Dynamics of plant populations in *Heteropogon contortus* (black speargrass) pastures on a granite landscape in southern Queensland. 1. Dynamics of *H. contortus* populations

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Abstract

The dynamics of *Heteropogon contortus* (black speargrass) populations were measured in a subset of treatments contained within an extensive grazing study conducted between 1990 and 1996 in *H. contortus* pasture in southern Queensland. This subset included 2 landscape positions and 3 stocking rates in both native pasture and legume-oversown native pasture.

Severe drought conditions throughout much of the study necessitated ongoing adjustments to the original stocking rates and, as a result, drought was the major influence on the dynamics of *H. contortus* populations. Plant density and basal area in the silver-leaved ironbark landscape were consistently higher than those in the narrow-leaved ironbark landscape. There was limited evidence of any impact by either light or moderate stocking rate but there was evidence of an impact at the heaviest stocking rate. There was minimal impact of legume oversowing.

Relatively large fluctuations in plant density occurred during this study resulting from the death of existing plants, due mainly to drought, and seedling recruitment. Similarly, there were relatively large fluctuations in basal area caused mainly by changes in plant size. Rates for turnover of plant numbers were relatively high whereas plant turnover rates of basal areas were relatively low. Regular seedling recruitment appeared necessary to ensure the persistence of this species. Despite the high turnover, populations were maintained at reasonable levels indicating the overall resilience of *H. contortus.*

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Introduction

Heteropogon contortus (black speargrass) pastures are an important forage resource for the breeding and finishing of 3–4 million beef cattle in Queensland and are, therefore, of considerable economic importance (Burrows *et al*. 1988). These pastures occupy 25 M ha and occur on a wide variety of soil types which receive between 700 and 1200 mm of annual rainfall (Weston *et al.* 1981). However, recent evidence (Tothill and Gillies 1992) indicates that these pastures have undergone deleterious changes in pasture composition under some current grazing management practices.

Plant population dynamics is the study of individual plants within a population and how plant numbers change with time (Harper 1977). Little is known of the dynamics of *H. contortus* populations under grazing despite their economic importance. Mott *et al*. (1985) reviewed the dynamics of perennial grass populations in Australian savannas and reported that 60% of *H. contortus* plants die within 5 years in southern Queensland and that high seed production allows many seeds to germinate, establish and so maintain populations.

Prior to white settlement the dominant perennial grass throughout what is now *H. contortus* pastures was *Themeda triandra* (kangaroo grass). The shift from *T. triandra* to *H. contortus* in southern Queensland resulted from increased grazing pressure together with changes in burning regimens between 1840 and 1880 (Fox 1967). More recently, grazing pressures have increased further because of economic pressures on commercial producers, the introduction of *Bos indicus* cattle, the use of dietary supplements and prolonged drought (Tothill and Gillies 1992). Despite the economic importance of these pastures, little is known on the impacts of increasing grazing pressure on population dynamics of *H. contortus*.

Extensive native pastures are usually highly organised landscape systems that range from a scale of metres to kilometres and this structure functions to conserve water and nutrients (Ludwig and Tongway 1997). In southern Queensland, landscapes supporting *H. contortus* pastures are often organised as a topographic sequence of *Eucalyptus maculata* (spotted gum) on ridge crests, *E. crebra* (narrow-leaved ironbark) on upper slopes, *E. melanophloia* (silver-leaved ironbark) on lower slopes with *E. tereticornis* (blue gum) in creek lines (Taylor and Cook 1993). Despite this, little is known of how landscape position influences *H. contortus* populations.

Oversowing *H. contortus* pastures with grazing-tolerant, introduced legumes is a potential avenue for increasing animal production from these pastures. However, such legume oversowing may lead to an imbalance in the proportion of the legume and perennial grasses in the pasture (Miller and Stockwell 1991).

This paper reports the dynamics of *H. contortus* populations in response to landscape position and stocking rate in both native pasture and legume-oversown native pasture in an extensive grazing study conducted between 1990 and 1996. Further papers in this series report seed production and soil seed banks of *H. contortus* (Orr *et al*. 2004a), dynamics of *Aristida* spp. populations (Orr *et al*. 2004b) and impacts of spring burning on *H. contortus* and *Aristida* spp. populations (Orr 2004). Other papers from this grazing study include MacLeod and McIntyre (1997) and MacLeod and Cook (2004) which report animal production and economic aspects of legume oversowing, respectively.

Materials and methods

Grazing study

A grazing study was established in 1988 on "Glenwood" station, 50 km west of Mundubbera (25°41′S, 150°52′E), which has a 100-year history of commercial cattle grazing. The soils are granite-derived, mainly yellow podzolics with a coarse-textured surface (Barton 1991). The vegetation is *E. crebra–E. melanophloia* woodland with an understorey of *H. contortus*. Average annual rainfall is 708 mm with 70% falling in October–March, inclusive (Cook and Russell 1983). The site was burnt in spring 1988 and remained ungrazed until grazing treatments commenced in December 1989. Grazing treatments continued until March 1996.

The overall study (described by MacLeod and McIntyre 1997) consisted of 4 land classes based on the dominant tree species and 3 stocking rates on either native pasture or legume–oversown native pasture. This paper will focus on a subset of data including 2 land classes (narrow-leaved ironbark and silver-leaved ironbark), at 3 nominal stocking rates (0.3, 0.6 and 0.9 beasts/ha) in both native pasture and legume-oversown native pasture. There were 2 replicates of the 0.3 and 0.6 beasts/ha stocking rates for the native pasture and legume-oversown native pasture in both land classes. However, there was only 1 replicate for the 0.9 beasts/ha treatment in each of the 2 land classes and only for the legume-oversown native pasture.

The depth of the soil A horizon varied but was typically 20–30 cm in the narrow-leaved ironbark and 40–50 cm in the silver-leaved ironbark (A. Barton, personal communication). Fences were located so that paddocks contained only 1 land class. Paddock sizes (6.6, 3.3 and 2.2 ha) were varied so that 2 animals grazed each paddock. Initially, 2 weaner Belmont Red steers grazed each paddock for the first year and one of these was replaced at the end of this first year. The remaining steer was replaced after 2 years with another weaner and this procedure continued with animals remaining for 2 years.

