. ewartiana* and *C. fallax* are similar to those in central Queensland (Jones *et al*. 2009).

Although a higher *Aristida* spp. density was recorded in the rotational treatment; this simply reflects an initial higher density of this species in one replicate which was maintained throughout this study. Although rainfall had a major impact on *Aristida* spp., surprisingly, there was no effect of grazing. This conflicts with the indication (Rolfe *et al*. 1997; Tothill *et al*. 2008) that *Aristida* spp. increase with grazing pressure. However, other data (Orr *et al*. 2004*b*, 2010*b*; Silcock *et al*. 2005) report that *Aristida* spp. is most common under light grazing. Highest densities of *Aristida* spp. at Wambiana were similar to densities of 6–14 plants/m^2 in southern Queensland (Orr *et al*. 2004*b*).

Fluctuations in *P. effusum* and *H. contortus* densities in this study were large compared with those for *B. ewartiana* and *C. fallax* although no comparative density data are available for *P. effusum*. However, *H. contortus* densities recorded here are much lower than that in both southern (Orr *et al*. 2004*a*) and central Queensland (Jones *et al*. 2009; Orr *et al*. 2010*a*).

Recruitment

Recruitment for all five species varied among years due to variable rainfall. This finding is consistent with other studies of seedling recruitment (Orr *et al*. 2004*a*, 2004*b*, 2010*a*; Jones *et al*. 2009). Recruitment of *B. ewartiana* and *C. fallax* was, however, very low (<2 and 0.5 seedling/m^2, respectively), and even at the light stocking rate was insufficient to maintain the initial densities of both species. Similar low recruitment for these species has been reported by both McIvor (2007) and Jones *et al*. (2009). Importantly, some *B. ewartiana* recruitment was not 'seedling' recruitment but arose from layering from the nodes of decumbent stems of existing, mature plants. Seedling recruitment of *C. fallax* may be rare because of small soil seed banks and slow seedling emergence (Silcock 1999).

Recruitment of *Aristida* spp. varied widely among years. This seasonal variation and lack of grazing impact is consistent with *Aristida* spp. recruitment in southern Queensland (Orr *et al*. 2004*b*). However, the highest *H. contortus* recruitment was very low compared with other studies with the highest levels of 4 seedlings/m^2 in 2000 following spring burning in 1999 being much lower than the 20 and 150 seedlings/m^2 following spring burning in southern and central Queensland, respectively (Orr *et al*. 1997, 2010*a*).

Survival

The survival of all species declined with time. Although the rate of this response varied widely among species, the rate of decline generally accelerated through the lower rainfall years from 2002 to 2007. This accelerated plant death due to drought is consistent with similar patterns recorded for *Astrebla* spp. during drought (Orr 1998). In contrast, a regular pattern of death was reported by Jones *et al*. (2009) where seasonal rainfall was consistently favourable for perennial grass growth.

Survival of *B. ewartiana* was further reduced by heavy grazing. Paradoxically, moderate grazing and rotational spelling further reduced the survival for *C. fallax* during drought. Jones *et al*. (2009) also reported reduced survival of *B. ewartiana* with heavy grazing; however, there was no grazing impact on *C. fallax*. As noted earlier, the reduced survival of *C. fallax* reported here probably reflects the longer time span of the present study combined with far drier seasonal conditions. Estimated life spans for original *B. ewartiana* plants were as high as 28 and 30 years for moderate grazing and rotational spelling and were similar to the 25 years for light grazing reported by Jones *et al*. (2009). Such life spans are within the range of life spans for perennial grasses reported for northern American grasslands (Wright and Van Dyne 1976; Lauenroth and Adler 2008).

The drought and low rainfall through 2002–07 resulted in the death of all *P. effusum* and *H. contortus* and all but one *Aristida* spp. plants. This is consistent with the finding (Wright and Van Dyne 1976) that long-term drought plays an important role in the mortality of otherwise long-lived plants. The mass mortality of *H. contortus* in the present study contrasts with its survival through drought and its relative longevity in both southern and central Queensland (Orr *et al*. 2004*a*, 2010*a*). Nevertheless, McIvor (2007) reported a similarly short life span for *H. contortus* on two land types in the Charters Towers region. *Aristida* spp. also survived through drought in southern Queensland with reported life spans of at least 6 years (Orr *et al*. 2004*b*). Few comparative data are available on the survival of *P. effusum*.

