CSIRO PUBLISHING
www.publish.csiro.au/journals/cp Crop & Pasture Science, 2010, 61, 255–267

Impacts of grazing management options on pasture and animal productivity in a *Heteropogon contortus* (black speargrass) pasture in central Queensland. 2. Population dynamics of *Heteropogon contortus* and *Stylosanthes scabra* cv. Seca

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Abstract. The dynamics of *Heteropogon contortus* and *Stylosanthes scabra* cv. Seca populations were studied in a subset of treatments in an extensive grazing study conducted in central Queensland between 1988 and 2001. These treatments were 4 stocking rates in native pasture and 2 of these stocking rates in legume oversown and supplement/spring burning treatments. For the 1999–2000 summer, population data for *H. contortus* in 5 of these native pasture and supplement/burning treatments were compared with those for an additional burnt treatment. Seasonal rainfall throughout this study was below the long-term mean and mean annual pasture utilisation ranged from 24 to 61%. Increasing stocking rate from 5 to 2 ha/steer in native pasture reduced *H. contortus* plant density. Increasing stocking rate reduced seedling recruitment as a result of its effect on soil seedbanks. Seedling recruitment was the major determinant of change in plant density, although some individual *H. contortus* plants did survive throughout the study. Burning in spring 1999, particularly at light stocking rate, promoted seedling recruitment above that in both unburnt native and legume oversown pasture and resulted in increased *H. contortus* plant density. In the legume oversown treatments, *S. scabra* cv. Seca density increased rapidly from 15 plants/m^2 in 1988 to 140 plants/m^2 in 2001 following a lag phase between 1988 and 1993. This increased *S. scabra* density was associated with an eventual decline in *H. contortus* plant density through reduced seedling recruitment. It was concluded that *H. contortus* population density is sustainable at stocking rates of 4 and 5 ha/steer (30% pasture utilisation) and that spring burning at light stocking rate can promote *H. contortus* populations. Increasing densities of *S. scabra* need to be managed to prevent its dominance.

Additional keywords: stocking rate, legume oversowing, burning.

Introduction

In an earlier paper, Orr *et al*. (2010) reported the effects of stocking rate, legume oversowing, and supplements/burning treatments on changes in pasture yield and composition in a *Hetropogon contortus* pasture in central Queensland. Increasing stocking rate reduced total pasture yields, tended to reduce the occurrence of *H. contortus*, and increased the occurrence of a range of 'increaser' species. Oversowing introduced legumes increased their presence, particularly that of the perennial *Stylosanthes scabra* cv. Seca, which increased to be 50% of the pasture composition by the end of the study. Stocking rate was more influential than pasture type (native, legume oversown, or supplement/burning) in effecting these pasture changes despite large increases in *S. scabra* cv. Seca plant density in the legume oversown treatments.

Oversowing introduced legumes into *H. contortus* pastures has resulted in substantial improvement in cattle liveweight gain in central Queensland (Middleton *et al*. 1993), although Miller and Stockwell (1991) indicated the need for improved management guidelines to maintain the grass: legume balance. Subsequently, Noble *et al*. (2000) suggested that managing pasture composition to prevent stylo dominance is the most important option to counteract increasing soil acidification in legume oversown pastures. Burning in spring together with deferred summer grazing has been shown to increase the proportion of *H. contortus* in southern Queensland (Orr and Paton 1997).

Plant population dynamics are the study of the effect of recruitment and death of individual plants on plant density, with density being the accumulated result of these processes (Jones and Mott 1980). Few data are available on the population dynamics of *H. contortus* or *S. scabra* under grazing, although Orr *et al*. (2004*a*) highlighted the need for regular seedling recruitment of *H. contortus* in southern Queensland to maintain plant density so as to offset death of existing plants.

A preliminary paper (Orr *et al*. 2001) reported changes in the density of *H. contortus* in native pasture, legume oversown native pasture, and animal diet supplement/spring burnt native pasture

 10.1071/CP09194 1836-0947/10/030255

and *S. scabra* cv. Seca in the legume oversown pasture between 1988 and 1996. This paper expands on this preliminary paper and reports the population dynamics of *H. contortus* and *S. scabra* cv. Seca in relation to these grazing management options between 1988 and 2001 and on the effect of spring burning on *H. contortus* seedling recruitment.

Methods

Grazing study

A study was conducted between 1988 and 2001 in a *H. contortus* pasture at Galloway Plains, Calliope (24°10′S, 150°57′E), in central Queensland. The original design was a randomised block with 2 replications of 11 treatments: 5 stocking rates (8, 5, 4, 3, and 2 ha/steer) in native pasture and 3 stocking rates (4, 3, and 2 ha/steer) in both native pasture oversown with introduced legumes and native pasture with dry-season protein supplement to the steers (Table 1). The 2 predominant soil types were a low fertility duplex (Dy3) and a grey clay (Ug5), with the study designed so that 1 replicate block was located on each of these 2 dominant soil types. The legumes *Stylosanthes scabra* cv. Scabra, *S. hamata* cv. Verano, and *Chamaecrista rotoundifolia* cv. Wynn were surface sown in October 1987, and *C. rotoundifolia* cv. Wynn was resown into cultivated strips in August 1988. Five *Bos indicus* crossbred steers grazed each treatment, with paddock sizes from 10 to 40 ha to achieve the designated stocking rates, although 6 steers were included in some of the later drafts in order to accelerate stocking rate effects. Steers were replaced annually (Burrows *et al*. 2010).

In 1992, the dry-season supplement treatments were replaced by spring burning treatments. However, by 1996, the combination of burning and heavy stocking rate resulted in inadequate fuel loads and this situation was further compounded by below-average rainfall. At 2 and 3 ha/steer, burning was possible in spring 1992 and 1999 only. As a result, in 1996, the 8 ha/steer native pasture treatment was reassigned to evaluate the effect of spring burning at a stocking rate of 5 ha/steer. Further details are provided in Orr *et al*. (2010).

Population dynamics of H. contortus

The dynamics of *H. contortus* were measured between 1988 and 2001 on a subset of treatments that included the 5, 4, 3, and 2 ha/steer stocking rates in native pasture and the 4 and 3 ha/steer stocking rates in the legume oversown and supplement/burning treatments. In 1988, 25 permanent quadrats, each 0.5 by 0.5 m, were established in 3 nests (8, 8, and 9 quadrats) in each of these 8 grazing treatments. These quadrats were subjectively selected to contain a total of 60 *H. contortus* plants that represented the existing range of plant diameters and plant densities. These 25 quadrats were positioned in the 'interzone' between *H. contortus* and *Aristida* spp. 'patches' (Wandera 1993) in order to monitor the fate of individual plants. The location and diameter of these *H. contortus* plants were recorded in autumn 1988 using a pantograph (Orr *et al*. 2004*a*). Where plants were not circular, the width was measured first along the widest diameter and second along the diameter perpendicular to the first diameter. Subsequently, each autumn between 1989 and 2001, 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 (Orr *et al*. 2004*a*).

Basal area of *H. contortus* was calculated on an individual quadrat basis as the area occupied by all *H. contortus* plants in that quadrat by assuming that plants were 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 2 diameters measured for that plant. Individual plant size, for both the original plants and annual seedling cohorts, 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 those plants) in that quadrat. Plant turnover for plant number and for basal area was calculated as 1 minus the fraction of the population not turning over during the period of the study, expressed as a percentage. The fraction not turning over was the number of individual plants or basal area present in 1988 and still present in 2001 (after O'Connor 1994).