Legume oversowing

The 6 legumes, sown by band seeder (Cook *et al*. 1993), were *Macroptilium atropurpureum* (Siratro), *Chamaecrista rotundifolia* (Wynn cassia), *Stylosanthes guianensis* var. *intermedia* (Fine stem stylo), *S. scabra* (Seca stylo), *Aeschynomene falcata* (Bargoo joint-vetch) and *Lotononis bainesii* (lotononis). Molybdenised superphosphate fertiliser was applied at 45 kg/ha at sowing. The legumes were oversown twice: initially in November 1989 and again in February 1993 because severe drought (see below) had precluded satisfactory legume establishment from the 1989 sowing.

Stocking rates

The severe drought conditions experienced throughout this study and the need to resow the legumes in February 1993 necessitated changes to the notional stocking rates of 0.3, 0.6 and

0.9 beasts/ha (Table 1). Stocking rates were halved in all paddocks over 4 periods, for a cumulative total of 22 months from December 1989–February 1993. All paddocks were destocked from February–April 1993 when some grazing treatments were altered.

From June 1993 until grazing concluded in March 1996, all native pasture treatments were grazed at the original stocking rates. Treatments designated as 0.9 beasts/ha with legume-oversown native pasture were grazed at 0.9 beasts/ha. However, treatments designated as 0.3 and 0.6 beasts/ha with oversown native pasture were stocked at half the originally proposed stocking rates. Subsequently, continuing drought and a severe feed deficit, particularly in late winter in 1994, necessitated supplementation with a ration of pasture hay (detailed in MacLeod and Cook 2004).

Measurements

Twenty permanent quadrats, each 0.5 × 0.5 m, were established in 2 nests each of 10 quadrats in each paddock in autumn 1990. These 20 quadrats were subjectively selected to contain a total of approximately 60 *H. contortus* plants which were selected to represent the range of plant sizes and plant densities. These 20 quadrats were positioned in the "interzone" between *H. contortus* and *Aristida* spp. "patches" (Wandera 1993) in order to monitor the fate of individual plants. In the oversown native pasture, quadrats were located on the undisturbed pasture between the bands that were disturbed by the sowing of the legumes (Cook *et al*. 1993).

Previous attempts to monitor individual *H. contortus* plants (J. C. Tothill, personal communication) indicated that plants fragment with increasing age (Samuel and Hart 1995) and it is difficult to follow the fate of plant segments. Consequently, we delineated individual plants in the permanent quadrats using a pantograph (Williams 1970) to record these plants together with any plant segments.

Commencing in autumn 1990, the position of individual *H. contortus* plants in each quadrat was charted and the diameter measured firstly along the widest diameter and secondly the diameter in the perpendicular direction to this widest diameter. All plants of *H. contortus* were classified as mature or seedlings (<1 cm diameter). Subsequent recordings were made annually in autumn when the survival and size of existing plants were recorded along with any seedling recruitment. [We acknowledge that this seedling recruitment measured in autumn fails to account for those seedlings which emerge and then die prior to autumn (Orr and Paton 1997). This fact is highlighted in the discussion of a subsequent paper in this series (Orr 2004)].

Calculations

Basal area of *H. contortus* was calculated on an individual quadrat basis as the area occupied by all *H. contortus* plants in the quadrat by assuming plants to be circular. (When the plant was not circular, the diameter was assumed to be the mean of the 2 diameters measured for that plant). Individual plant size was determined as the area covered by each plant and was calculated by

Table 1. Actual stocking rate history for 3 nominal stocking rate treatments over the study period from November 1989–March 1996.

Nominal stocking rate	NP[1] 0.3	NP 0.6	NP+Leg[2] 0.3	NP+Leg 0.6	NP+Leg 0.9
Period			(beasts/ha)		
Nov 89–Mar 90	0.3	0.6	0.3	0.6	0.9
Mar 90–Jul 90	0.15	0.3	0.15	0.3	0.45
Jul 90–Jan 91	0.3	0.6	0.3	0.6	0.9
Jan 91–Jun 91	0.15	0.3	0.15	0.3	0.45
Jun 91–Aug 91	0.3	0.6	0.3	0.6	0.9
Aug 91–Jul 92	0.15	0.3	0.15	0.3	0.45
Jul 92–Dec 92	0.3	0.6	0.3	0.6	0.9
Dec 92–Feb 93	0.15	0.3	0.15	0.3	0.45
Feb 93–Apr 93	nil	nil	nil	nil	nil
Apr 93–Jun 93	0.3	0.3	0.3	0.3	0.45
Jun 93–Mar 96	0.3	0.6	0.15	0.3	0.9

[1] NP = native pasture.
[2] NP+Leg = native pasture plus legume.

dividing the total basal area per quadrat by the number of individual plants (incorporating the number of segments making up each of these 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 (after O'Connor 1994). The fraction not turning over was the number of individual plants or basal area present in 1990 and still present in 1996. Plant survival was analysed using a proportional hazards survival model (Cox 1972).

Statistical analysis

Paddocks were located on either side of Hogarth Creek with, generally, 1 replicate on the eastern slope and 1 on the western slope. However, the 2 paddocks grazed at 0.6 beasts/ha in the narrow-leaved ironbark, native pasture treatment had both replicates on the eastern slope. The land class and stocking rate treatments were assumed to be completely randomised within a 'replicate'.

The 0.9 beasts/ha stocking rate treatment was excluded from all statistical analyses because it was not present for the native pasture treatments and was not replicated for the legume-oversown native pasture treatments. However, results from this treatment have been included for illustrative purposes.

The data were analysed by residual maximum likelihood (REML) with models including the fixed effects of pasture type (native pasture and oversown native pasture), land class (silver-leaved ironbark and narrow-leaved ironbark) and stocking rate (0.3 and 0.6 beasts/ha) and the random effects of replicate and paddocks within replicate. Significance of effects in the model would normally be tested by the Wald statistic. However, the Wald statistic has an asymptotic chi-squared distribution, and tends to lead to an upward bias in the significance levels for smaller data sets. Therefore, an approximate F-test based on the Wald statistic was used to test effects in the model.

Due to the sequential nature of the Wald statistic, the 3-way interaction was tested first and was almost always non-significant. Therefore, the 3-way interaction was removed from the model and the 2-way interactions were tested. The model was reduced by stepwise elimination of non-significant (P>0.05) interactions until only main effects and significant interactions were present. Predicted means for the significant interactions were tabulated. Finally, as only a few interactions were significant, interactions were removed from all models and the main effects tested and predicted means tabulated.

