Dynamics of plant populations in *Heteropogon contortus* (black speargrass) pastures on a granite landscape in southern Queensland. 2. Seed production and soil seed banks of *H. contortus*

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Abstract

Seed production and soil seed banks of *H. contortus* were studied in a subset of treatments within an extensive grazing study conducted in *H. contortus* pasture in southern Queensland between 1990 and 1996.

Seed production of *H. contortus* in autumn ranged from 260 to 1800 seeds/m^2 with much of this variation due to differences in rainfall between years. Seed production was generally higher in the silver-leaved ironbark than in the narrow-leaved ironbark land class and was also influenced by a consistent stocking rate × pasture type interaction.

Inflorescence density was the main factor contributing to the variable seed production and was related to the rainfall received during February. The number of seeds per inflorescence was unaffected by seasonal rainfall, landscape position, stocking rate or legume oversowing. Seed viability was related to the rainfall received during March.

Soil seed banks in spring varied from 130 to 520 seeds/m^2 between 1990 and 1995 with generally more seed present in the silver-leaved ironbark than in the narrow-leaved ironbark land class. There were poor relationships between viable seed production and the size of the soil seed bank, and between the size of the soil seed bank and seedling recruitment.

This study indicates that *H. contortus* has the potential to produce relatively large amounts of seed and showed that the seasonal pattern of rainfall plays a major role in achieving this potential.

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Introduction

In an earlier paper (Orr *et al*. 2004a), we reported the impacts of landscape position, stocking rate and legume oversowing on the dynamics of *Heteropogon contortus* (black speargrass) populations in the southern speargrass region of Queensland. That study indicated that seedling recruitment was a major contributor to maintaining population density and basal area. Seedling recruitment was generally higher in the silver-leaved ironbark (*Eucalyptus melanophloia)* than the narrow-leaved ironbark (*E. crebra)* land class, tended to be higher in native pasture than in legume-oversown native pasture but was not consistently affected by stocking rate. We considered that these differences in seedling recruitment reflected differences in the size of the soil seed banks, which, in turn, reflected flowering of existing plants and subsequent seed production.

This paper reports changes in seed production and soil seed banks of *H. contortus* over 6 years in both native pasture and native pasture oversown with legumes as affected by landscape position and stocking rate.

Materials and methods

Grazing study

A grazing study was conducted between December 1989–March 1996 in a *H. contortus* pasture on a granite-derived soil at "Glenwood" station, 50 km west of Mundubbera (25°41′S, 150°52′E). The overall study consisted of 4 land classes 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. This grazing study was severely impacted by drought and further details are presented in Orr *et al*. (2004a).

Measurements

Seed production. Seed production of *H. contortus* was calculated as the product of inflorescence density and seeds per inflorescence. Inflorescence density was measured during late March each year between 1991 and 1996 in 20 permanent quadrats (Orr *et al*. 2004a) following the main flowering period for *H. contortus* which occurs during March (Tothill and Knox 1968). The number of seeds per inflorescence was determined annually from 5 inflorescences collected at random from each paddock. In 1996, plants flowered in late January and seeds per inflorescence data were unavailable. The mean value for each paddock for the period 1991–1995 was used to calculate seed production data for 1996.

Seed germination. Inflorescences containing fresh seed of *H. contortus* were collected at random from within the grazing study in April each year and stored in a laboratory. The germination of this seed was tested following 12 months storage because seed of *H. contortus* is dormant when produced and requires at least 6 months to overcome this dormancy (Tothill 1977). Three replicates each of 25 seeds were germinated in a germination cabinet set at 12 h day/12 h night and temperature of 30/20°C. Germinating seeds were counted and removed daily for 7 days and total germination was calculated as the cumulative total of daily germinations.