Table 1. Experimental design for stocking rate and pasture type treatments at Galloway Plains between 1988 and 2001

Stocking rate (ha/steer)	Native pasture	Native pasture with legume	Native pasture with dry-season supplement/burning
8	+[A]		
5	+		+[B]
4	+	+	+
3	+	+	+
2	+	+	+

[A]Treatment conducted between 1988 and 1996.
[B]Treatment conducted between 1996 and 2001.

Impacts of burning on H. contortus

In spring 1996, an additional 25 permanent quadrats were located in the newly established 5 ha/steer, burnt treatment to compare this stocking rate treatment with the existing stocking rates. *H. contortus* plants in these quadrats were monitored in the same manner as the original quadrats. Data presented here are limited to the soil seedbanks in spring 1999 and the subsequent *H. contortus* seedling recruitment in autumn 2000 following burning in spring 1999.

Population dynamics of S. scabra cv. Seca

The dynamics of *S. scabra* were monitored in the 4 and 3 ha/steer in legume oversown treatments (*S. hamata* cv. Verano persistence was limited and *Chamaecrista rotoundifolia* cv. Wynn failed to persist). During autumn 1988, the position of all *S. scabra* plants present in the 25 quadrats established to monitor *H. contortus* was recorded together with *H. contortus*, using a pantograph. Subsequently, each autumn between 1989 and 2001, further recordings were made of the survival of these initial plants together with seedling recruitment over the previous year. However, following the 1993–94 summer, *S. scabra* density increased substantially, making it difficult to subsequently identify these newly recruited plants. Consequently, starting in 1994, only plants from the initial recording and those from the 1989–93 cohorts were monitored individually together with the total *S. scabra* density in each quadrat.

Soil seedbanks

The soil seedbanks of *H. contortus* and of *S. scabra* were measured annually to interpret treatment differences in seedling recruitment. Soil cores were collected in spring between 1989 and 2000 and the soil seedbank determined by germinating seed contained in soil cores collected from the area surrounding the permanent quadrats. Four soil cores, each 5 cm diameter and 5 cm deep, were bulked to produce each sample and there were 15 samples (i.e. 60 cores; 5 samples from each of 3 nests) from each paddock. In the following summer, when *H. contortus* 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). *H. contortus* and *S. scabra* seedlings were identified and counted and only one wetting cycle was conducted on each set of cores (Orr 1999).

S. scabra seed contains a proportion of 'hard' seed such that not all viable seed present germinates during only one wetting period. Using the soil cores collected in spring 1996, we estimated this proportion of 'hard' seed using the separation technique of Jones and Bunch (1988) following the completion of the normal wetting period.

Statistical analyses

The overall grazing experiment was a randomised complete block design consisting of 2 replicates of 11 treatments. For the permanent quadrats, population data were measured at 4 stocking rates (5, 4, 3, and 2 ha/steer) in native pasture and at 2 stocking rates (4 and 3 ha/steer) in the 3 pasture types with 4 treatment combinations missing. The spring burning study analyses were based on 3 stocking rates (5, 4, and 3 ha/steer) and 2 pasture types (native pasture and burnt native pasture). Data were analysed separately for each year and, given the lack of balance in the treatment structure, data were analysed using analysis of variance with an appropriate nested factorial structure in GENSTAT (GENSTAT 2002). A logarithmic transformation was used for seedling recruitment data.

In evaluating the effects of treatments 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 by time) model. The significance of the splines was evaluated by a chi-square test on the change in deviance. Subsequently, the fixed effects were assessed for overall trends. Plant survival was analysed using a proportional hazards survival model (Cox 1972). Results presented in this paper are limited to those demographic parameters where treatment differences were significant ($P < 0.05$). For those parameters where no results are presented, treatment differences were not significant ($P > 0.05$).

Results

Rainfall

Trends in the 5-year moving average summer (October–March) rainfall for Calliope Station (20 km from the Galloway Plains) indicate that the experiment was conducted during the driest period of the last 100 years. Summer rainfall in some years, e.g. 1990–91 and 1996–97, approached the long-term mean rainfall, while other years, e.g. 1992–93 and 1994–95, were very much below the long-term mean. Further details are provided in Orr *et al.* (2010).

Pasture utilisation

Mean annual pasture utilisation increased with increasing stocking rate in the 4 native pasture treatments from 24% at 5 ha/steer to 61% at 2 ha/steer. Utilisation was consistently higher on the duplex soil than on the clay reflecting lower pasture yields on the duplex soil. Further details are provided in Orr *et al.* (2010).

Population dynamics of H. contortus

Plant turnover

For the 13 years of recording the original 8 treatments, a total of 6235 *H. contortus* plants were recorded: 946 original plants in 1988 and 5289 seedlings recruited between 1989 and 2001. Mean turnover rate after 13 years for plant number was 94.7% and the mean turnover rate for basal area was 95.9%, and there were no differences ($P > 0.05$) in either plant or basal area turnover due to either stocking rate or pasture type.

Plant density

Spline analyses revealed different ($P < 0.001$) season × treatment interactions. In native pasture, there was a year × treatment interaction ($P < 0.001$) where *H. contortus* plant density increased at 5 and 4 ha/steer and declined at 3 and 2 ha/steer. Increasing stocking rate reduced ($P < 0.05$) density between 1993 and 1999 and this trend ($P < 0.1$) was apparent in 1992 and 2001 also (Fig. 1*a*). There was also a year × treatment interaction ($P < 0.001$) for stocking rate × pasture type. *H. contortus* plant density was highest in 2000 and 2001 for the 4 ha/steer treatments and particularly under burning (Fig. 1*b*). Generally, *H. contortus* plant density was lowest in the legume oversown treatments. These differences in density resulted from changes in both seedling recruitment and plant survival.

Plant survival

The survival of all cohorts of *H. contortus* was reduced ($P < 0.05$) with time. In native pasture, survival of the original plants was influenced ($P < 0.05$) by stocking rate, being generally highest at 5 ha/steer and lowest at 2 and 4 ha/steer (Fig. 2*a*). For pasture types, survival of the original plants was influenced ($P < 0.05$) by a stocking rate × pasture type interaction with survival highest at 4 ha/steer burnt and lowest at 4 ha/steer in native pasture (Fig. 2*b*). Survival of the 1989 cohort was influenced also ($P < 0.05$) by a stocking rate × pasture type interaction (Fig. 2*c*). In 1992, in native pasture, seedling recruitment was higher at 5 and 4 ha/steer but fewer ($P < 0.05$) of these seedlings survived compared with those at 3 and 2 ha/steer (Fig. 2*d*). Few seedlings of any cohort survived more than 2 years.

Seedling recruitment

H. contortus seedling recruitment varied markedly among years. In native pasture, recruitment in 1990 was highest ($P < 0.05$) at 2 ha/steer but this situation was reversed in 1993, 1996, 1998 and 2001 when recruitment was higher ($P < 0.05$) at 5 and 4 ha/steer than at 3 and 2 ha/steer (Fig. 3*a*). Recruitment in 2001 was higher

