

Demography of three perennial grasses in a central Queensland eucalypt woodland

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Abstract. The population dynamics of the palatable, perennial grasses *Bothriochloa ewartiana* (Domin) C.E.Hubb. (desert Mitchell grass), *Chrysopogon fallax* S.T.Blake (golden beard grass) and *Heteropogon contortus* (L.) P.Beauv. ex Roem. & Schult. (black speargrass), were studied in an extensive grazing study conducted in a eucalypt woodland within the *Aristida–Bothriochloa* pasture community in central Queensland between 1994 and 2000. Treatments were three grazing pressures based on light, medium and heavy utilisation of forage available at the end of summer and two timber treatments (trees intact and trees killed). Seasonal rainfall throughout this study was generally favourable for plant growth with no severe drought periods. Grazing pressure had a greater overall impact on plant dynamics than timber treatment, which had minimal impact. Grazing pressure had a large impact on *H. contortus* dynamics, an intermediate impact on *B. ewartiana* and no impact on *C. fallax*. Fluctuations in plant density of both *B. ewartiana* and *C. fallax* were small because both species were long lived with low levels of seedling recruitment and plant death, whereas fluctuations in *H. contortus* density were relatively high because of its relatively short life span and higher levels of both recruitment and death. Heavy grazing pressure increased the recruitment of *B. ewartiana* and *H. contortus* in some years but had no impact on that of *C. fallax*. Heavy grazing pressure reduced the survival of the original plants of both *B. ewartiana* and *H. contortus* but not of *C. fallax*. For *H. contortus*, the size of the original plants was larger where trees were killed than where trees were left intact and plants of the 1995 seedling cohort were larger in 1998 at heavy compared with those at light and medium grazing pressure. Grazing had a minor negative impact on the soil seed bank of *H. contortus*. Populations of all three species remained stable throughout this study, although the favourable seasonal rainfall experienced and the short duration of this study relative to the life span of these species may have masked longer term, deleterious impacts of heavy grazing pressure.

Additional keywords: *Bothriochloa ewartiana*, *Chrysopogon fallax*, *Heteropogon contortus*, plant, seedling recruitment.

Introduction

The extensive pastoral industries of Australia rely on native perennial grasses that provide much of the forage for grazing animals, particularly during the dry season. In recent years there has been increased interest in the sustainability of native pasture communities, with research focused on the dynamics of those perennial grasses which dominate these pasture communities. The dynamics of some important perennial grasses have been described by Orr (1998), Orr *et al.* (2004a, 2010), Hodgkinson and Muller (2005), Orr and O'Reagain (2005, 2008) and McIvor (2007).

Pasture communities in Qld have been classified into 14 different communities based on soil type and herbaceous vegetation structure (Weston *et al.* 1981), and these 14 communities form part of 27 pasture communities across northern Australia (Tohill and Gillies 1992). In Qld, the *Aristida–Bothriochloa* pasture community occupies 33.5 million ha and is a composite of eight more localised pasture types which occur as *Eucalyptus* spp. woodlands on generally non-

agricultural soils where both *Aristida* spp. (wiregrasses) and *Bothriochloa* spp. (bluegrasses) are common. Detailed floristic descriptions and dynamics of this *Aristida–Bothriochloa* community are lacking and are generally limited to lists of commonly occurring species (Tohill and Gillies 1992). Walker (1997) identified a need to develop sustainable grazing management strategies for this community.

This paper reports the dynamics of three perennial grass species in response to grazing utilisation and timber management treatments in an extensive grazing study conducted in a central Qld *Aristida–Bothriochloa* pasture community between 1994 and 2000 (Silcock *et al.* 2005). Results are discussed in terms of sustainable grazing management.

Materials and methods

Grazing study

A grazing study was established in 1994 in a *Eucalyptus melanophloia* F.Muell. (silver-leaved ironbark) dominant, open woodland community at Keilembete (23°22'30" S, 147°35'15" E),

60 km west north-west of Emerald, central Qld (Fig. 1). Mean annual rainfall for Anakie (20 km south-east) is 652 mm with 75% occurring between October and March. (Monthly rainfall at Keilembete during this study was compared with the long-term monthly means for Anakie). The highest mean daily maximum temperature is 34.5°C in December and the lowest mean daily minimum temperature is 7.6°C in July. Frosts occur between June and August.

The grazing study was located in the Peak Vale land system which is described as undulating country with *E. melanophloia* woodland on texture contrast soils on granite exposed below the Tertiary weathered zone (Gunn *et al.* 1967). The soil was uniform across the site and is described as a red duplex (Dr2.12) (Northcote *et al.* 1975). The Peak Vale land system covers 185 000 ha in central Qld (between Rubyvale and Clermont) and is also described as Regional Ecosystem 11.12.2 (Sattler and Williams 1999). At the start of this study in 1994, the pasture was in good condition because of the dominance of *Bothriochloa ewartiana* (Domin) C.E.Hubb. (desert Mitchell grass) and both *Chrysopogon fallax* S.T.Blake. (golden beard grass) and *Heteropogon contortus* (L.) P.Beauv. ex Roem. & Schult. (black spargrass) were major contributors to total pasture yield.

Treatments

The experimental design was a randomised block design with three grazing pressures and two timber treatments each with two replicates. Year long grazing pressures were either light (25%),

medium (50%), or heavy (75%) utilisation of pasture available each autumn. The aim of these treatments was for cattle to consume these proportions of the pasture available each autumn over the following 12 month period. In November 1994, a group of weaner steers commenced grazing and these animals were replaced every 12 months in autumn when stocking rates were varied for each paddock to consume the desired proportion of available pasture over the next 12 months. Timber treatments were either trees left intact (treed) or trees killed in March 1994 by stem injection with Velpar (DuPont, Sydney, NSW), except along water courses. Paddock sizes were 21.5, 11 and 7 ha in the trees intact and 11, 5.5 and 3.5 ha in the trees killed for the light, medium and heavy utilisations and treatments, respectively.