Results

Seasonal conditions

The overriding climatic condition throughout this study was drought with 6 consecutive years of below average rainfall (Figure 1). Overall, the site experienced moderate drought (395–441 mm received in 12 months) for 39 months and severe drought (less than 395 mm received in 12 months) for 21 months as determined by RAINMAN (Clewett *et al*. 1994). By 1993, the previous 4 consecutive growing seasons had been the driest since district rainfall records commenced in 1887. Furthermore, total rainfall for the 5 years to June 1994 was the lowest for any continuous 5-year period. Thus, the results should be interpreted accordingly.

Table 2. Plant turnover[1] of: (a) plant number and (b) basal area of *H. contortus* between 1990 and 1996 in relation to land class, stocking rate and pasture type in *H. contortus* pasture in southern Queensland.

(a)

Variable	Treatment	Plant number
Land class	Narrow-leaved ironbark	78.5a[2]
	Silver-leaved ironbark	64.5b
Stocking rate × Pasture type	0.3 beasts/ha, native pasture	69.3ab
	0.3 beasts/ha, NP + legume	76.6a
	0.6 beasts/ha, native pasture	79.6a
	0.6 beasts/ha, NP + legume	59.5b

(b)

Variable	Treatment	Basal area
Land class	Narrow-leaved ironbark	16.9a
	Silver-leaved ironbark	–21.8b
Stocking rate	0.3 beasts/ha	–8.4a
	0.6 beasts/ha	3.5a
	0.9 beasts/ha	48.1[3]
Pasture type	Native pasture	–8.9a
	NP + legume	4.0a

[1] Plant turnover for plant number and 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 (after O'Connor 1994). The fraction not turning over was the number of individual plants or basal area present in 1990 and still present in 1996.
[2] Within parameters, values followed by the same letter are not significantly different (P>0.05).
[3] Data included for completeness only.

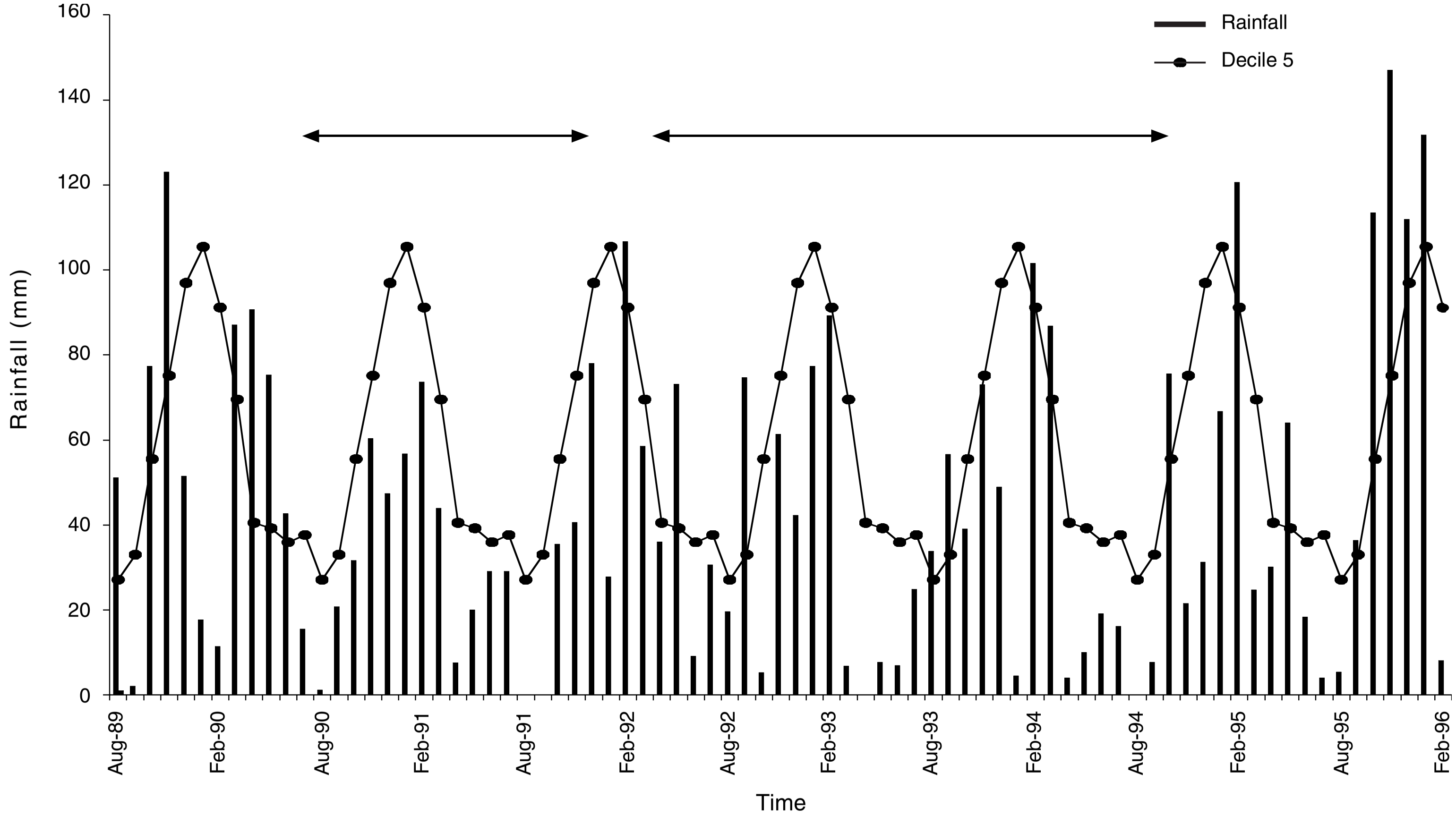

Figure 1. Monthly rainfall recorded at "Glenwood" (bars) between August 1989 and February 1996 compared with decile 5 rainfall (continuous). Arrows (← →) indicate times of drought during the experimental period as defined by RAINMAN (Clewett *et al*. 1994).

Plant turnover

Over the 6 years of this study, a total of 3909 *H. contortus* plants were studied — 1880 plants present in 1990 plus 2029 seedlings recorded between 1991 and 1996. Turnover for plant numbers was higher (P<0.05) for the narrow-leaved ironbark than for the silver-leaved ironbark land class and there was an interaction between stocking rate and pasture type (Table 2a). Turnover for basal area was also higher (P<0.05) for the narrow-leaved ironbark than for the silver-leaved ironbark land class (Table 2b). Negative values for the silver-leaved ironbark land class, 0.3 beasts/ha stocking rate and for native pastures indicate that basal area in these treatments was higher in 1996 than in 1990.