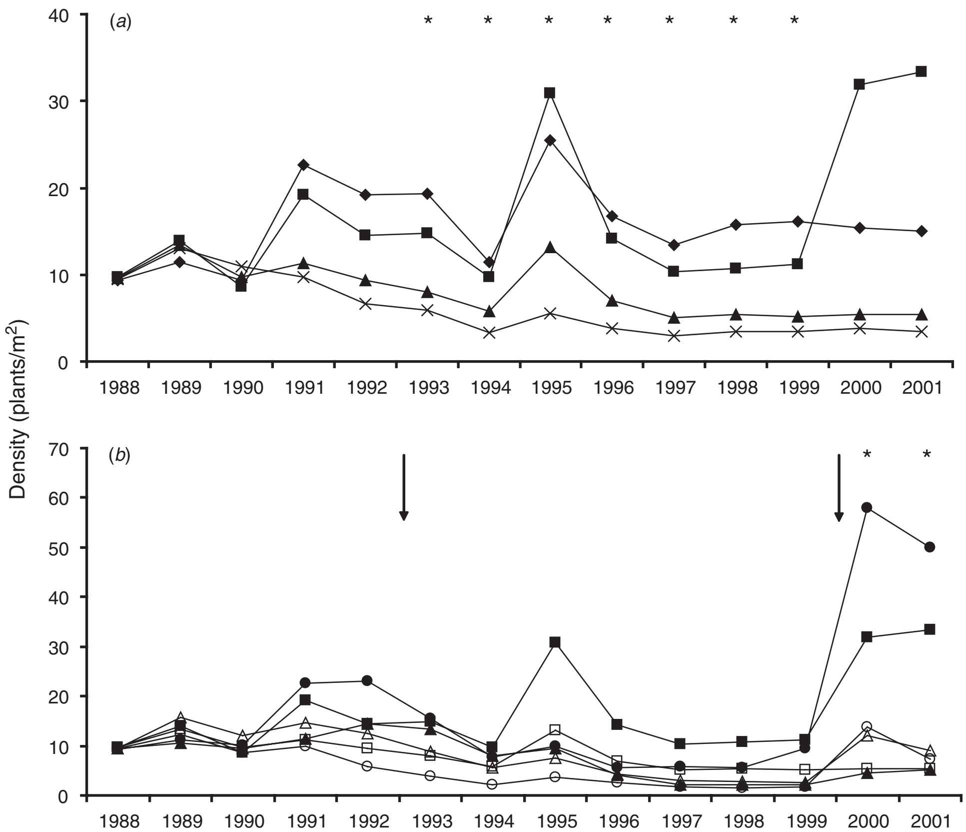

Fig. 1. Changes in density (plants/m^2) of *H. contortus* at (*a*) 4 native pasture stocking rates (◆ 5; ■ 4; ▲ 3; ✕ 2 ha/steer), (*b*) stocking rate × pasture type interaction (■ 4; □ 3/ha/steer native pasture; ▲ 4; △ 3 ha/steer legume oversown; ● 4; ○ 3 ha/steer supplement/burnt) in autumn between 1988 and 2001. Within years, asterisks indicate differences ($P < 0.05$) between treatments. Arrows indicate time of spring burning for the supplement/burnt treatment.

($P < 0.05$) at 4 ha/steer than at the other 3 stocking rates. For pasture types, there were few differences in recruitment within years, although in 2000 it was higher ($P < 0.05$) in the supplement/burning than in the other 2 pasture types. In 2001, recruitment was higher ($P < 0.05$) in both supplement/burning and native pasture than in the legume oversown treatment (Fig. 3*b*).

Soil seedbanks

Soil seedbanks also varied markedly among years. In native pasture, soil seedbanks at 5 and 4 ha/steer were generally higher ($P < 0.05$) than those at 3 and 2 ha/steer between 1994 and 2000 (Fig. 4*a*). For pasture types, there were no differences ($P > 0.05$) in the soil seedbank, although there was a consistent trend for seedbanks to be highest in native pasture and lowest in the legume oversown treatments (Fig. 4*b*).

Basal area

Basal area of *H. contortus* in native pasture doubled from 1% in 1988 to 2% in 1989 and declined to 0.5% in 1990 and remained around this level until 2001 (Fig. 5*a*). Basal area was higher ($P < 0.05$) at 5 ha/steer in 1991 and during the period 1995–99. For pasture types, basal area of *H. contortus* also fluctuated between 1988 and 1990 and there was a stocking × pasture type interaction ($P < 0.05$) in 1996 when basal area was highest at 4 ha/steer in native pasture and also in 2001 when basal area was highest at 4 ha/steer in the supplement/burning treatment (Fig. 5*b*).

Plant size

The persisting 1988 plants in native pasture displayed no major change in size between 1988 and 2001 and there were no differences ($P > 0.05$) among the 4 stocking rates (Fig. 6*a*). Plants from the 1991 cohort generally increased in size with time while stocking rate influenced ($P < 0.05$) size only in 1996, with plants at 4 ha/steer being larger than at the other 3 stocking rates (Fig. 6*b*). Plants from the 1994 cohort were larger ($P < 0.05$) in 1994 and 1999 at 2 ha/steer than at the other 3 stocking rates (Fig. 6*c*). Similarly, plants from the 1995 cohort were larger ($P < 0.05$) in 1996 at 2 ha/steer than at the other 3 stocking rates (Fig. 6*d*).

Effect of burning on recruitment

Soil seedbanks of *H. contortus* in spring 1999 were reduced ($P < 0.05$) by increasing stocking rate but not by pasture type (Fig. 7*a*). In contrast, following burning in spring 1999, seedling recruitment in autumn 2000 was influenced ($P < 0.05$) by a stocking rate × pasture interaction, with seedling recruitment highest at the 5 ha/steer, burnt and lowest at the 2 ha/steer in native pasture treatments (Fig. 7*b*).