Population dynamics

Population dynamics of the perennial grasses, *B. ewartiana*, *C. fallax* and *H. contortus* were monitored in 15 permanently marked quadrats, each 1 × 1 m, in each treatment. Initially, ~50 plants of each species were identified and located within these 15 quadrats which were located in three nests of five quadrats each which were distributed across each paddock. Quadrat locations were selected in midslope positions with soil and vegetation structure representative of the paddock.

The location and diameter of all individual *B. ewartiana*, *C. fallax* and *H. contortus* tussocks in each quadrat was charted in autumn 1994. Where plants were not circular, the width was

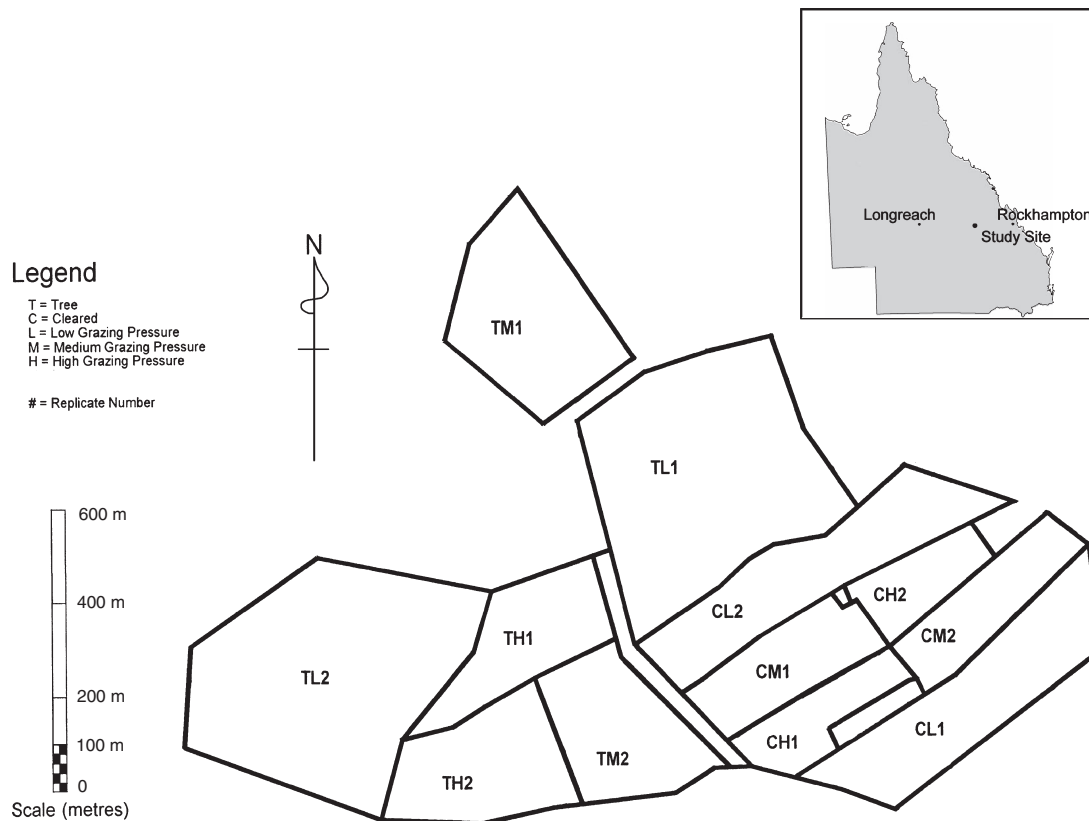


Fig. 1. Location of study site in Queensland, and layout of grazing paddocks for the Keilembete grazing study.

measured first along the widest diameter and second along the diameter perpendicular to the first diameter. Subsequently, each autumn between 1995 and 2000, further recordings were made of the survival and size of these initial plants together with any new plants that had been recruited during the previous year. Individual plant size for each species was calculated as the area occupied by each plant (including all segments making up that plant) by assuming plants were circular (Orr *et al.* 2004a).

Plant turnover was calculated as $1 - (\text{the fraction of the population not turning over during the period of study}) \times 100$ (O'Connor 1994). The fraction not turning over was the number of individual plants present in 1994 and still present in 2000. The estimated life spans for the original plants were calculated based on the survival of these original plants between 1994 and 2000 (Sarukhan and Harper 1973), and plant survival was analysed using a proportional hazards survival model (Cox 1972).

Soil seed banks

Germinable soil seed bank was measured annually between 1994 and 2000 by germinating seed contained in soil samples collected adjacent to the permanent quadrats. In spring each year, four cores, each 5.3 cm diameter and 5 cm deep were bulked to produce a sample with a total of 12 samples per treatment replicate. Samples were stored in a dark, dry location. In the following summer each year, samples were sieved (to remove stones) and then spread as a 2 cm layer on compacted sand in 15 cm diameter, drained pots. Pots were watered by overhead sprinkler for 12 weeks and germinated seeds were identified, counted and removed (Orr *et al.* 1996).

Statistical analysis

All analysis was completed in GENSTAT (VSN International, Hemel Hempstead, UK). Each measurement, within a sampling date, was analysed using ANOVA. Statistical differences were determined at the $P > 0.05$ level. Plant survival was analysed using a proportional hazards model (Cox 1972).

Results

Rainfall

Rainfall during the 2 years before the commencement of this study (1992–93) was extremely low as indicated by rainfall received at nearby Anakie (Fig. 2). Summer (January–March) rainfall was well above the long-term mean in 1995 and 1997 but below this mean in 1994, 1996 and 1998. Winter (July–September) rainfall was greatly above the long-term mean in 1998 but well below this mean in all other years. Rainfall for the period July 1996 to June 1997 was very high (decile 9). There were no severe drought periods where growing season rainfall was below the mean for extended periods.

Treatment interactions

Examination of the statistical analyses indicated few significant ($P < 0.05$) grazing pressure \times timber management interactions. Grazing pressure had the predominant influence on plant dynamics of all three species while the effects of timber management were few, accordingly, results presented here concentrate on the main effects of grazing pressure.