Survival of plants of both *Aristida* spp. and *P. effusum* from the 2008 and 2009 cohorts were higher than that from the 2003 and 2004 cohorts indicating that seasonal rainfall influences the survival of annual cohorts of these species. Similarly, Orr and Paton (1997) reported seasonal rainfall resulted in differences in survival for annual cohorts of *H. contortus*.

Basal area and plant size

Basal area of all species responded strongly to rainfall by increasing in good rainfall years and declining in drought. These changes result largely from tiller dynamics within individual plants with basal area increases following favourable rainfall resulting from new tiller production which, in turn, leads to increased plant size (Orr 1998; Orr *et al*. 2004*a*; Jones *et al*. 2009). In contrast, drought causes tiller death, particularly older tillers, and reduces plant size. For both *B. ewartiana* and *C. fallax* these basal area changes with seasonal rainfall interacted with grazing. For *B. ewartiana*, basal area was further reduced by heavy grazing resulting from a reduction in both plant survival and size. For *C. fallax*, basal area changes were further reduced by moderate grazing and rotational spelling resulting from a reduction in plant survival but not plant size. The recovery of basal area after 2007 of *B. ewartiana* and *C. fallax* from existing plants highlights the importance of maintaining a residual population throughout drought to allow recovery to occur. Similarly, Fair *et al*. (2001) concluded that the continuing dominance of the long-lived North American grass *Bouteloua gracilis* was related to its ability to survive despite partial plant mortality.

In complete contrast to *B. ewartiana* and *C. fallax*, basal area recovery in the short-lived *Aristida* spp. and *P. effusum* resulted from increases in the size of newly recruited plants. For both *Aristida* spp. and *P. effusum*, plants recruited in 2003 and 2004 (during the drought) and again in 2008 and 2009 rapidly increased in size after 2007 resulting in large increases in basal area.

Plants of *B. ewartiana* and *C. fallax* reached maximum sizes of 160 and 80 cm^2/plant respectively, which are much larger than the 60 and 15 cm^2/plant in central Queensland (Jones *et al*. 2009). Similarly, *H. contortus* reached 120 cm^2/plant compared with 30–80 cm^2/plant in southern and central Queensland (Orr *et al*. 2004*a*, 2010*a*; Jones *et al*. 2009). The large variability in plant size of all five species resulting from the overriding influence of rainfall recorded in this study supports the suggestion (McIvor 2007; Lauenroth and Adler 2008) that age, especially for grasses, is a better predictor of survival than size.

It is noteworthy that despite 3 years of above-average summer rainfall up until 2010, plant size and basal area of both *B. ewartiana* and *C. fallax* had still failed to reach the levels achieved in 2001 after a similar 3-year period of above-average summer rainfall. Reasons for these differences are not readily apparent but perennial grass growth during these wet summers may possibly have been limited by available nitrogen. Winter rainfall in 2007, 2008 and 2009 was substantially above average, which stimulated the growth of cooler season C_3 dicotyledonous species. These plants possibly utilised soil nitrogen that would otherwise have been available for C_4 perennial grasses, such as *B. ewartiana* and *C. fallax*, following above-average summer rainfall. High summer rainfall in these later years may also have reduced soil nitrogen availability through leaching or through denitrification when soils were saturated, reducing the growth of grasses. Whatever the reason, the growth of these C_4 perennial grasses in these years was lower than might have been expected given favourable rainfall.

Seed banks

The very low germinable seed bank of perennial grasses recorded here is consistent with other studies of perennial grass seed banks in this area (McIvor and Gardener 1994; McIvor 2004). McIvor (2004) reported perennial grasses such as *B. ewartiana* and *C. fallax* were often dominant in the pasture but had few seeds present in the seed bank. Elsewhere in Queensland, soil seed banks of 130 seeds/m^2 have been reported for *B. ewartiana* (Jones *et al*. 2009) while that for *H. contortus* have been reported as high as 670 seeds/m^2 (Orr *et al*. 2004*c*).

Managing Aristida-Bothriochloa *pastures*

This study indicates that these *Aristida-Bothriochloa* pastures contain a range of perennial grass species with differing plant dynamics. The accelerated plant death of *B. ewartiana* with heavy grazing during prolonged drought reported here is consistent with the thesis that perennial grasses are at risk of local extinction through the co-occurrence of drought and heavy grazing (O'Connor 1995). These results emphasise the importance of grazing management, particularly the application of moderate pasture utilisation rates during drought (O'Connor 1995). The present data also provided supporting evidence for simulation studies of historical degradation episodes such as that in north-east Queensland during the 1980s, which occurred 'in response to heavy utilisation and variable rainfall' (McKeon *et al*. 2004).