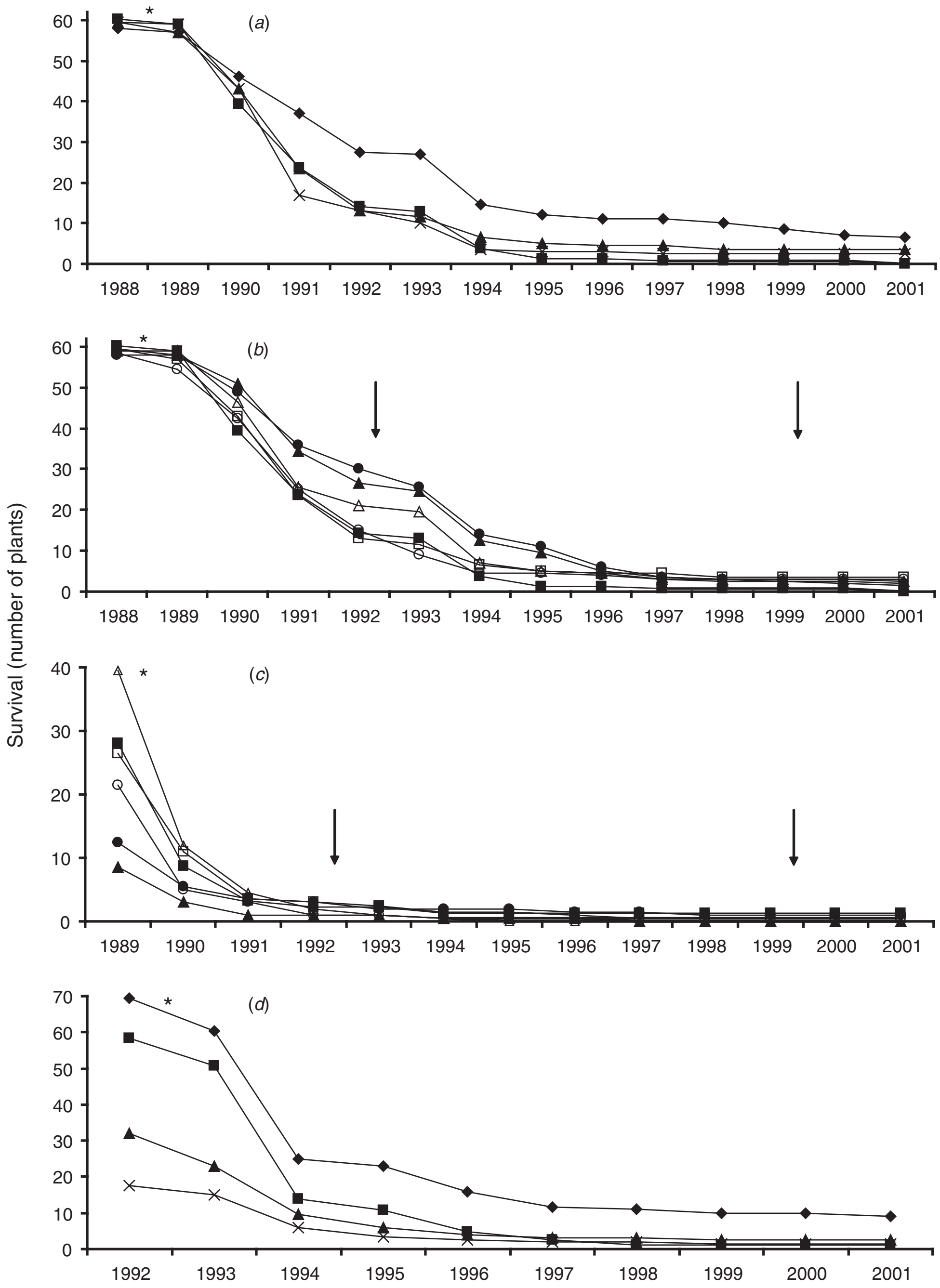

Fig. 2. Changes in survival (number of plants) of *H. contortus* plants between 1988 and 2001 for (*a*) original plants at 4 native pasture stocking rates (◆ 5; ■ 4; ▲ 3; ✕ 2 ha/steer), (*b*) original plants for pasture type × stocking rate interaction (■ 4; □ 3/ha/steer native pasture; ▲ 4; △ 3 ha/steer legume oversown; ● 4; ○ 3 ha/steer supplement/burnt), (*c*) 1989 cohort for pasture type × stocking rate interaction (■ 4; □ 3/ha/steer native pasture; ▲ 4; △ 3 ha/steer legume oversown; ● 4; ○ 3 ha/steer supplement/burnt), (*d*) 1992 cohort 4 native pasture stocking rates (◆ 5; ■ 4; ▲ 3; ✕ 2 ha/steer). Asterisks indicate differences ($P < 0.05$) in survival across time between treatments. Arrows indicate time of spring burning for the supplement/burnt treatment.

Population dynamics of S. scabra

Plant density

The initial *S. scabra* plant densities of 15 plants/m^2 increased slowly to be 20 plants/m^2 in 1993, after which time, densities increased rapidly so that, by 2001, densities were 150 and 140 plants/m^2 at 4 and 3 ha/steer respectively, with no differences ($P < 0.05$) between stocking rates (Fig. 8). Very high densities in 1997 resulted from large numbers of seedling plants, most of

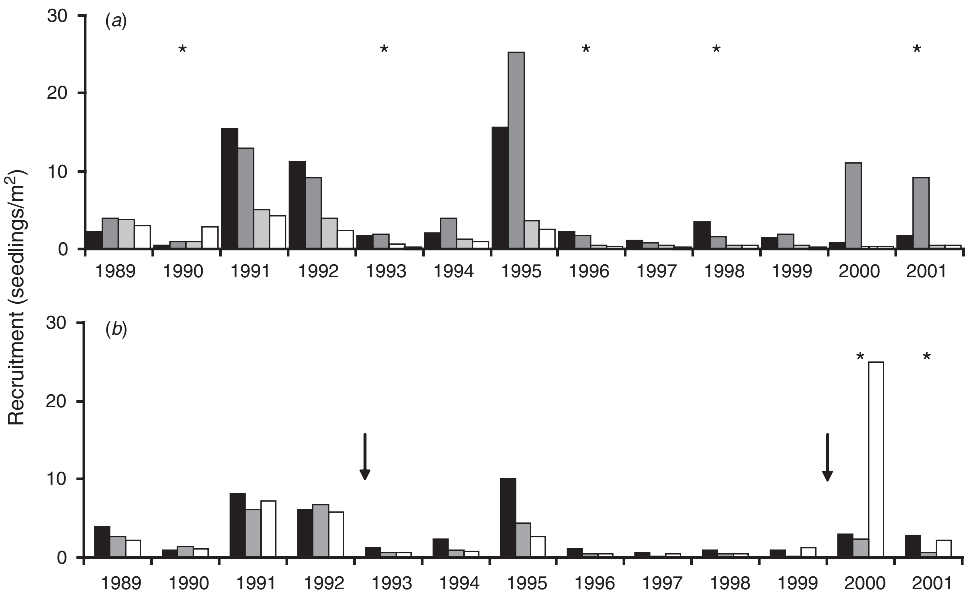

Fig. 3. Changes in seedling recruitment (seedlings/m^2) of *H. contortus* at (*a*) 4 native pasture stocking rates (5 ha/steer, solid; 4, dark grey; 3, light grey; 2, open) and (*b*) 3 pasture types for 2 stocking rates (native pasture, solid; legume oversown, grey; supplement/burnt, open) in autumn between 1989 and 2001. Within years, asterisks indicate differences ($P < 0.05$) between treatments. Analyses performed on logarithmic transformed data. Arrows indicate time of spring burning for the supplement/burnt treatment.

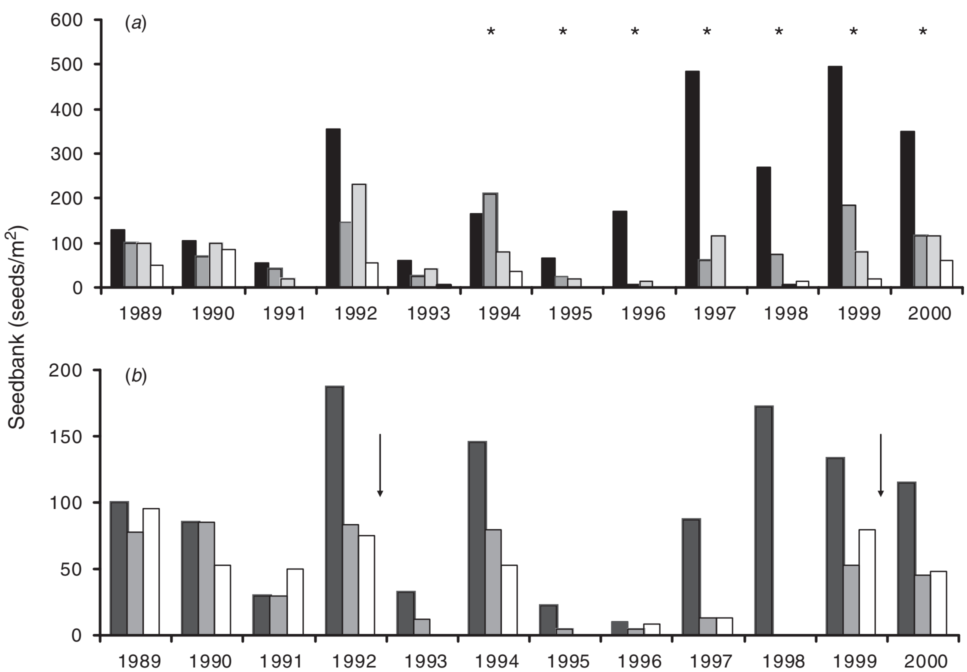

Fig. 4. Changes in soil seedbanks (seeds/m^2) of *H. contortus* in spring between 1989 and 2000 in relation to (*a*) 4 native pasture stocking rates (5 ha/steer, solid; 4, dark grey, 3, light grey; 2, open) and (*b*) 3 pasture types for 2 stocking rates (native pasture, solid; legume oversown, grey; supplement/burnt, open) in spring. Within years, asterisks indicate differences ($P < 0.05$) between treatments. Arrows indicate time of spring burning for the supplement/burnt treatment.

which failed to survive until 1998. The rapidly accelerating rate of *S. scabra* density increase after 1993 corresponded with our inability to differentiate individual plants. This accelerating rate of *S. scabra* density increase was also associated with an overall increase in its frequency from 18 and 36% at 4 and 3 ha/steer in 1988 to 100% in 2001 (data not presented).