Germinable soil seed bank. The germinable soil seed bank of *H. contortus* was measured in spring each year between 1990–1995 by germinating seed contained in soil cores collected from the areas surrounding the permanent quadrats. Four cores, each 5cm diameter and 5 cm deep, were bulked to produce each sample and there were 15 samples (*i.e*. 60 cores) from each paddock. In the subsequent summer (when seed dormancy had been overcome), each sample was spread as a 2 cm thick layer on top of compacted sand in a 15 cm diameter drained plastic pot and seed in these samples was germinated by watering with an overhead sprinkler for 30 minutes daily in a glasshouse (Orr *et al*. 1996). After 6 weeks, seedlings of *H. contortus* were identified and counted. Only 1 wetting cycle was conducted as most seeds of *H. contortus* are recorded in this first wetting cycle (Orr 1999).

Statistical analysis

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.

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. Further details are presented in Orr *et al*. (2004a).

Linear regressions were used to investigate relationships between rainfall in February and inflorescence density, rainfall in March and seed germination, viable seed production and soil seed bank, and viable seed production and recruitment.

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

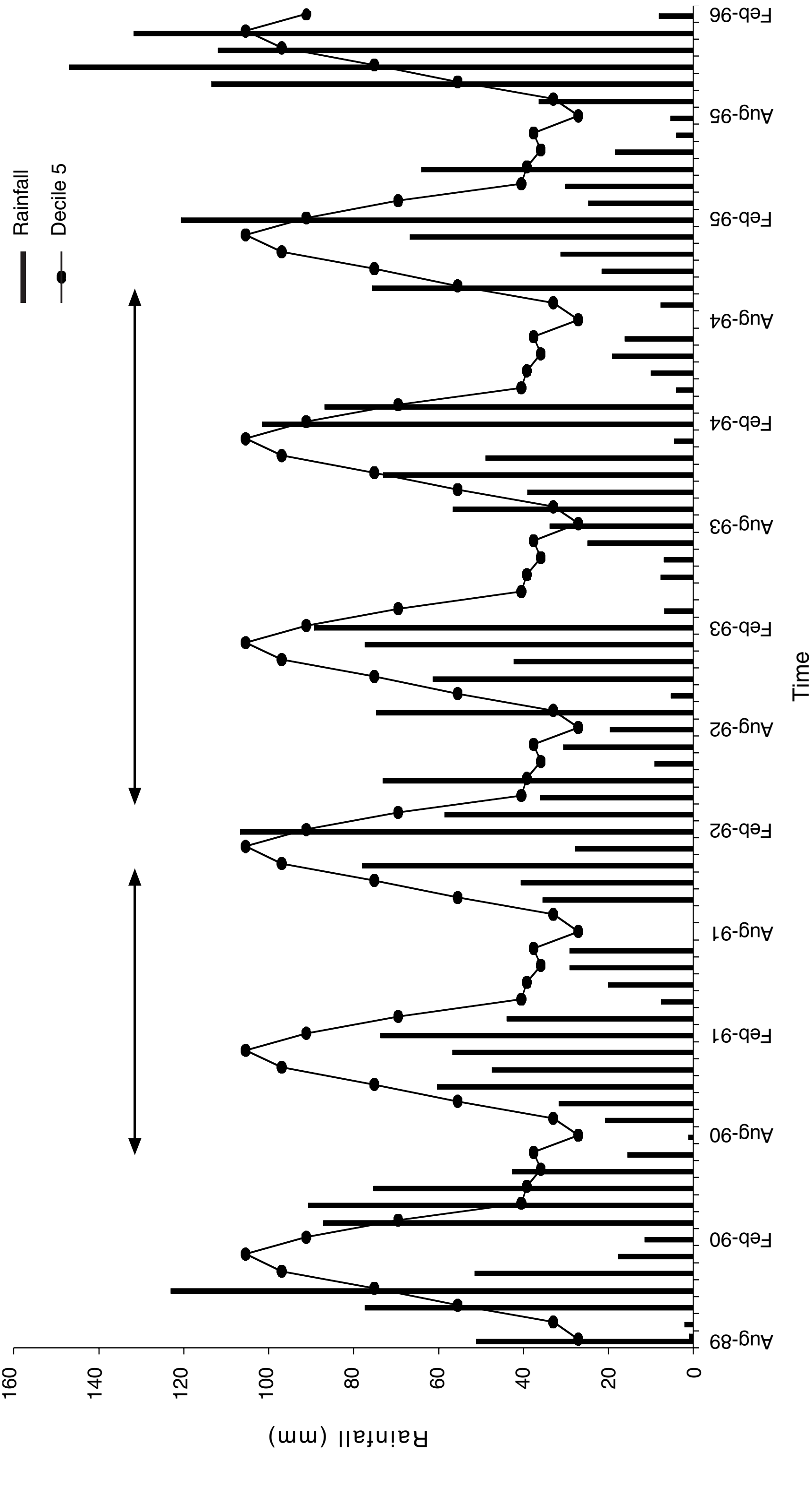

Figure 1. Monthly rainfall recorded at "Glenwood" (bars) between August 1989 and February 1996 compared with decile 5 rainfall (continuous). Arrows (← →) indicate times of drought during the experimental period as defined by RAINMAN (Clewett *et al.* 1994).

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.

Seed production

Seed production of *H. contortus* varied greatly between years and ranged across all treatments from 260 seeds/m^2 in 1991 to 1800 seeds/m^2 in 1995. Generally, more seed was produced in the silver-leaved ironbark than in the narrow-leaved ironbark land class (Figure 2a). There was a significant (P<0.05) interaction between stocking rate and pasture type in 1992, 1994 and 1995 (Figure 2b). Seed production was consistently higher for 0.3 beasts/ha than 0.6 beasts/ha in native pasture but this trend was not evident in oversown pasture.