Population density

The density of *H. contortus* plants varied greatly between years with the density in 1990, 1991 and 1995 being considerably higher than in 1992 and 1993. Density was greater (P<0.05) in the silver-leaved ironbark than in the narrow-leaved ironbark land class in 1990 and from 1992 to 1994 (Figure 2a). There was a significant (P<0.05) interaction between stocking rate and pasture type from 1992–1994 with weaker evidence (P<0.10) of the interaction in 1995 (Figure 2b). The density of *H. contortus* plants in these years was less for 0.3 beasts/ha in the oversown native pastures than for the other 3 treatments.

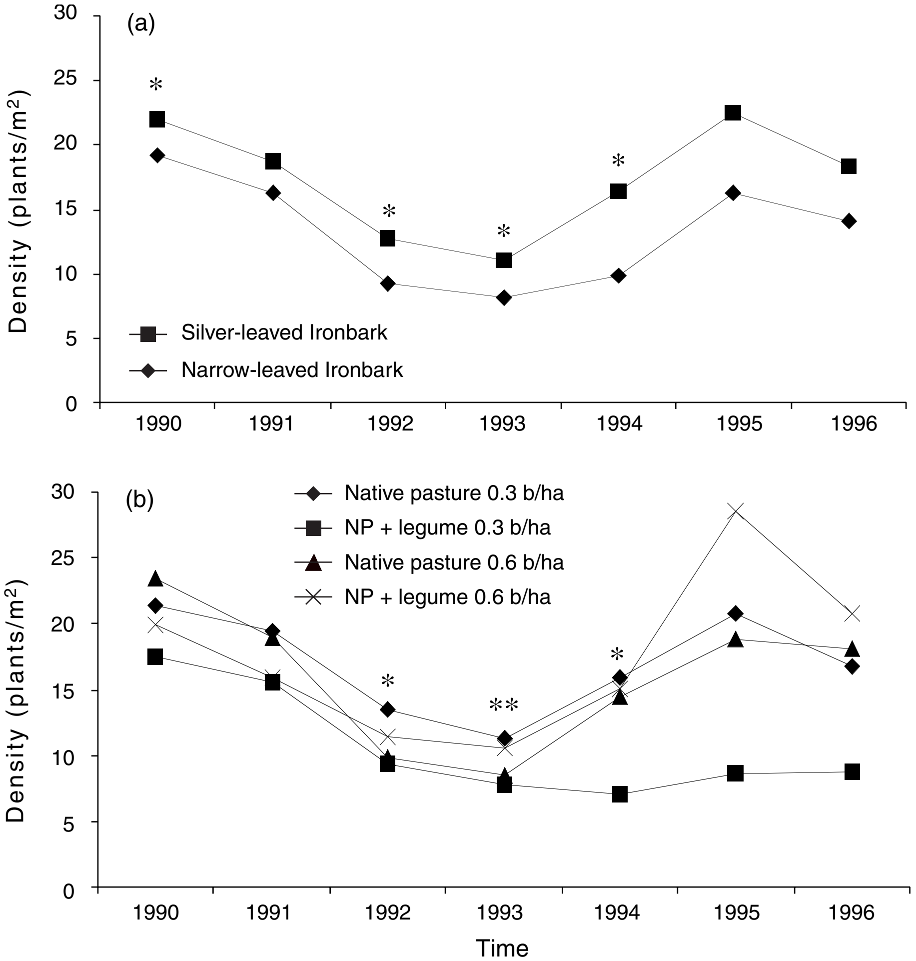

Figure 2. Changes in density of *H. contortus* in autumn between 1990 and 1996 in relation to: (a) land class; and (b) stocking rate × pasture type in *H. contortus* and oversown pasture in southern Queensland. Within years, asterisks indicate that significant (P<0.05) differences occurred between treatments.

Seedling recruitment

There were no significant interactions between treatments for recruitment of *H. contortus.* Recruitment was generally greater for the silver-leaved ironbark than the narrow-leaved ironbark land class although the difference was significant ($P<0.05$) only in 1993. There were no consistent effects of stocking rate on recruitment (Figure 3b). Native pasture had greater recruitment than oversown pasture in 1992 ($P<0.10$), 1994 ($P<0.05$) and 1996 ($P<0.10$)(Figure 3c).

Plant survival

There were few differences in survival of the original *H. contortus* plants between 1990 and 1996 (Figures 4a, 4b, 4c). Survival of these original plants was higher ($P<0.05$) in the silver-leaved ironbark than the narrow-leaved ironbark land class and was also influenced ($P<0.05$) by a stocking rate 3 pasture type interaction. Survival of plants from the 1991, 1992 and 1994 seedling cohorts between the time of their recruitment and 1996 was similar (Figures 4d–4l). The 1993 recruitment was very small and there was limited time for the 1995 cohort so these data are not presented. For the 1991 and 1992 plants, survival was influenced ($P<0.05$) by a stocking rate 3 pasture type interaction whereas survival of the 1994 plants showed a land class effect being higher ($P<0.05$) in the narrow-leaved ironbark than in the silver-leaved ironbark land class.

Changes in basal area

Basal area of *H. contortus* declined between 1990 and 1992 and then increased until 1996. Basal area was consistently greater in silver-leaved ironbark than in the narrow-leaved ironbark land class (Figure 5a). There was a significant ($P<0.05$) interaction between stocking rate and pasture type from 1992–1995 with weaker evidence ($P<0.10$) of the interaction in 1996 (Figure 5b). Basal area in these years was greater for 0.6 beasts/ha than 0.3 beasts/ha in the oversown native pastures while there was no effect of stocking rate in the native pastures.

Changes in plant size

The original plants declined in area between 1990 and 1992 with no differences in size due to either land class, stocking rate or pasture type (Figure 6a). After 1992, these original plants increased in size although the difference was significant ($P<0.05$) only in 1995 when plants were larger ($P<0.05$) at 0.6 beasts/ha than at 0.3 beasts/ha. Increases in plant sizes were similar for the 1991, 1992 and 1994 seedlings with no differences due to land class, stocking rate or pasture type, although, for the 1991 and 1994 plants, plant size tended to be higher at 0.9 beasts/ha than at the other 2 stocking rates (Figures 6b, 6c, 6d).