Plant turnover

Over the 7 years of this study, a total of 2097, 1502 and 5254 plants of *B. ewartiana*, *C. fallax* and *H. contortus*, respectively, were encountered: 829, 950 and 817 original plants and 1268, 552 and 4437 seedlings, respectively, recorded between 1995 and 2000. Turnover for *B. ewartiana* was higher ($P < 0.05$) at heavy than at light and medium grazing pressure (Table 1). There were no differences ($P > 0.05$) in plant turnover with grazing pressure for either *C. fallax* or *H. contortus* and there were also no differences ($P > 0.05$) for any of the three species due to timber management.

Density

Between 1994 and 2000, the density of *B. ewartiana* increased slightly from 4 to 5 plants/m² and *C. fallax* remained relatively constant at 5 plants/m² with no differences ($P > 0.05$) between

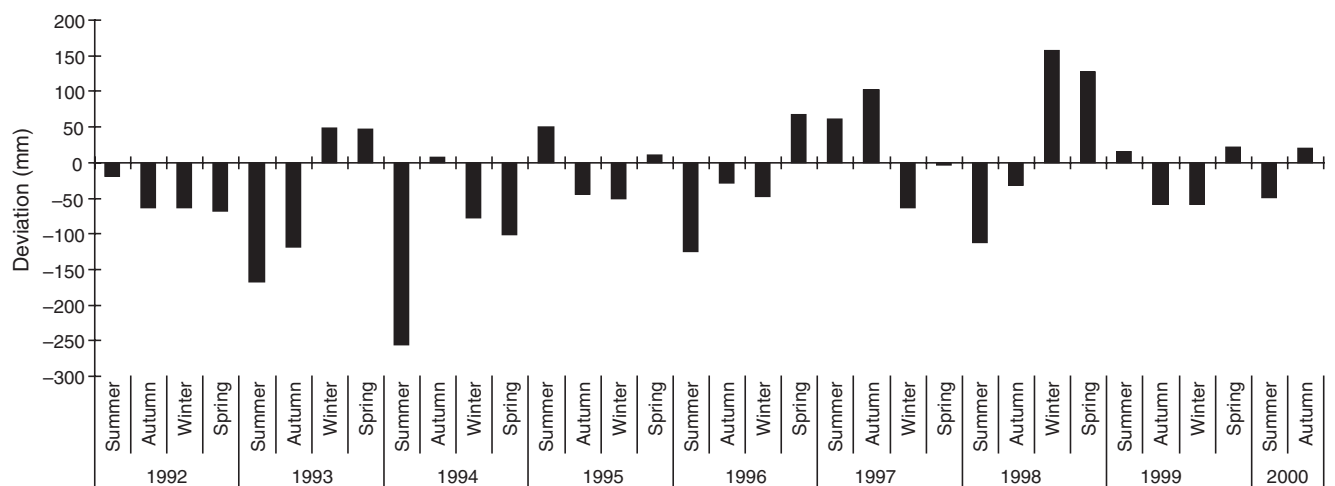


Fig. 2. Deviation (mm) of seasonal rainfall at Keilembete from long-term mean seasonal rainfall at Anakie between 1992 and 2001. (Data for 1992–93 from Rainman historical records.)

either species due to grazing or timber treatments (Fig. 3a, b). In contrast, the density of *H. contortus* fluctuated markedly between 5 and 18 plants/m² and was higher ($P < 0.05$) under heavy than

medium and light grazing pressure in 2000 (Fig. 3c). *H. contortus* density in 2000 was also higher ($P < 0.05$) in tree killed (14.6 plants/m²) than in the treed (10.4 plants/m²) treatment.

Table 1. Plant turnover^A of plant numbers for *Bothriochloa ewartiana*, *Chrysopogon fallax* and *Heteropogon contortus* between 1994 and 2000 in relation to grazing pressure and timber management in central Qld
 Within parameters, values followed by the same letters are not significantly different ($P > 0.05$)

Variable	Treatment	<i>Bothriochloa ewartiana</i>	<i>Chrysopogon fallax</i>	<i>Heteropogon contortus</i>
Grazing pressure	Light	24.7a	30.7	55.4
	Medium	31.1a	38.3	71.1
	Heavy	47.4b	30.6	74.7
Timber management	Timbered	34.2	33.1	70.6
	Cleared	34.5	33.3	63.5

^APlant turnover for plant number was calculated as $1 - (\text{the fraction of the population not turning over during the period of the study}) \times 100$ (after O'Connor 1994). The fraction not turning over was the number of individual plants present in 1994 and still present in 2000.