Although the 2003–07 drought in our study was not a 'major degradation event', our study recorded an overall decline in *B. ewartiana* even at moderate stocking rate with little subsequent recovery even after two periods of above-average rainfall. This finding does not support the McKeon *et al*. (2004) conclusion that these 'vegetation changes appear reversible'. Our results also contrast sharply with other results for a similar land type showing rapid recovery of perennial grasses even in dry years with light utilisation (Ash *et al*. 2011). Nevertheless, data from a range of other studies (O'Connor 1991) indicate that recovery in perennial grass communities can often take 5–10 years to occur after a degradation event. Recovery of *B. ewartiana* probably requires an increase in plant density; possibly through a germinable soil seed bank with subsequent recruitment (Jones *et al*. 2009). However, no such recruitment was recorded during the 12 years of our study.

Factors leading to the recruitment of long-lived species such as *B. ewartiana* are not apparent although Orr (1998) reported an exceptional recruitment event of 30 seedlings/m^2 during an 11-year study in *Astrebla* grassland. This single recruitment event provided the majority of the *Astrebla* spp. plants for the next 20 years (D. M. Orr, unpubl. data). The failure of seedling recruitment to maintain *B. ewartiana* density in the present study, together with the fact that the original plants still contributed 88% of total basal area in 2010, indicates a need to study seed production (Orr *et al*. 2004*c*) and seedling recruitment of *B. ewartiana* in this environment. This lack of recovery further emphasises the critical importance of maintaining the existing population of perennial grass tussocks through good grazing management. Given the productivity and reliability of perennial grasses like *B. ewartiana*, any loss of these tussocks will inevitably reduce long-term forage production and obviously reduce productivity and profitability.

The failure of this study to demonstrate any impact of wet season spelling on survival, recruitment or basal area of any species is surprising considering the accepted importance of spelling in grazing management (Scanlan and McIvor 2010). One possible reason is that the detrimental effects of the increased grazing pressure that occurred in the remainder of the paddock while one section was spelled outweighed the beneficial effects of the spelling *per se* (Scanlan *et al*. 2011). This is likely to have occurred in this study given the slightly higher stocking rate initially applied to the spelling treatment, the run of dry years encountered and the problems resulting from the ill-timed fire in November 2001. Whatever the reason, the present results do not support the contention Ash *et al*. (2011) that wet season spelling may allow modest increases in stocking rates without adverse effects on pasture condition.

This study highlights substantial differences in the dynamics of *H. contortus* compared with central and southern Queensland. One probable reason for these differences is the relative length and severity of the dry season at Wambiana (Orr *et al*. 2004*a*, 2010*a*; Jones *et al*. 2009). At more southern sites, the dry season is less pronounced with annual rainfall more evenly distributed probably providing more favourable conditions for *H. contortus* growth than at Wambiana. These considerations further highlight the importance of managing stocking rates for rainfall variability in the harsher, more variable environment of north Queensland.

The accelerated decline in *B. ewartiana* density reported here with drought, especially with heavy stocking, adds further support to two overall conclusions emerging from this grazing study (O'Reagain and Bushell 2008; O'Reagain *et al*. 2009, 2011). First, moderate stocking at or near the long-term carrying capacity to manage for climate variability gave good individual animal performance and was both sustainable and profitable despite an extended sequence of below-average rainfall years. Second, high stocking rates are neither sustainable nor profitable in a variable climate and inevitably lead to a decline in pasture productivity and composition.

Conclusion

This study provides important quantitative data on the dynamics of a range of short- and long-lived perennial grasses in an *Aristida-Bothriochloa* pasture in northern Australia. This study highlights rainfall variability as having a major impact on the dynamics of all five perennial grass species with this effect being greatest on plant survival and size and with this effect being most evident on the shorter-lived species *Aristida* spp., *P. effusum* and *H. contortus*. The impact of grazing was greatest on the long-lived *B. ewartiana* and *C. fallax* and this effect of grazing was accentuated by drought.

Acknowledgements

We are grateful to the Lyons family of 'Wambiana' for their continuing interest and support in the conduct of this grazing study. This study was established via funding from the Australian Government's Drought Regional Initiative. Further funding support has been provided by Meat and Livestock Australia, the Natural Heritage Trust, the Great Barrier Reef Marine Park Authority and the CRC for Tropical Savanna Management. We thank Ms Christina Playford who provided statistical advice and Ms Madonna Hoffman who prepared the figures.

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Manuscript received 23 November 2010; accepted 18 May 2011