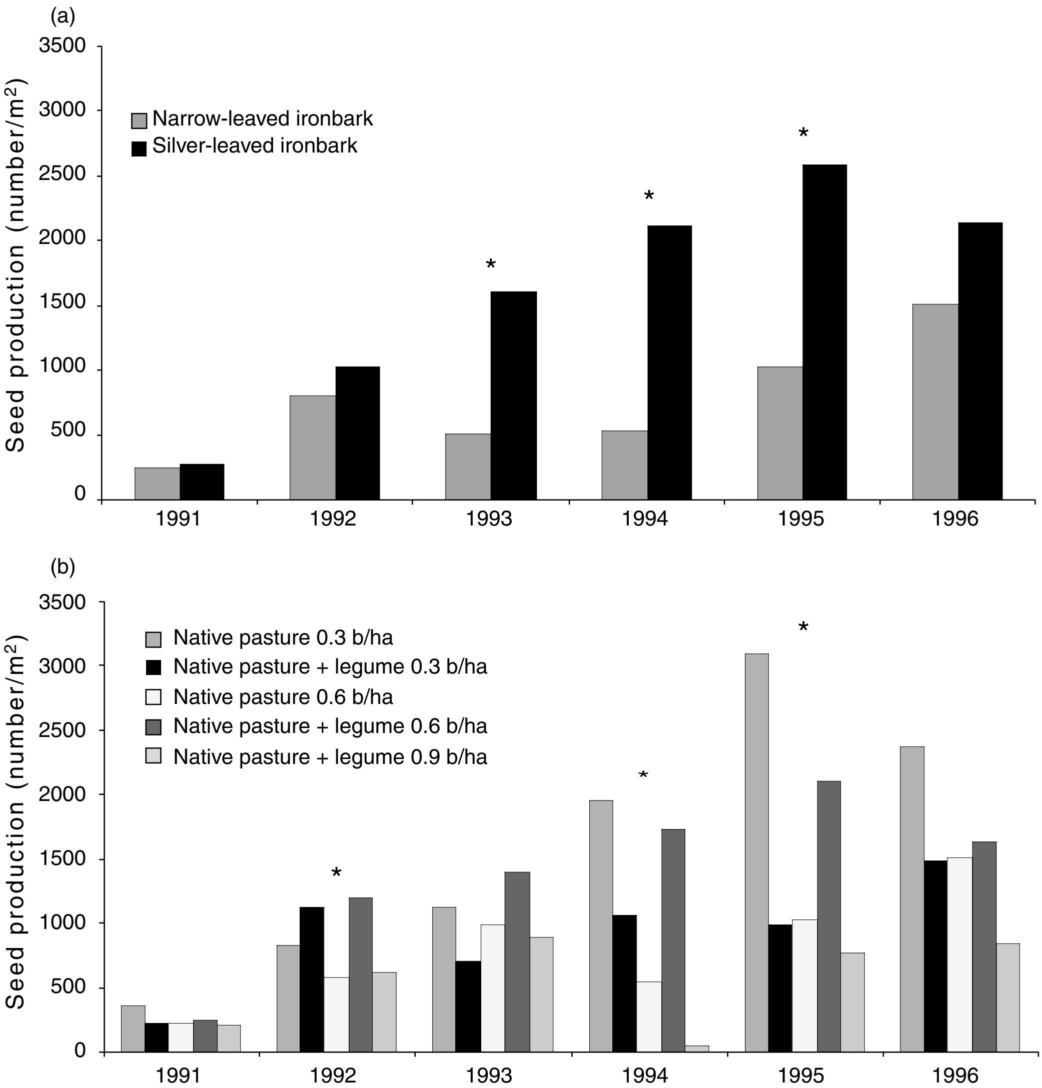

Figure 2. Seed production of *H. contortus* measured in autumn (1991–1996) in relation to: (a) land class; and (b) stocking rate × pasture type interaction in *H. contortus* pasture in southern Queensland. Within years, asterisks indicate that significant differences (P<0.05) occurred. Data for the unreplicated 0.9 beasts/ha stocking rate are included for completeness only.

Inflorescence density was the major factor influencing seed production and ranged from 23 inflorescences/m^2 in 1991 to 153 inflorescences/m^2 in 1995. As with seed production, inflorescence density was generally higher in the silver-leaved ironbark than in the narrow-leaved ironbark land class (Figure 3a). Inflorescence density measured in March was linearly related to rainfall recorded in February (Figure 4). Seed production was independent of the number of seeds per inflorescence which varied from 10.6–12.7 seeds/inflorescence with no significant differences between years, land classes, stocking rates or pasture types (data not presented).

Seed germination

Seed germination was linearly related to the rainfall recorded in March (Figure 5). Seed collected from land class, stocking rate and pasture type treatments in 1995 and germinated in 1996 indicated that these factors did not differentially influence seed germination.

Germinable soil seed banks

The soil seed bank of *H. contortus* varied from 130 in 1990 to 520 in 1994 and was higher (P<0.05) in the silver-leaved ironbark than in the narrow-leaved ironbark land class in 1992 and