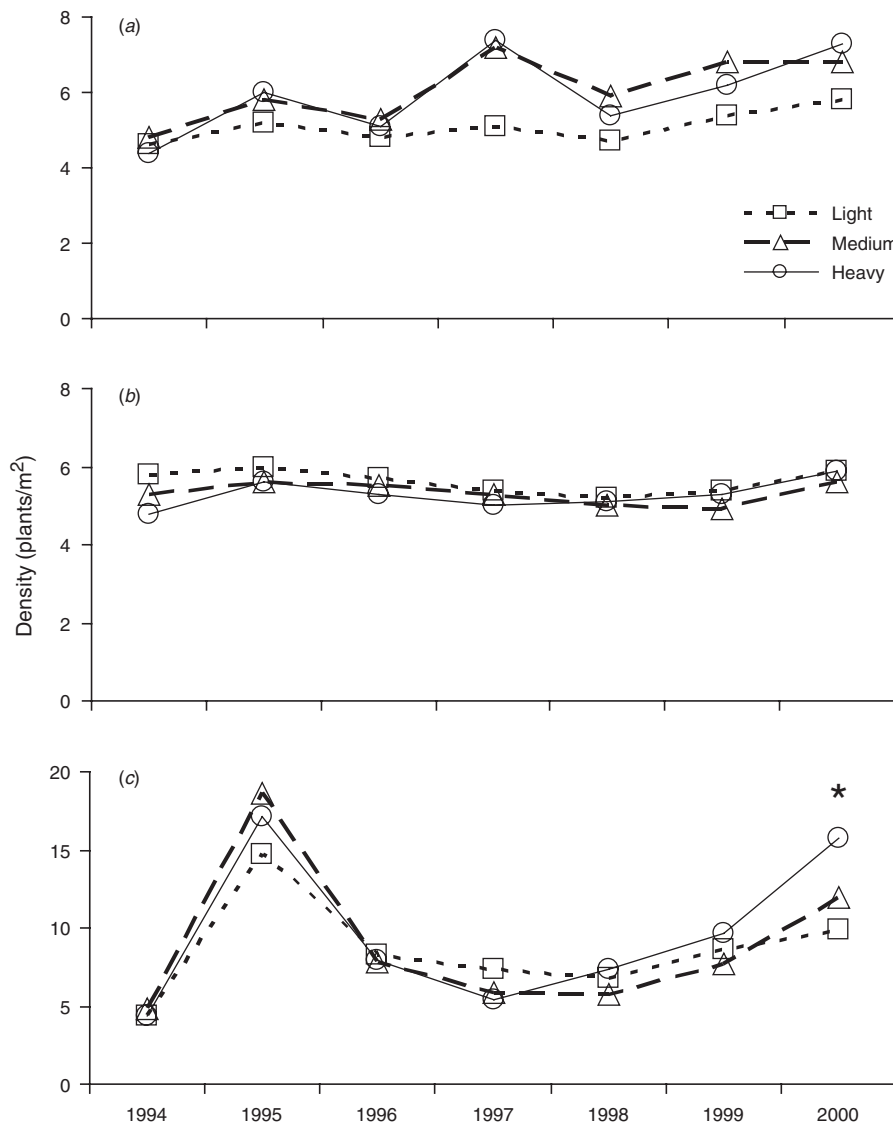


Fig. 3. Changes in the density in autumn of (a) *Bothriochloa ewartiana*, (b) *Chrysopogon fallax*, and (c) *Heteropogon contortus* in relation to three grazing pressure treatments between 1994 and 2000. Within years, significant differences between treatments are indicated: * $P < 0.05$.

Recruitment

Recruitment of all three species varied among years. Recruitment of both *B. ewartiana* and *C. fallax* was consistently low across all years with fewer than 3.5 and 1.5 seedling/m², respectively (Fig. 4). Recruitment of *B. ewartiana* was higher ($P < 0.05$) at heavy than at light grazing pressure in both 1995 and 1997 (Fig. 4a), and was also higher ($P < 0.05$) in the trees killed (2.2 seedling/m²) than in the tree (1.1 seedling/m²) treatment in 1995. Recruitment of *H. contortus* varied widely between 15 seedlings/m² at medium grazing pressure in 1995 and 0.5 seedlings/m² in 1996 and was higher ($P < 0.05$) at heavy than at light grazing pressure in both 1998 and 2000 (Fig. 4c).

Survival

The survival of all cohorts of all three species was reduced ($P < 0.05$) with time. Survival of the 1994 *B. ewartiana* and of *H. contortus* plants was reduced more ($P < 0.05$) at heavy than at light and medium grazing pressure, and the survival of the original *C. fallax* plants was unaffected ($P > 0.05$) by grazing treatment (Fig. 5a–c). Estimated life spans for the original

B. ewartiana plants were 25, 20 and 13 years and for *H. contortus* plants were 12, 9 and 8 years for the light, medium and heavy grazing treatments, respectively. The mean estimated life span for *C. fallax* across all treatments was 20 years.

Survival of the 1995 *B. ewartiana* cohort was reduced more ($P < 0.05$) by heavy than light and medium grazing pressure (Fig. 5d) although survival of *C. fallax* and *H. contortus* cohorts remained unaffected by grazing pressure (Fig. 5e, f). Grazing pressure failed to influence the survival of the 1997 cohort for any of the three species (Fig. 5g–i). Survival of all cohorts of all three species was unaffected by timber treatment (data not shown).

Plant size

The size of the original 1994 plants was small, consistent with below average rainfall in 1992 and 1993 (Fig. 2). Between 1994 and 2000, these original plants of both *B. ewartiana* and of *H. contortus* substantially increased in size but that of *C. fallax* changed little and there was no ($P > 0.05$) impact of grazing pressure (Fig. 6a). Between 1998 and 2000 the original plants