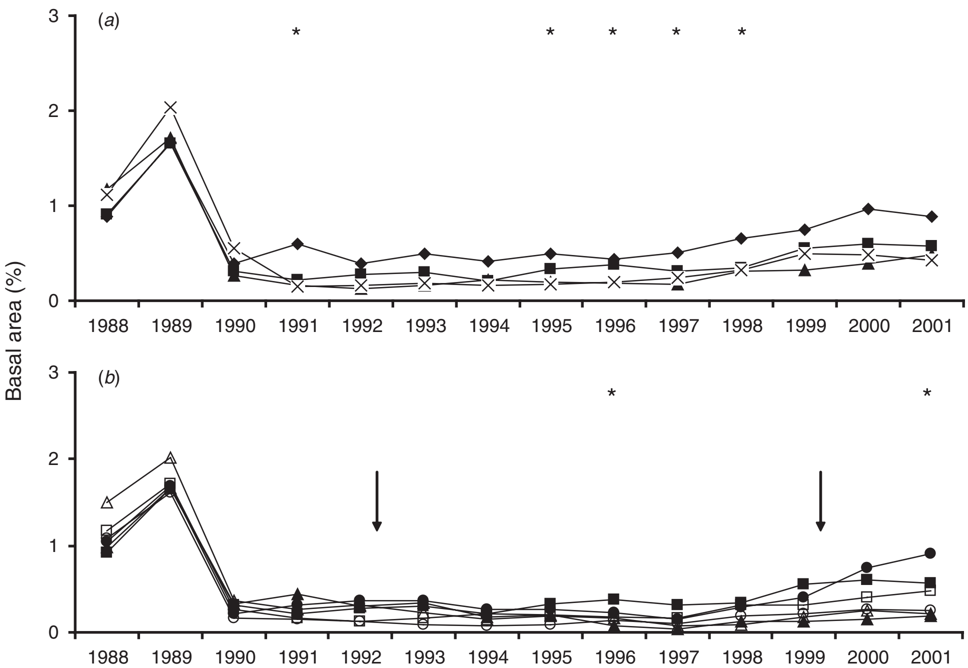

Fig. 5. Changes in basal area (%) of *H. contortus* at (*a*) 4 native pasture stocking rates (◆ 5; ■ 4; ▲ 3; ✕ 2 ha/steer) and (*b*) 2 stocking rates in 3 pasture types (■ 4; □ 3 ha/steer native pasture; ▲ 4; △ 3 ha/steer legume oversown; ● 4; ○ 3 ha/steer supplement/burnt) in autumn between 1988 and 2001. Within years, asterisks indicate differences ($P<0.05$) between treatments. Arrows indicate time of spring burning for the supplement/burnt treatment.

Recruitment and survival

Seedling recruitment of *S. scabra* varied among years between 1989 and 1993 and there were no differences ($P>0.05$) between the 2 stocking rates although recruitment was generally greater at the higher stocking rate (Fig. 9). Similarly, there were no differences ($P>0.05$) in the survival of the initial plants (Fig. 10*a*), although a comparison of the survival of successive annual cohorts on a standardised basis indicated that survival was reduced with successive annual cohorts (Fig. 10*b*).

Stylo seedbanks

Little germinable *S. scabra* seed was recorded in the soil seedbank until 1994 (Fig. 11) despite *S. scabra* seedling recruitment occurring each year between 1989 and 1993 (Fig. 9). By 1994, the soil seedbank had increased to 600 seeds/m^2 at 4 ha/steer and fluctuated among years and, although being consistently higher at this lighter stocking rate, these differences were generally not significant ($P>0.05$). Physical separation of 'hard' seed from the spring 1996 sampling indicated that this germinable seedbank represented 70% of the total *S. scabra* seedbank.

Discussion

Effects of stocking rate and pasture type

Increasing stocking rate from 5 to 2 ha/steer in native pasture reduced *H. contortus* density through reduced seedling recruitment which, in turn, reflected reduced soil seedbanks. Compared with stocking rate, pasture type had a smaller effect on *H. contortus* density, although burning substantially increased *H. contortus* seedling recruitment over the 1999–2000 summer compared with that in unburnt native pasture and this effect was accentuated at the lightest stocking. Legume oversowing gradually reduced *H. contortus* density as seedling recruitment failed to replace those existing plants which died. This reduced *H. contortus* density was associated with increased *S. scabra* density, which was particularly rapid after 1993, while *S. scabra* dominated the legume oversown quadrats in 2001 with plant densities of 140 plants/m^2. Results presented here provide further data and are consistent with earlier results from this study (Orr *et al*. 2001).

This study was conducted through the driest period of the last 100 years so that the effects of increasing stocking rates recorded here can be expected to be reduced during periods of 'normal' or 'above normal' rainfall. During such periods of higher rainfall, *H. contortus* density could be expected to increase through reduced pasture utilisation which, in turn, would lead to higher seed production, resulting in higher seedling recruitment and plant survival, while individual plants would increase in size leading to higher basal area.

Population dynamics of H. contortus

Reduced *H. contortus* density with increasing stocking rates reported here is consistent with a similar study of *H. contortus* dynamics at Glenwood in southern Queensland (Orr *et al*. 2004*a*). However, at Glenwood, the trend of declining *H. contortus* density with increasing stocking rate was not consistent, probably because first, the Glenwood study was relatively short (1990–96), and second, the drought at Glenwood was more severe than at Galloway Plains. Thus, the 13-year time frame of the Galloway Plains study more accurately reflects the