Discussion

Effects of treatments

The major result from this study is the overriding impact of rainfall — as reflected in the most severe drought in over 100 years of rainfall recordings — and the relative lack of treatment effects. This result reflects a similar finding regarding the performance of sown legumes at this site over the same time period (Jones *et al*. 2000). Similarly, this overriding impact of drought on population dynamics supports a similar conclusion by O'Connor (1994), who reported that the dynamics of populations of perennial grasses in southern Africa was also more strongly influenced by rainfall variability than by grazing. Furthermore, O'Connor (1985) reviewed those factors influencing fluctuations in species abundance in African grassland savannas and concluded that soil moisture was the major determinant of botanical change. Nevertheless, the current study does indicate that the population dynamics of *H. contortus* are also influenced by landscape position and, to a lesser extent, stocking rate and legume oversowing.

There was a clear trend for most population parameters of *H. contortus* to be consistently higher in the silver-leaved ironbark than in the narrow-leaved ironbark land class and this is further reflected in reduced population turnover rates for both plant density and basal area. These differences are probably associated with soil differences. Soils supporting silver-leaved ironbark generally have greater depth, better moisture-holding capacity and marginally higher fertility than the narrow-leaved ironbark land class.

There was a general trend for density, survival and basal area of *H. contortus* to be influenced by a stocking rate 3 pasture type interaction

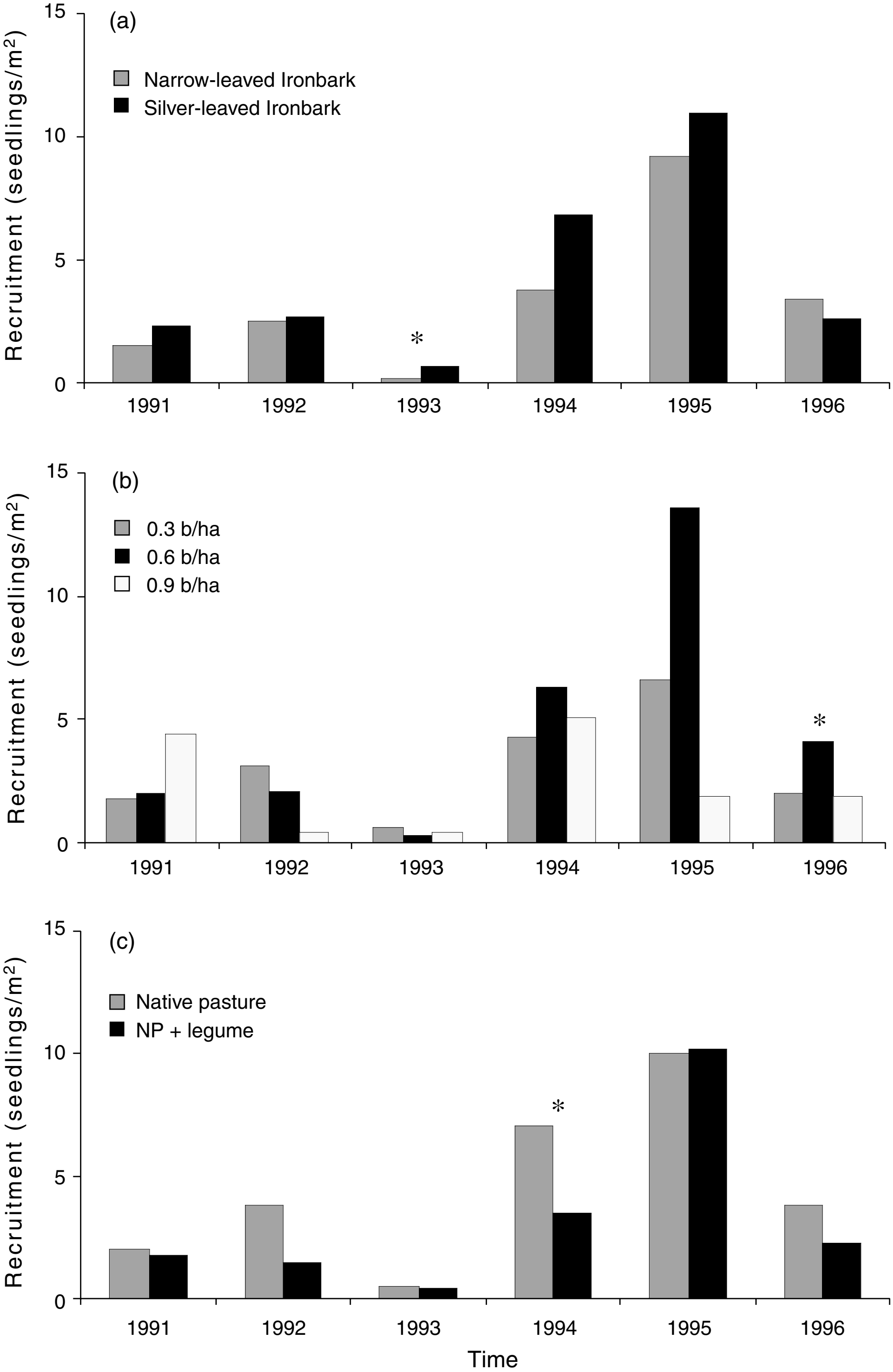

Figure 3. Changes in seedling recruitment of *H. contortus* measured in autumn between 1991 and 1996 in relation to: (a) land class; (b) stocking rate; and (c) pasture type in *H. contortus* and oversown pasture in southern Queensland. Within years, asterisks indicate that significant (P<0.05) differences occurred between treatments. Data for the unreplicated 0.9 beasts/ha stocking rate are included for completeness only.