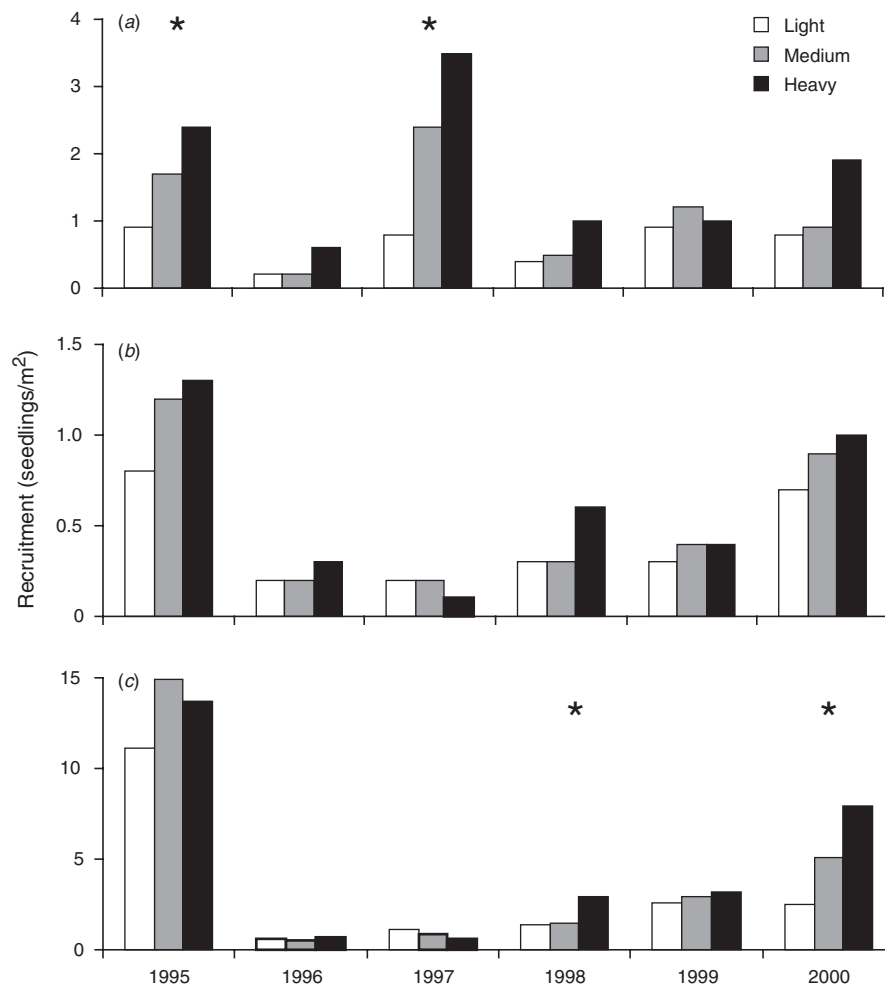


Fig. 4. Changes in seedling recruitment in autumn of (a) *Bothriochloa ewartiana*, (b) *Chrysopogon fallax*, and (c) *Heteropogon contortus* in relation to three grazing pressure treatments between 1994 and 2000. Within years, significant differences between treatments are indicated: * $P < 0.05$.

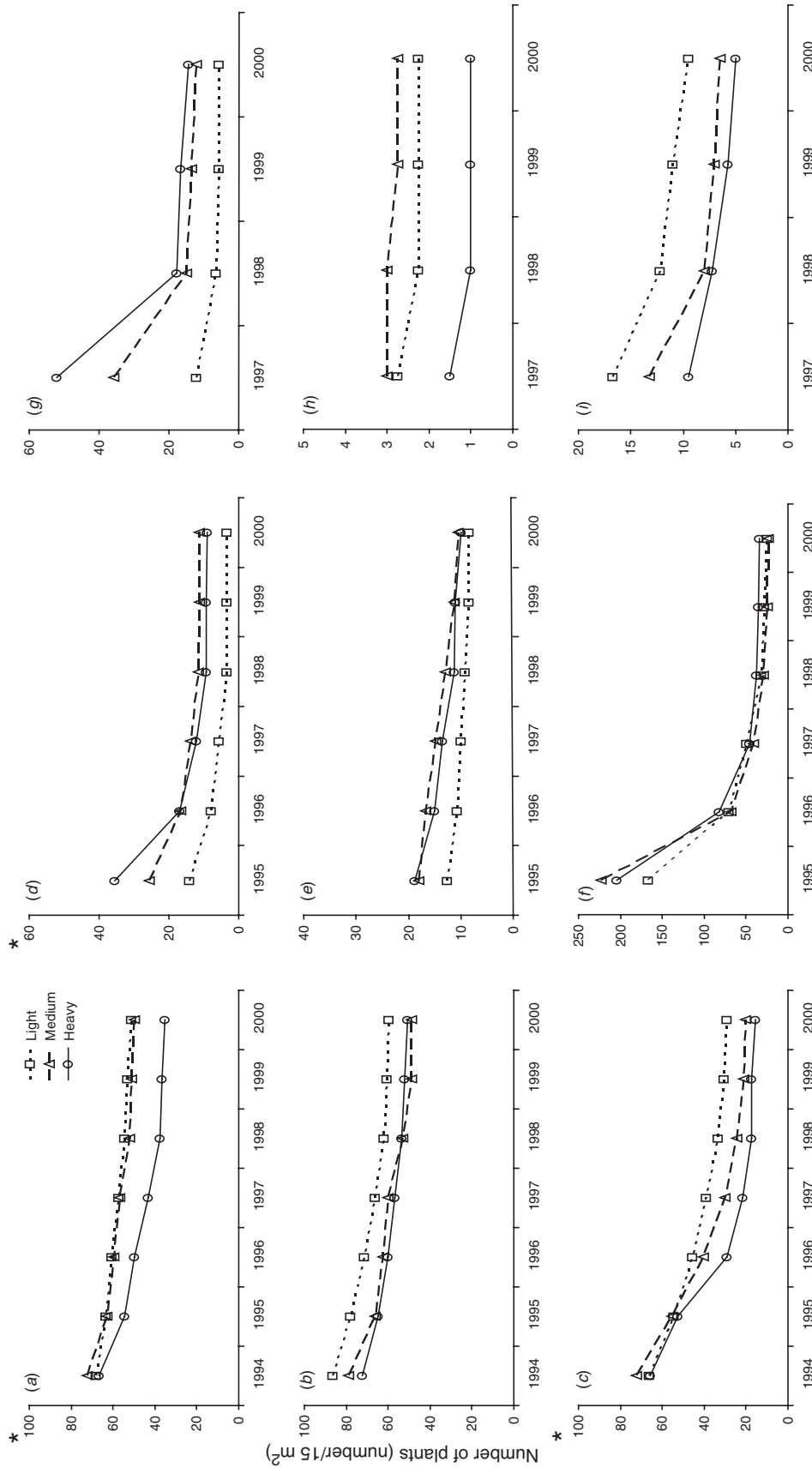


Fig. 5. Changes in the survival of the original plants of (a) *Bothriochloa ewartiana*, (b) *Chrysopogon fallax*, (c) *Heteropogon contortus*, of the 1995 cohorts of (d) *B. ewartiana*, (e) *C. fallax*, (f) *H. contortus* and of the 1997 cohorts of (g) *B. ewartiana*, (h) *C. fallax*, and (i) *H. contortus* in relation to three grazing pressure treatments between 1994 and 2000. Significant differences between treatments for a given species are indicated: * $P < 0.05$.