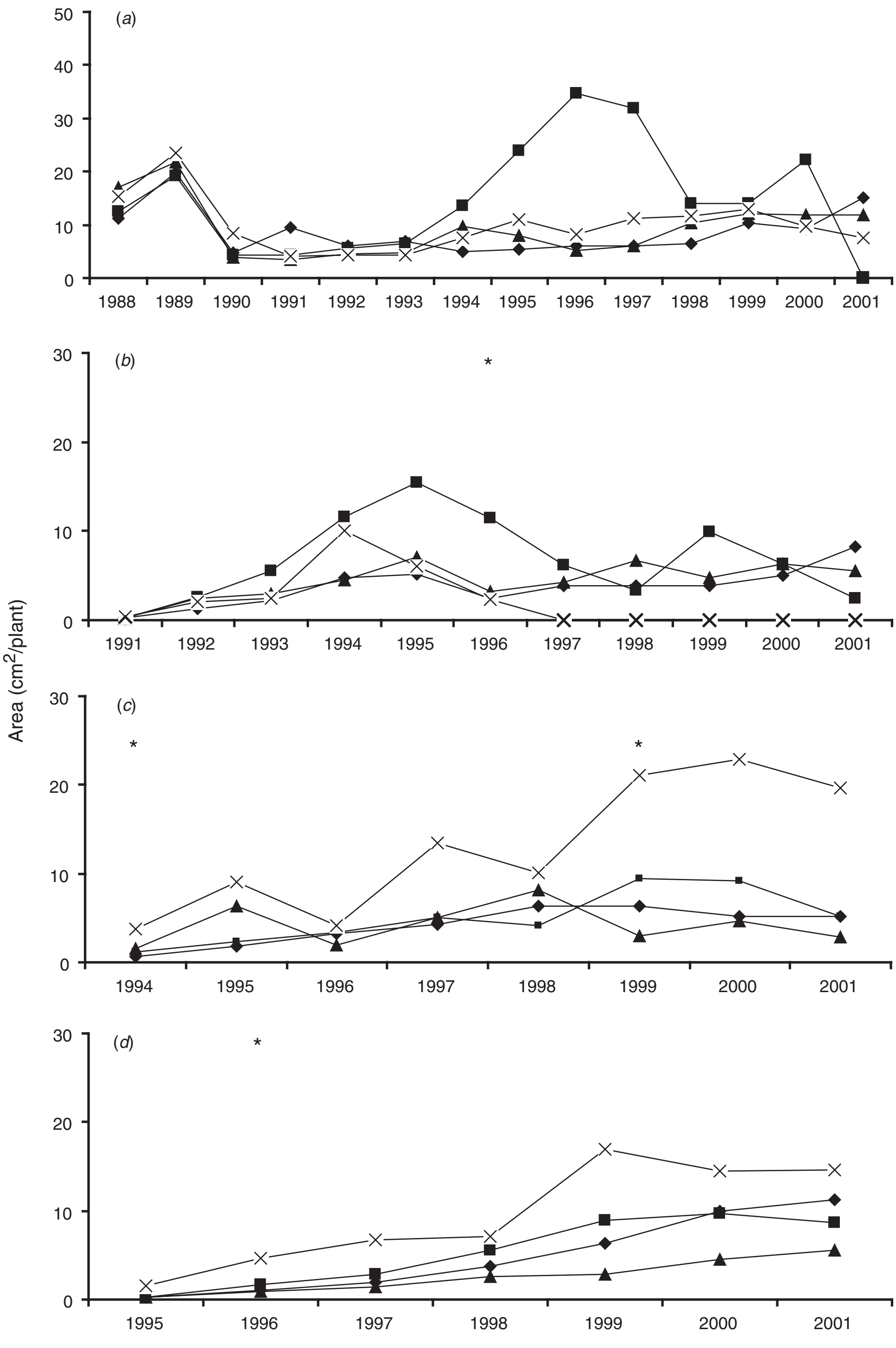

Fig. 6. Changes in plant size (cm^2/plant) of *H. contortus* plants in relation to 4 stocking rates in native pasture for (*a*) original plants (◆ 5; ■ 4; ▲ 3; ✕ 2 ha/steer), (*b*) 1991 cohort, (*c*) 1994 cohort, (*d*) 1995 cohort between 1988 and 2001. Within years, asterisks indicate differences ($P < 0.05$) between treatments.

expected impact of increasing stocking rate in reducing *H. contortus* density. Densities at Galloway Plains generally ranged over 5–20 plants/m^2 and were less than the 10–25 plants/m^2 at Glenwood, although the 60 plants/m^2 recorded in the 5 ha/steer, burnt treatment in 2000 was much higher than that recorded with burning at Glenwood (Orr 2004).

Large fluctuations in *H. contortus* density occurred relatively rapidly, particularly at 5 and 4 ha/steers, and this fluctuation is

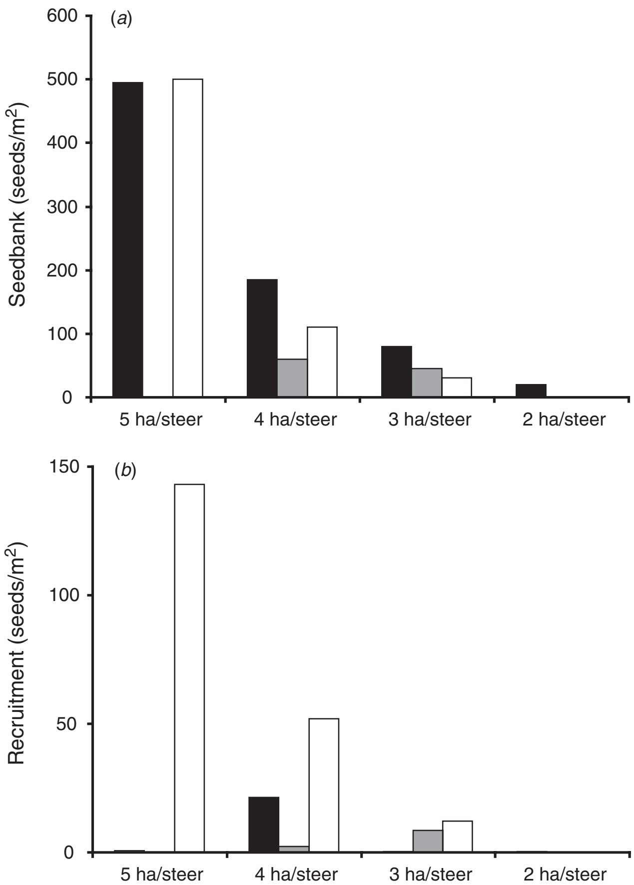

Fig. 7. Effects of fire on (*a*) seedbank (seeds/m^2) in spring 1999 (native pasture, solid; legume oversown, grey; supplement/burnt, open) and (*b*) recruitment (seedlings/m^2) in autumn 2000 in 4 stocking rates in native pasture, legume oversown and supplement/burnt pasture. Data for the 2 ha/steer native pasture and the legume oversown treatments are included only for illustrative purposes.

consistent with similar fluctuations at both Glenwood (Wandera 1993; Orr *et al*. 2004*a*) and at Keilambete in central Queensland (Jones *et al*. 2009), and also in southern Africa (O'Connor 1994). These large population fluctuations resulted chiefly from large fluctuations in seedling recruitment, which varied among years, stocking rates, and pasture types. Recruitment at Galloway Plains ranged over 0–20 seedlings/m^2 in the absence of burning, and was similar to that at both Glenwood (Wandera 1993; Orr *et al*. 2004*a*) and at Keilambete (Jones *et al*. 2009). Initially, recruitment at Galloway Plains was higher at 2 ha/steer than at the other 3 stocking rates, but this trend was reversed with the continuing effect of heavy grazing. This overall trend was consistent with a similar pattern recorded at both Glenwood (Orr *et al*. 2004*a*) and in southern Africa (O'Connor 1994). Therefore, the general trend is for *H. contortus* recruitment to decline with increasing stocking rate and this trend was consistent with reduced soil seedbanks with increased stocking rate. However, this overall trend for recruitment to decline with increasing grazing pressure was not recorded at Keilambete where recruitment was highest at the heaviest grazing pressure in 2 of the last 3 years of this 8-year study. This effect probably arose because there had been little reduction in soil seedbanks (Jones *et al*. 2009) under better seasonal rainfall, unlike that reported in these 3 other studies.

Large differences in *H. contortus* seedling recruitment, particularly at heavy stocking rates and irrespective of pasture type, mirrored differences in the size of the soil seedbank. Soil seedbanks of 0–500 seeds/m^2 for *H. contortus* at Galloway Plains were similar to the 40–670 seeds/m^2 at Glenwood (Orr *et al.* 2004*b*) but were higher than the 10–350 seeds/m^2 at Keilambete (Jones *et al*. 2009). However, all these figures were higher than the 60 seeds/m^2 averaged over 5 years for *H. contortus* near Townsville (McIvor 1987) and higher than the total perennial grass seedbank of 210 seeds/m^2 recorded in a range of both native and oversown pastures near Charters Towers (McIvor 2001).