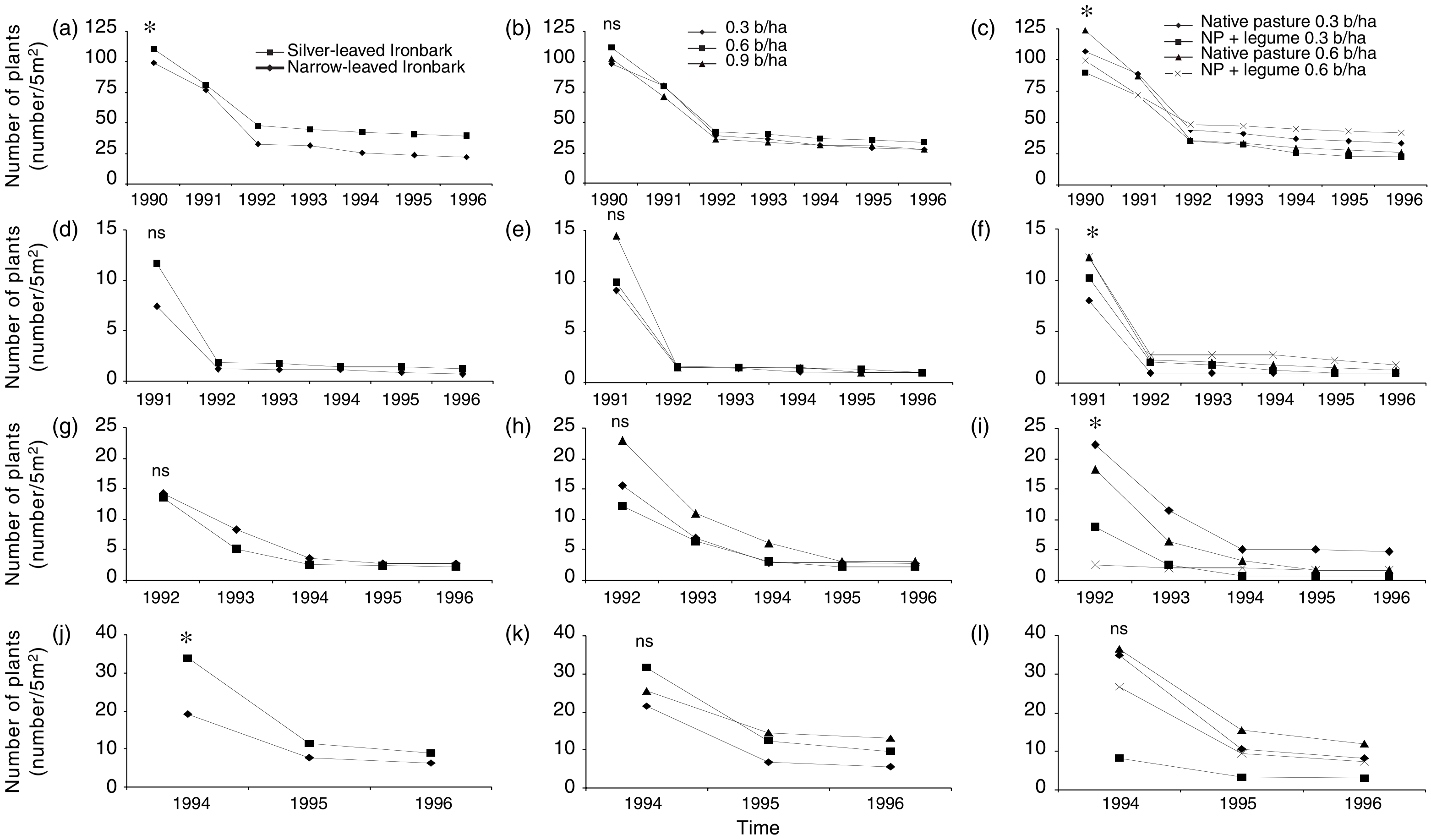

Figure 4. Changes in the survival of *H. contortus* plants between 1990 and 1996 for (1) the original plants in relation to: (a) land class; (b) stocking rate; and (c) stocking rate × pasture type; (2) the 1991 seedling cohort in relation to: (d) land class; (e) stocking rate; and (f) stocking rate × pasture type; (3) the 1992 seedling cohort in relation to: (g) land class; (h) stocking rate; and (i) stocking rate × pasture type; and (4) the 1994 seedling cohort in relation to: (j) land class; (k) stocking rate; and (l) stocking rate × pasture type in *H. contortus* and oversown pasture in southern Queensland. Asterisks indicate that significant ($P<0.05$) differences in survival occurred. Data for the unreplicated 0.9 beasts/ha stocking rate are included for completeness only.

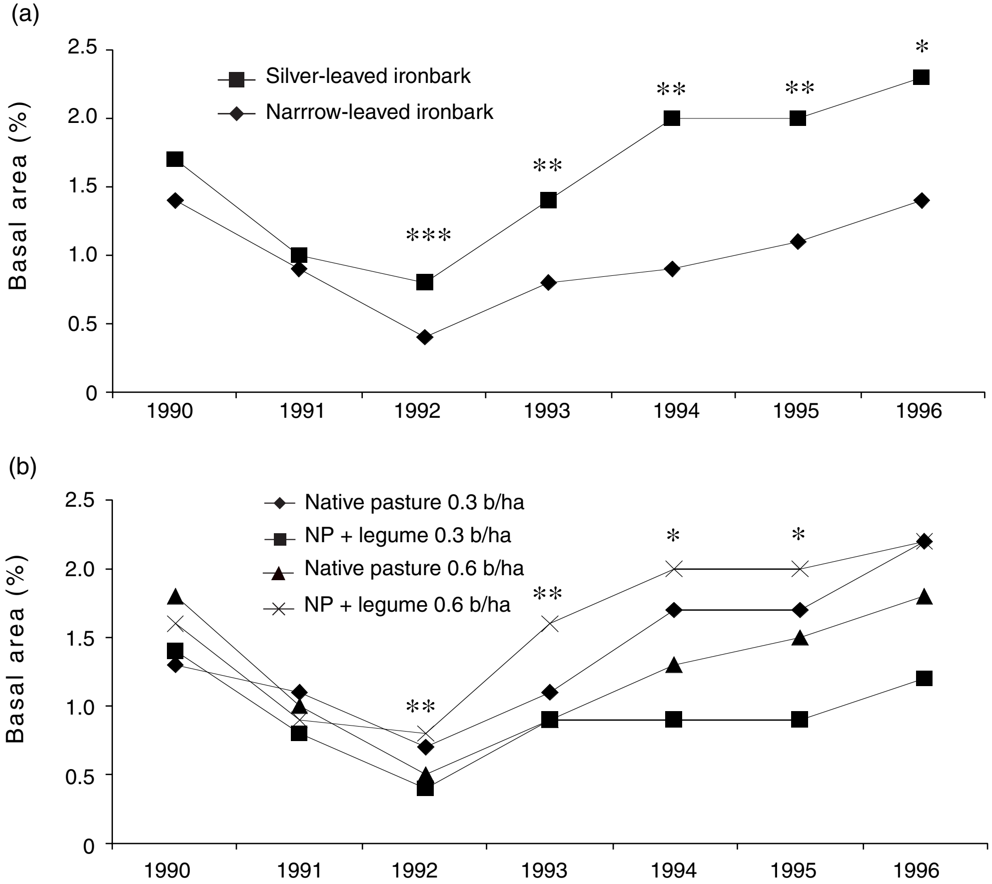

Figure 5. Changes in the basal area of *H. contortus* in autumn between 1990 and 1996 in relation to: (a) land class; and (b) stocking rate × pasture type in *H. contortus* and oversown pasture in southern Queensland. Within years, asterisks indicate that significant (P<0.05) differences occurred between treatments.

although there is no clear biological explanation for this interaction. This stocking rate 3 pasture type interaction was also evident in *H. contortus* seed production (Orr *et al*. 2004a). Since overall legume establishment was low and highly variable, part of this interaction may be a reflection of *H. contortus* responding to the reduced plant competition resulting from the application of herbicide associated with the band sowing of the legumes.