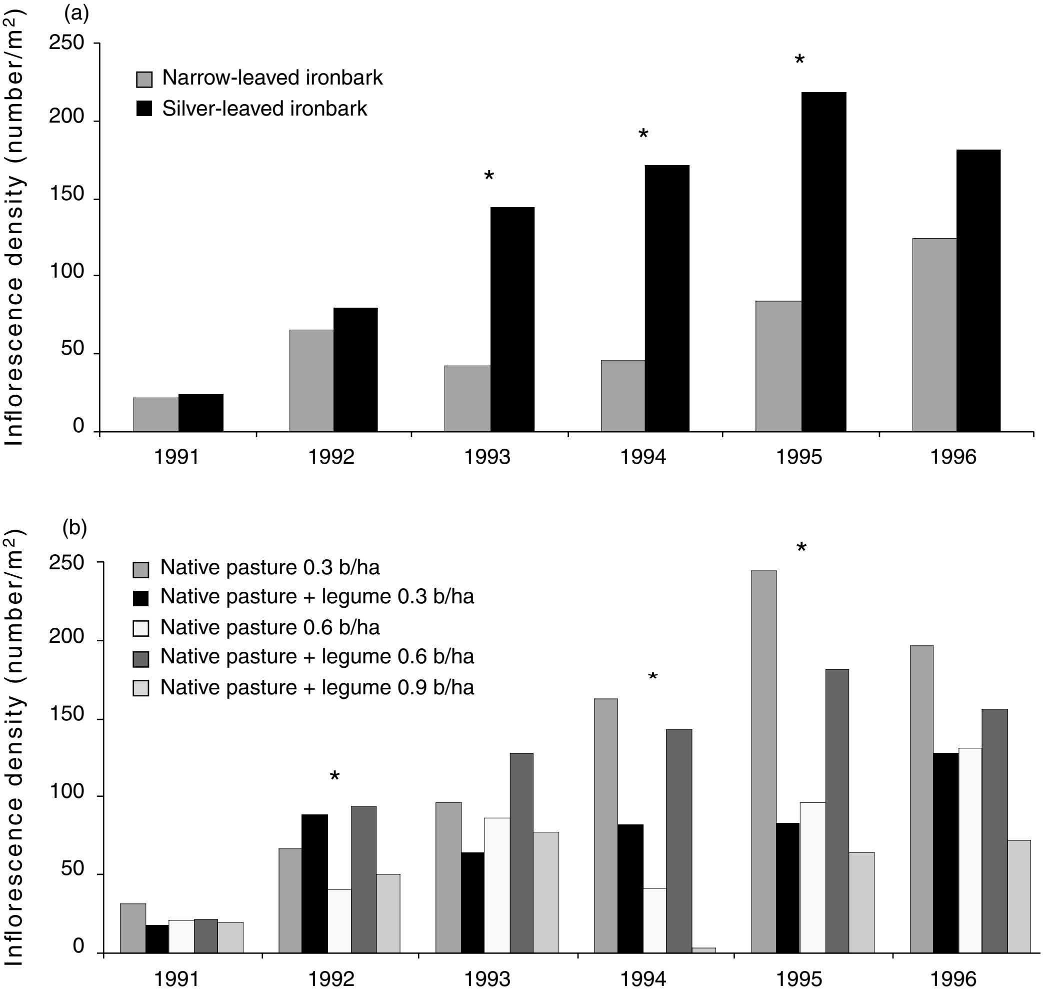

Figure 3. Inflorescence density of *H. contortus* measured in autumn (1991–1996) in relation to: (a) land class; and (b) stocking rate × pasture type interaction in *H. contortus* pasture in southern Queensland. Within years, asterisks indicate that significant differences (P<0.05) occurred. Data for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

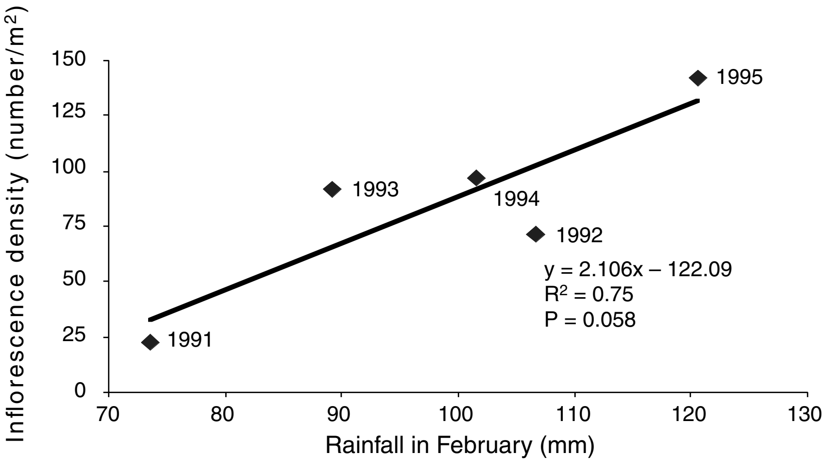

Figure 4. Relationship between inflorescence density of *H. contortus* in March (1991–1995) and rainfall during February in *H. contortus* pasture in southern Queensland.