This study has clearly demonstrated that increasing stocking rate reduced the size of the soil seedbank. Orr *et al.* (2004*b*) suggest that such a reduction results from the increasing

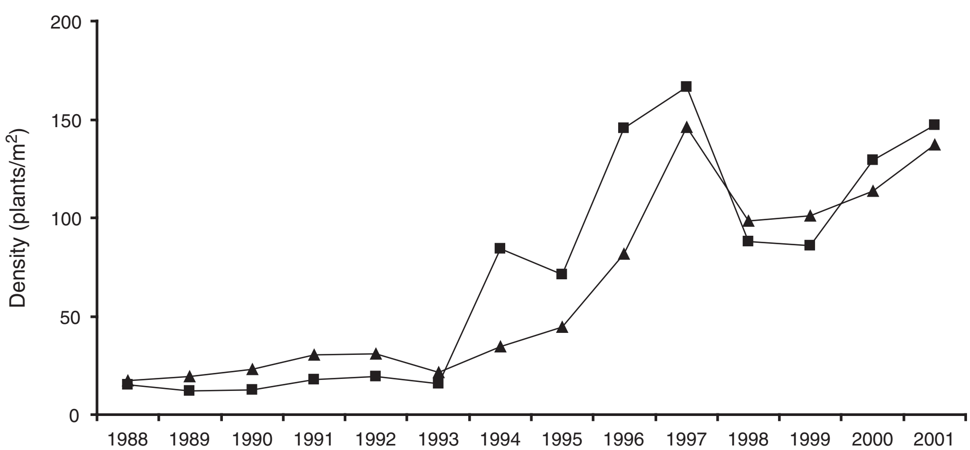

Fig. 8. Changes in density (plants/m^2) of *S. scabra* cv. Seca at 2 stocking rates (■ 4; ▲ 3 ha/steer) in legume oversown native pasture in autumn between 1988 and 2001.

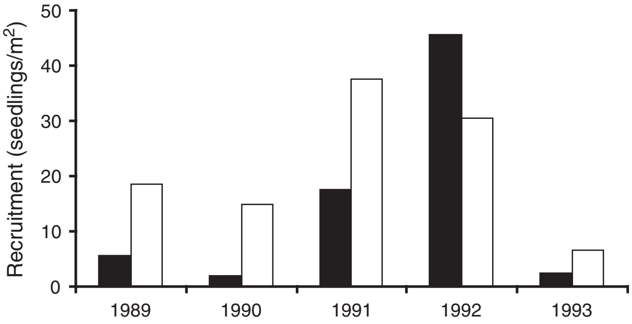

Fig. 9. Changes in seedling recruitment (seedlings/m^2) of *S. scabra* cv. Seca at 2 stocking rates (4 ha/steer, solid; 3 ha/steer, open) in legume oversown native pasture in autumn between 1989 and 1993.

consumption by cattle of tillers that would otherwise produce inflorescences in the previous autumn because inflorescence density is the major determinant of seed production. Such a finding is consistent with the conclusion (Wandera 1993) that seed production of *H. contortus* is the parameter most susceptible to increasing stocking rate.

Burning markedly increased *H. contortus* seedling recruitment, especially at light stocking rate where soil seedbanks were higher than at heavy stocking rate. Burning increases seedling recruitment (Orr and Paton 1997; Orr *et al*. 1997) because fire directly stimulates the germination of *H. contortus* (Campbell 1996). However, the current study further highlights the role of light grazing in promoting recruitment after burning because of the creation of higher soil seedbanks compared with heavy grazing.

Increasing stocking rate also reduced *H. contortus* density by reducing plant survival; however, the effect of reduced survival was less than that of seedling recruitment. Survival rates of the original plants at Galloway Plains were similar to those at both Glenwood (Orr *et al*. 2004*a*) and Keilambete (Jones *et al*. 2009), although the longer study period at Galloway Plains compared with these other 2 studies indicates a life span of at least 13 years.

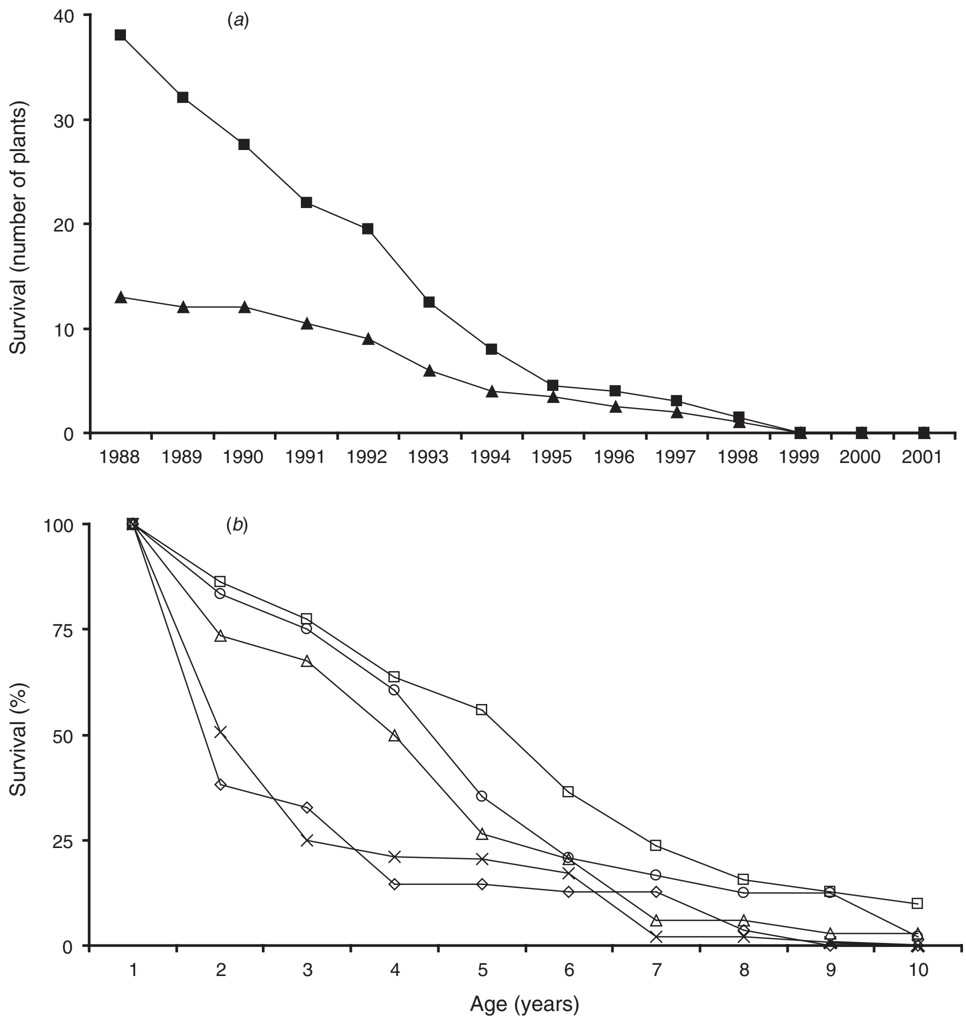

Fig. 10. Changes in survival (number of plants) of *S. scabra* stylo plants for (*a*) initial plants at 2 stocking rates (■ 4; ▲ 3 ha/steer); and (*b*) annual cohorts between 1988 and 1993 (□ 1988; ○ 1989; △ 1990; ◇ 1991; ✕ 1992) in legume oversown native pasture between 1988 and 2001.