Stocking rate (0.3 and 0.6 beasts/ha) had less impact than landscape position. One possible explanation is that any stocking rate effect may have been masked by the alterations to the original stocking rates that were necessary due to drought and the associated requirement to resow the legumes. A second, and more likely, reason for the limited impact of stocking rate is that this study did not run long enough. In a separate study in central Queensland, where drought conditions were less severe than at "Glenwood" (Orr *et al*. 2001), differences in *H. contortus* plant density due to increased stocking rate were not apparent until 6 years of stocking rate treatments.

Despite the limited impact of the 0.3 and 0.6 beasts/ha stocking rate treatments, there were indications of a stocking rate impact at 0.9 beasts/ha. Firstly, seedling recruitment in the initial year of our study was higher at 0.9 beasts/ha than at the other 2 stocking rates (Figure 3b) as found in the initial year of a similar study in southern Africa (O'Connor 1994). O'Connor demonstrated that this initial pattern was reversed with further heavy grazing which reduced seed production. A similar reversal also occurred in our study. Secondly, plants from the 1991 and 1994 seedling cohorts tended to be larger at 0.9 than 0.6 and 0.3 beasts/ha (Figures 6b, 6c, 6d), which is consistent with other

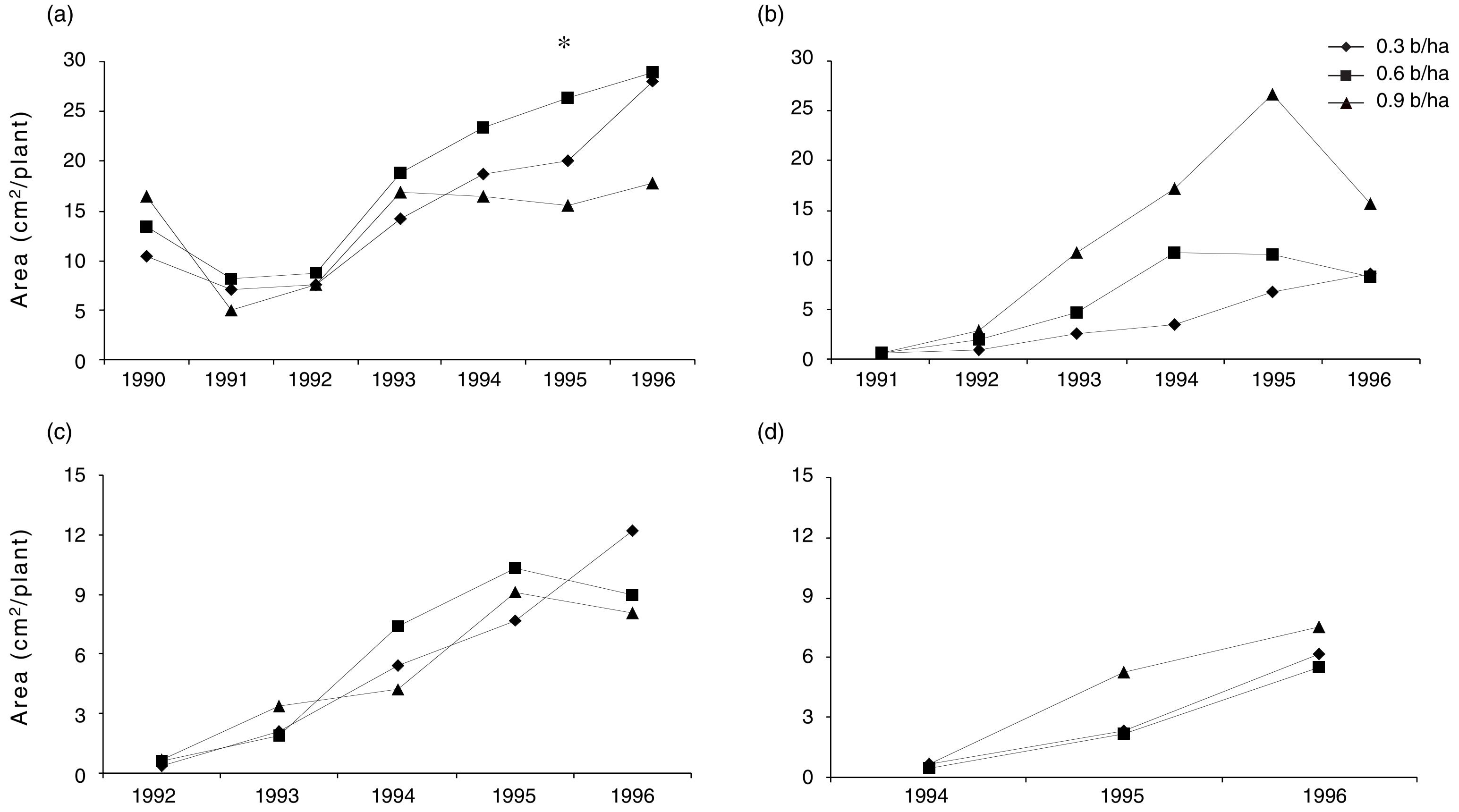

Figure 6. Changes in plant size of *H. contortus* between 1990 and 1996 in relation to stocking rate for: (a) original plants; (b) 1991 seedling cohort; (c) 1992 seedling cohort; and (d) 1994 seedling cohort in *H. contortus* and oversown pasture in southern Queensland. Within years, asterisks indicate that significant ($P<0.05$) differences occurred between treatments. Data for the unreplicated 0.9 beasts/ha stocking rate are included for completeness only.

data (Campbell 1996; Orr and Paton 1997), indicating that early defoliation, as occurs under heavy grazing, promotes tillering in *H. contortus.*

Legume oversowing had little apparent impact on the dynamics of *H. contortus* apart from a minor reduction in seedling recruitment. A probable reason is that, as with stocking rate, this study did not run long enough. While legume oversowing reduced *H. contortus* plant density in a separate study in central Queensland, this effect was apparent only after 8 years and was associated with increasing plant densities (> 25 plants/m^2) of *Stylosanthes scabra* cv. *Seca* (Orr *et al*. 2001). No such increases in legume density were recorded at "Glenwood".