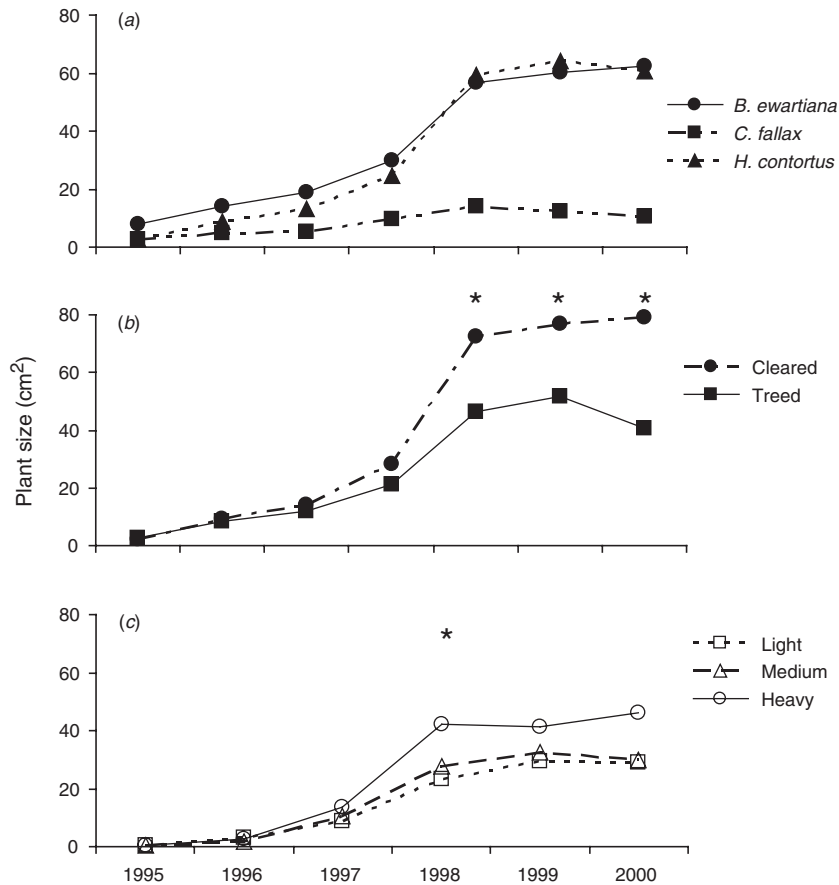


Fig. 6. Changes in the plant size of (a) original *Bothriochloa ewartiana*, *Chrysopogon fallax* and *Heteropogon contortus* (meaned across three grazing pressure treatments), (b) original *H. contortus* in relation to timber treatment, and (c) the 1995 cohort of *H. contortus* in relation to three grazing pressure treatments between 1994 and 2000. Within years, significant differences between treatments are indicated: * $P < 0.05$.

of *H. contortus* were larger ($P < 0.05$) in the cleared than the treed treatment (Fig. 6b). For the 1995 cohort of *H. contortus*, plants were larger ($P > 0.05$) in 1998 at heavy than the other two grazing pressures (Fig. 6c).

Seed banks

Seed banks of all three species displayed large variation among years (Fig. 7). Seed banks of both *B. ewartiana* and *C. fallax* were consistently low with fewer than 130 and 30 seeds/m², respectively, in any year with no ($P > 0.05$) differences between grazing pressures (Fig. 7a, b). The seed bank of *B. ewartiana* was higher in the trees killed (22.8 seeds/m²) than the treed treatment (9.5 seeds/m²) in 2000. The seed banks of *H. contortus* reached 350 seeds/m² during 1999 but < 50 seeds/m² in other years in the same treatments (Fig. 7c). There were few treatment differences although the seed bank at light grazing pressure was higher ($P < 0.05$) than at heavy grazing pressure in 1996.

Discussion

This study indicates that *B. ewartiana* and *C. fallax* are both long lived species with relatively small fluctuations in plant

density because of low levels of recruitment and death in most years. In contrast, *H. contortus* is a short lived species with relatively large fluctuations in plant density because, relative to the other two species, it has large annual variation in both recruitment and death. The overall impact of grazing pressure was greater than that of timber management, and this result is consistent with other pasture productivity data from this study (Silcock *et al.* 2005). The impact of grazing pressure on perennial grass dynamics was greatest on *H. contortus*, intermediate on *B. ewartiana* and least on *C. fallax*. The overall small impact of timber clearing on plant productivity in this study contrasts with other data indicating large impacts of timber clearing on pasture productivity in *Eucalyptus* spp. communities in Qld (Scanlan and Burrows 1990; McIvor 2007).

Local best practice in the area around Keilembete is that this woodland community should not be cleared because (i) subsequent regrowth can be a major problem, and (ii) there is no benefit to stocking rates (Clark *et al.* 1992). Seasonal rainfall throughout this study was favourable for perennial grass growth and there were increases in plant density and plant size. This favourable seasonal rainfall pattern contrasts with that during other perennial grass population studies (Orr 1998;