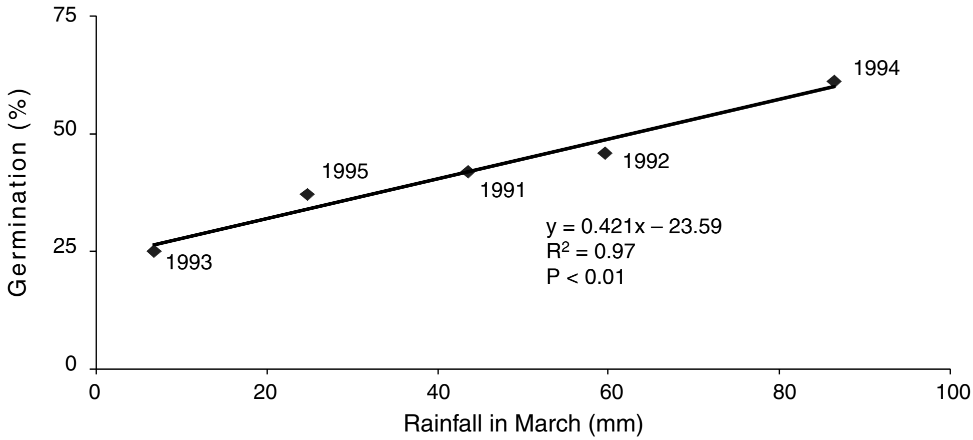

Figure 5. Relationship between germination of *H. contortus* seed at 12 months of age and rainfall during March when the seed was produced (1991–1995) in *H. contortus* pasture in southern Queensland.

1993 (Figure 6a). Soil seed banks tended to be higher at the lighter stocking rate (0.3 beasts/ha) but this trend was not significant ($P>0.05$) (Figure 6b). Seed banks were independent of pasture type (Figure 6c).

Relationships between seed production, seed banks and seedling recruitment

There was a poor relationship between viable seed production in autumn (*i.e.*, total seed production adjusted for variable seed germination) and the size of the soil seed banks measured in spring (Figure 7). The relationship between the size of the soil seed bank in spring and seedling recruitment in the subsequent autumn was also poor (Figure 8).

Discussion

This study has identified large variations in both seed production and soil seed banks of *H. contortus*. Inflorescence density and seed viability were major determinants of viable seed production and much of the variation in seed production results from the effects of rainfall in February and March on inflorescence density and seed viability, respectively. This study has also showed