Population processes

Recruitment. Plant recruitment measured in autumn occurred every year, even during the severe 1992–93 summer drought (Figure 3), and the large variation between years reflected differences in both rainfall and the size of the soil seed bank (Orr *et al.* 2004a). Wandera (1993) recorded similar levels of recruitment and similar large variation between years at "Glenwood". Orr and Paton (1993) recorded similar levels of *H. contortus* recruitment in central Queensland; however, in that study, recruitment declined with increasing stocking rate from 5 ha/beast to 2 ha/beast. In southern Africa, O'Connor (1994) recorded seedling recruitment of *H. contortus* up to 5 seedlings/m^2 in years with generally below average rainfall. All these values for seedling recruitment which were measured in autumn were substantially below the 80–100 seedlings/m^2 recorded in spring by Shaw (1957) and Orr *et al.* (1997). However, these studies involved spring burning and Campbell (1996) described how spring burning promoted *H. contortus* seedling recruitment.

Plant survival. Many of the *H. contortus* plants present at the commencement of the current study in 1990 persisted until the end of the study in 1996, despite apparently accelerated mortality between 1990 and 1992 due to drought (Figures 4a, 4b, 4c). These data indicate a maximum life span for individual tussocks of at least 6 years. Few comparable data are available for *H. contortus*. Canfield (1957) reported that, in Arizona, America *H. contortus* survived for 4 years under grazing and for 6 years in exclosures. This compares with survival of plants for at least 14 years in central Queensland, with longevity greatest at the lightest stocking rate (D. M. Orr, unpublished data). Clearly, maximum life span for *H. contortus* in the Australian environment is greater than that reported by Canfield (1957). Northup *et al*. (1999) highlighted the importance of persistence by perennial grass tussocks, such as *H. contortus*, in maintaining soil microbial processes and landscape function.

Seedlings of *H. contortus* survived well at all stocking rates despite persistent drought (Figures 4d–4l). These survival data, generally 20–40% survival over the first year, are similar to other data recorded at "Glenwood" (Wandera 1993). Such survival contrasts, for example, with the failure of *Themeda triandra* (kangaroo grass) seedlings to survive at Katherine, Northern Territory, where all seedlings died by the end of the following wet season with the majority dying over the dry season (Mott and Andrew 1985). Orr and Paton (1997) monitored the development of 2 cohorts of *H. contortus* seedlings across a range of grazing treatments over 2 years elsewhere in southern Queensland and reported few differences in survival due to grazing. However, large differences in seedling survival occurred between the 2 years and this was attributed to the effects of contrasting rainfall patterns in the initial 2-month period following germination. Data from both the current study and Orr and Paton (1997) indicate an initial rapid loss of seedlings followed by a period where the rate of loss of seedlings declines.

Tussock growth. Limited data are available on changes in plant size in *H. contortus*, which occur as a result of new tiller production. Mott *et al*. (1992) reported that most new tillers were produced at the start of the growing season when 60% of tiller buds present at the base of old tillers produced new tillers with reduced numbers of tillers being produced later in the summer. The increase in plant size at 0.9 b/ha (Figures 6b, 6c, 6d) attests to the inherent tillering ability of *H. contortus* and its ability to recover from the effects of drought. Plant sizes recorded in this study are consistent with the range of 1–12 cm^2 (1–4 cm diameter) for 18-month-old seedling plants in southern Queensland (Orr and Paton 1997) and 20–115 cm^2 (5–12 cm diameter) for *H. contortus* in northern Queensland (Northup *et al*. 1999). The original plants declined in size between 1990 and 1992 (Figure 6a), probably as a result of the death of tillers caused by severe drought. Similarly, death of tillers probably contributes to the increasing segmentation of older *H. contortus* tussocks.

Plant density. This study indicates that relatively large fluctuations in plant density occur over a relatively short period as a combination of the death of existing plants, due mainly to drought, and to seedling recruitment. Both the levels of plant densities and the relatively large fluctuations recorded in this study are consistent with those reported elsewhere in southern (Wandera 1993; Campbell 1996) and central (Orr *et al*. 2001) Queensland and southern Africa (O'Connor 1994).

Basal area. This study indicates that fluctuations in basal area also occur over a relatively short period and result from either increases or decreases in size of tussocks present in the pasture. The increase in basal area after 1992 indicates the capacity of *H. contortus* to respond to improved rainfall conditions and highlights the importance of maintaining populations so that these plants can respond to improved rainfall through tillering. The basal areas recorded here are similar to those recorded elsewhere in southern Queensland (Orr and Paton 1997) and in southern Africa (O'Connor 1994). A feature of the Orr and Paton (1997) study was that grazing regimen influenced basal area of *H. contortus*. As discussed above, the failure to detect any grazing effect on basal area in the current study probably reflects the major influence of below average rainfall.

Plant turnover. Rates for turnover (Table 2) of plant numbers are similar to the 60% turnover of plants within 5 years in southern Queensland (Mott *et al*. 1985) and for a similar time frame in South Africa (O'Connor 1994). In contrast, relatively lower turnover rates for basal area suggest that basal area is a less variable parameter in pastures. Furthermore, the negative rates for basal area turnover reflect the survival of the original (1990) plants together with the improved seasonal rainfall occurring after the 1991–92 summer. It is interesting that these negative values occur in the silver-leaved ironbark land class, at the lightest stocking rate and in the native pasture treatment and these are the 3 treatments where the impact of grazing can be expected to be the minimum.

Implications for grazing management

This study has demonstrated that *H. contortus* pastures have an appreciable turnover of individual plants within a relatively short time period due to continuing plant mortality and regular seedling recruitment. This highlights the importance of seedling recruitment for the persistence of this species and consequently the need for grazing management to optimise seedling recruitment.

Acknowledgements

Many people contributed to the setting up and overall conduct of the experiment as well as data collection and analysis. Particular acknowledgement is due to Mr D. McIvor, owner of "Glenwood", for making land and facilities available for this study and to Mr J. Ogden who competently maintained the experimental site throughout the study.

We thank colleagues in CSIRO and Department of Primary Industries for many useful discussions throughout the duration of the study and for assistance in data collection and interpretation. We are grateful to Mr R. M. Jones for constructive criticism of a draft of this manuscript and to Mr M. C. Yee who prepared the figures. Mr J. Hodgkinson kindly provided Figure 1.

This project was supported by the Meat Research Corporation (Project CS195) which is now Meat and Livestock Australia.

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(Received for publication March 10, 2003; accepted November 30, 2003)