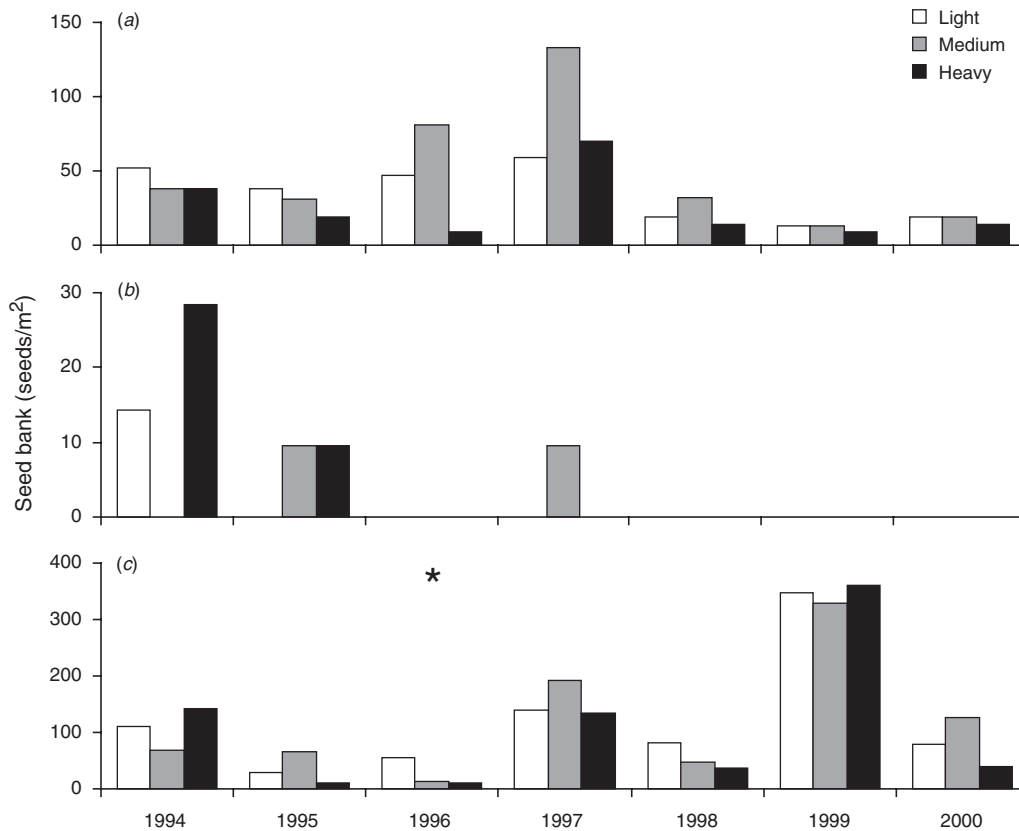


Fig. 7. Changes in the germinable soil seed banks of (a) *Bothriochloa ewartiana*, (b) *Chrysopogon fallax*, and (c) *Heteropogon contortus* in relation to three grazing pressure treatments between 1994 and 2000. Within years, significant differences between treatments are indicated: * $P < 0.05$.

Orr *et al.* 2004a; Hodgkinson and Muller 2005; Orr and O'Reagain 2005, 2008; McIvor 2007) where drought had a large impact on grass dynamics.

Plant turnover

Heavy grazing pressure increased plant turnover for *B. ewartiana* but not for *C. fallax* or *H. contortus*. Comparing turnover times at Keilembete with those for other grazing studies is difficult because of the different durations of other grazing studies and also differences in seasonal rainfall during those studies. However, plant turnovers of 34 and 33% at Keilembete for *B. ewartiana* and *C. fallax* are lower than the 44 and 55% measured for these two species over a similar time span (1998–2004) at Wambiana, Charters Towers, where no impact of grazing pressure was detected (D. M. Orr, unpubl. data). Mean turnover for *H. contortus* in the present study was 67% years over 6 years compared with 98% over a similar time span (1998–2004) at Wambiana (DM Orr, unpubl. data), 72% over 6 years (1990–96) at Glenwood in southern Qld (Orr *et al.* 2004a) and 95% for 13 years (1988–2001) at Galloway Plains in central Qld (Orr *et al.* 2010).

Density

Density of *B. ewartiana* and *C. fallax* remained relatively constant throughout this study as a result of both low seedling

recruitment and low mature death rates, in contrast with *H. contortus* which recorded relatively high fluctuations due to higher rates of both seedling recruitment and mature plant death. Little comparative plant density data are available for either *B. ewartiana* or *C. fallax* although the densities recorded for these two species in this study are similar to the 4–8 and 2–5 plants/m² for these two species at Wambiana, Charters Towers (D. M. Orr, unpubl. data). For *H. contortus*, plant densities of 5–15 plants/m² with relatively large fluctuation recorded here are similar to the 10–25 plants/m² recorded at Glenwood (Orr *et al.* 2004a) and 5–20 plants/m² recorded at Galloway Plains (Orr *et al.* 2010).

Recruitment

Large variation in recruitment of all three species was apparent among years and reflects variation in the size of the soil seed bank at the start of each summer together with rainfall during that summer. The overall recruitment of *B. ewartiana* and *C. fallax* was low at 0–3.5 and 0–1.5 seedling/m², respectively, and these data are consistent with other results (McIvor 2007) indicating similar low colonisation rates for both species in most years near Charters Towers. Large variation in recruitment of *H. contortus* of 0 to 15 seedling/m² is consistent with similar variable recruitment, although the levels of 0–12 seedling/m² at Glenwood (Orr *et al.* 2004a) and 0–20 seedling/m² at Galloway

Plains (Orr *et al.* 2010) were generally higher than that at Keilembete. The exception was the recruitment in 1995–96 where there had been generally favourable rainfall at Keilembete compared with below average rainfall at both Glenwood and Galloway Plains. McIvor (2007) reported intermediate colonisation rates of 0.5–4 seedling/m² for *H. contortus* at Hillgrove and Cardigan, Charters Towers. The consistently high recruitment of both *B. ewartiana* and *H. contortus* recorded at heavy grazing was consistent with similar initial findings for *H. contortus* in southern Africa (O'Connor 1994), at Glenwood (Orr *et al.* 2004a) and at Galloway Plains (Orr *et al.* 2010). In these three studies, this initial higher recruitment occurred because of reduced competition on developing seedlings from existing plants under heavy grazing although this situation in all three studies was reversed with time as this heavy grazing reduced seed production. However, such reduction in recruitment was not measured at Keilembete: this difference probably reflecting the reduced grazing pressure in all treatments in summer 1999 (as a result of poor 1998 summer rainfall) together with favourable spring 1998 rainfall. This situation at Keilembete contrasts with the drought and consistent stocking rates at the other three studies. The higher recruitment of *H. contortus* in 2000 under heavy grazing was associated with no differences in the size of the soil seed bank in spring 1999 although there was a large increase in the overall size of the soil seed bank in spring 1999.