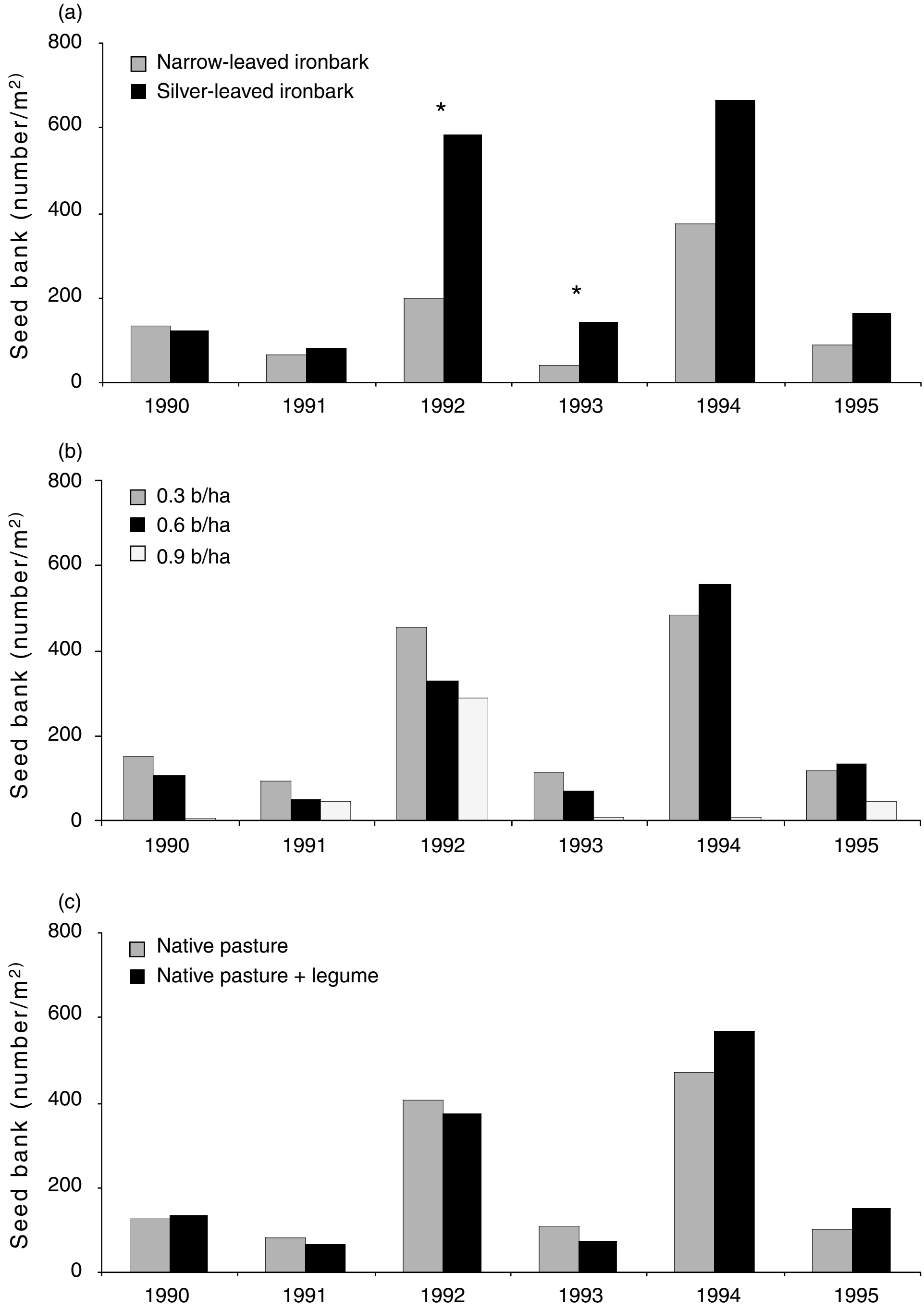

Figure 6. Soil seed bank of *H. contortus* in spring (1990–1995) in relation to: (a) land class; (b) stocking rate; and (c) pasture type in *H. contortus* pasture in southern Queensland. Within years, asterisks indicate that significant differences ($P<0.05$) occurred. Data