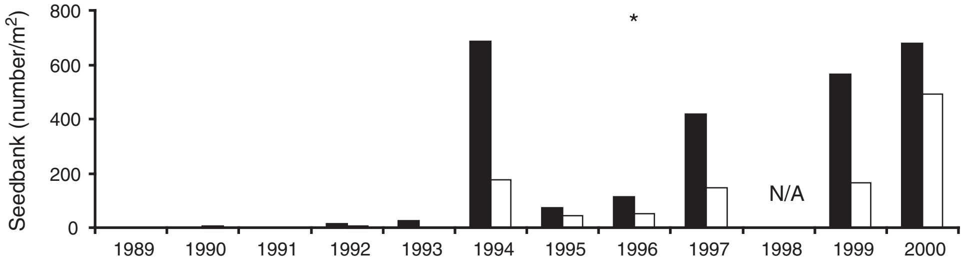

Fig. 11. Changes in germinable seedbanks (seeds/m^2) of *S. scabra* stylo at 2 stocking rates (4 ha/steer, solid; 3 ha/steer, open) in legume oversown native pasture between 1989 and 2000. N/A means no data available.

Given that survival was reduced by increased stocking rate, life spans of *H. contortus* in excess of this 13-year life span are likely. These life spans are longer than the 4-year life span under grazing and 6 years in exclosure respectively, reported for this species in Arizona, USA (Canfield 1957). Orr *et al*. (2004*c*) compared survival of *H. contortus* across a north–south spread of sites in Queensland and demonstrated that its life span in the northern region is substantially less than in central and southern regions. Annual seedling cohorts of *H. contortus* survived well at all stocking rates and pasture types, with survival generally 20–40% over the first year and this was consistent with similar seedling survival rates at both Glenwood (Wandera 1993; Orr *et al*. 2004*a*) and Keilambete (Jones *et al*. 2009).

Basal area of *H. contortus* varied markedly between 1988 and 1990, after which time basal area was reduced with heavy stocking rate in native pasture. Basal area values at Galloway Plains were generally around 0.5% and were lower than the 1–2% at Glenwood (Orr *et al*. 2004*a*).These differences probably reflect the fact that *H. contortus* density was consistently higher at Glenwood and where *H. contortus* contributed 50% of total pasture yield at Glenwood compared with only 20% at Galloway Plains (Orr *et al*. 2010). The sizes of mature plants at Galloway Plains were similar to that at Glenwood (Orr *et al*. 2004*a*). There were few consistent differences between stocking rates in the size of seedling plants at Galloway Plains in contrast with larger seedlings under heavy grazing (Orr and Paton 1997; Orr *et al*. 2004*a*) and with heavy defoliation (Campbell 1996).

Overall, the reduction in density of *H. contortus*, particularly under heavy grazing and also with legume oversowing, resulted from the failure of adequate seedling recruitment to replace those plants which died. In this way, the permanent quadrats that initially contained *H. contortus* plants often became devoid of *H. contortus* plants at high stocking rates leading to a decline in both density and frequency.

Measuring H. contortus *change using different sampling methods*

Substantial stocking rate effects on *H. contortus* density measured in permanent quadrats in this study contrast with the few treatment differences in the occurrence of *H. contortus* measured by Botanal (Orr *et al*. 2010) and also perennial grass basal area measured by the wheel point (Tidmarsh and Havenga 1955) (R. L. Clem, unpubl. data). These differences probably reflect the 2 different scales at which *H. contortus* was measured. At the community scale, Botanal sampling measured *H. contortus* in random quadrats spaced 40–50 m apart, while wheel point sampling measured basal area as 'strikes' on live grass tussocks with points spaced at ~1-m intervals. In contrast, at the individual plant scale, permanent quadrats measured individual *H. contortus* plants in permanently located quadrats in the 'interzone' between patches where *H. contortus* plant density was high and those patches where *H. contortus* was low or absent (Wandera 1993). During this Galloway Plains study, these 'interzones' expanded at 5 and 4 ha/steer as *H. contortus* density increased, but contracted at 3 and 2 ha/steer as *H. contortus* density decreased. Under these circumstances, these 'interzone' patches more accurately reflect change in both plant density and frequency of *H. contortus* than if the permanent quadrats had been randomly distributed across the paddock. Thus, the Botanal and wheel point methods assessed the occurrence of *H. contortus* independently of these 'interzones'.

Population dynamics of S. scabra

The slow initial increase in *S. scabra* density was followed by a rapid increase to reach 140 plants/m^2 in 2001 as the soil seedbank increased, and this pattern was consistent with a similar increase reported for this species in northern Queensland (McIvor and Gardener 1998), although the density increase was not as rapid in southern Queensland (Jones *et al*. 2000). The *S. hamata* sown at Galloway Plains displayed limited persistence, whereas McIvor and Gardener (1998) reported that *S. hamata* density initially increased rapidly to 50 plants/m^2 before declining as the density of *S. scabra* increased. This finding further supports Middleton *et al*. (1993) who reported that *S. hamata* is less suitable in central compared with northern Queensland. Plant densities of 140 plants/m^2 for *S. scabra* after 13 years in the current study – despite below-average rainfall – and 120 plants/m^2 after 6 years in northern Queensland (McIvor and Gardener 1998), attest to this species' ability to eventually dominate *H. contortus* pastures in the absence of specific management intervention (McIvor *et al*. 1996; Noble *et al*. 2000).

Survival of the initial *S. scabra* plants indicated a life span of 10 years and this was higher than the 8 years reported in northern Queensland (Gardener 1984; McIvor and Gardener 1998) and the 4-years for southern Queensland (Jones *et al*. 2000). At Galloway Plains, plants from the annual 1989–92 cohorts had life spans similar to the initial plants, although the trend for decreasing survival of successively later cohorts suggests that existing *S. scabra* plants increasingly compete with later emerging cohorts. Such competition probably also limits the establishment of *H. contortus* seedlings. Stocking rate failed to affect this increasing *S. scabra* density at Galloway Plains and McIvor and Gardener (1998) reported only a small effect of stocking rate on plant density in northern Queensland. Soil seedbanks up to 700 seeds/m^2 at Galloway Plains were at the low end of the range of 600–7000 seeds/m^2 for this species at a range of sites throughout Queensland (McIvor *et al*. 1996).

Managing H. contortus *pastures*

Seedling recruitment is critical to the maintenance of *H. contortus* density and this study indicates that management systems can be devised to maintain plant density. In native pasture, reduced grazing pressure in autumn to promote seed production (Orr *et al*. 2004*b*) followed by spring burning in association with a favourable Southern Oscillation Index (Orr 2004) will enhance seedling recruitment and promote *H. contortus* density. In legume oversown pasture, 2 distinct phases of legume density are apparent: an initial establishment phase where legume density builds up slowly followed by a later phase of rapid legume density increase. In both phases, reduced grazing pressure in autumn combined with spring burning can be used to manage both *H. contortus* and *S. scabra* density. However, this study has not identified what should be a desirable or manageable legume plant density.

Conclusions

This study has indicated that increasing stocking rate from 5 to 2 ha/steer reduces *H. contortus* density through reduced seedling recruitment which, in turn, results from reduced seed production. Spring burning is effective in promoting *H. contortus* seedling recruitment and this effect is most effective at lower stocking rates. Oversowing *S. scabra* results in a gradual reduction in *H. contortus* density and this reduction is associated with the inevitable increase in legume density.

Acknowledgments

Special acknowledgment is made to the Neill-Ballantine family (Galloway Plains Pastoral Co.) for their ready co-operation and for the long-term use of land on which the study was based. Many people contributed to the overall conduct of this grazing study during its 13-year duration and it is impossible to comprehensively list all these people here. We would especially acknowledge the large number of Department of Primary Industries and Fisheries and Department of Natural Resources and Water staff who provided major contributions to this study's success. A Producer Advisory Group readily gave constructive advice throughout the study. Funding was provided by Meat and Livestock Australia.

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Manuscript received 3 July 2009, accepted 11 December 2009