Seed banks

Soil seed banks in this study were not consistently affected by grazing pressure in contrast with other studies indicating that increasing grazing pressure reduces soil seed banks of *H. contortus* (Orr *et al.* 2010). This failure of grazing pressure to reduce soil seed banks probably reflects the generally favourable rainfall, the short time frame of this study (relative to long lived *B. ewartiana* and *C. fallax*) and the fact that these pastures were in good condition at the start of this study. No data are available on the size of soil seed banks for *B. ewartiana* although soil seed banks of the closely related *Bothriochloa bladhii* at Galloway Plains varied among years between 5–150 seeds/m² (D. M. Orr, unpubl. data). Seed banks of *H. contortus* ranging between 10–350 seeds/m² in the present study were generally lower than the 40–670 seeds/m² at Glenwood (Orr *et al.* 2004a) and 0–500 seeds/m² at Galloway Plains (Orr *et al.* 2010) despite the generally favourable rainfall during the present study.

The soil seed bank of *C. fallax* reported here is probably an artefact of the sampling process, since some soil cores contained rhizomatous fragments which resulted in 'seedling' plants. McIvor and Gardener (1994) recorded no viable seed of *C. fallax* in 20 native pasture communities near Collinsville while no germinable seed of *C. fallax* was recorded over 6 and 12 years of soil seed bank sampling at Glenwood and Galloway Plains, respectively (D. M. Orr, unpubl. data). Silcock (1999) grew *C. fallax* plants from both seed and detached rhizomes and concluded that the absence of true seedling recruitment seems due to small soil seed banks together with slow seedling emergence resulting from slow elongation of the coleoptile.

Survival

Heavy grazing reduced the survival of both *B. ewartiana* and *H. contortus* consistent with similar reductions with heavy

grazing for *B. ewartiana* at Wambiana (Orr and O'Reagain 2008) and *H. contortus* at Galloway Plains (Orr *et al.* 2010). Survival of *C. fallax* was not influenced by grazing in this study although its survival was increased with heavy grazing at Wambiana (Orr and O'Reagain 2008) between 1998 and 2007 (compared with 6 years at Keilembete) which included prolonged drought. Survival of all three species at Keilembete showed a regular pattern of death over time, contrasting with the accelerated death of *H. contortus* plants due to drought at Glenwood during 1990–92 (Orr *et al.* 2004a) and 1993–94 at Galloway Plains (Orr *et al.* 2010). Similarly, accelerated death of *B. ewartiana* plants at Wambiana due to drought during 2002–04 was reported by Orr and O'Reagain (2008).

Estimated life spans for the original *B. ewartiana* plants varied from 13 to 25 years depending on grazing pressure while that for *C. fallax* plants was 20 years irrespective of grazing treatment. Little other data are available on the life spans of these two species although data from Wambiana for a similar time period (1998–2004) indicates life spans of 15 years for both (D. M. Orr, unpubl. data). Elsewhere in northern Qld, McIvor (2007) suggested that *C. fallax* was long lived (more than 50% survival after 4 years), *B. ewartiana* had intermediate survival (10–50% survival after 4 years) but *H. contortus* was short lived (less than 10% survival after 4 years).

Estimated life spans for the original *H. contortus* in this study varied from 8 to 12 years depending on grazing pressure. Such life spans are shorter than those at Galloway Plains where some original plants survived throughout that study from 1988 to 2001 (Orr *et al.* 2010). Orr *et al.* (2004b) suggested that *H. contortus* life spans were higher in southern compared with northern Qld because of the increased severity of the dry season in the north.

Plant size

Plants of both *B. ewartiana* and *H. contortus* rapidly increased in size, particularly during 1997–98, with the generally favourable rainfall throughout this study although *C. fallax* failed to increase in size. The ability of *H. contortus* to increase plant size through tillering (Orr *et al.* 2004a, 2010) is an important factor in the persistence of this species just as it is also for other perennial C₄ grasses such as *Astrebla* spp. (Mitchell grass) (Orr 1998). The similar large increase in plant size of *B. ewartiana* attests to its capacity to produce new tillers when seasonal conditions are favourable. The size of the 1995 *H. contortus* cohort was higher at heavy compared with light and medium grazing pressure and this finding is consistent with other studies of *H. contortus* plant size (Orr and Paton 1997; Orr *et al.* 2004a, 2010). Orr and Paton (1997) suggested that early defoliation of seedling plants, as occurs with heavy grazing, promotes tillering that leads to increased size relative to those plants which are lightly defoliated as occurs with light grazing pressure.

At the Keilembete site in 1994, the original *B. ewartiana* plant size was only 8 cm²/plant and this was probably due to drought immediately before the start of this study. Despite this, these plants increased in size throughout the study to be 60 cm²/plant in 2000. This maximum plant size for *B. ewartiana* at Keilembete was much smaller than the maximum of 160 cm²/plant at Wambiana (Orr and O'Reagain 2005) although size at

Keilembete remained unaffected by drought in contrast with drought at Wambiana during 2002–03 which reduced plant size from 160 cm²/plant to only 25 cm²/plant. Maximum plant size for *H. contortus* in the present study was 80 cm²/plant for the original plants in the intact trees treatment which is within the range 20 to 115 cm²/plant indicated for this species at Cardigan, Charters Towers (Northup *et al.* 1999). Further south, plant size was usually smaller with maximum sizes of 40 cm²/plant at Galloway Plains (Orr *et al.* 2010) and 30 cm²/plant at Glenwood (Orr *et al.* 2004a). For *C. fallax*, Northup *et al.* (1999) reported sizes up to 440 cm²/plant, although such tussocks usually contained standing dead stems and litter.

Conclusions

This *Aristida–Bothriochloa* pasture community contains a mixture of both long and short lived perennial grasses with different plant dynamics. The impact of grazing pressure was greatest on *H. contortus* because grazing pressure influenced both recruitment and original plant survival whereas increased grazing pressure reduced the survival of original *B. ewartiana* plants. *C. fallax* remained unaffected by grazing pressure. Killing trees had only a minor impact on plant dynamics. Relatively stable populations of these three perennial grasses during this study may mask longer term, deleterious impacts of persistent heavy grazing pressure because there was no severe drought experienced and because of the short duration of this study relative to the long life span of these perennial grasses.

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