for the unreplicated 0.9 beasts/ha stocking rate are included for completeness only.

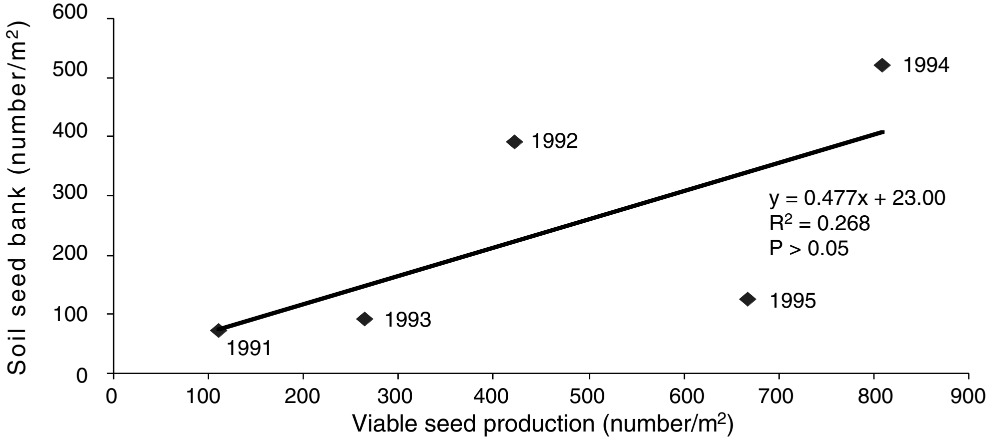

Figure 7. Relationship between the size of the soil seed bank in spring and viable seed production in the previous autumn (1991–1995) in *H. contortus* pasture in southern Queensland.

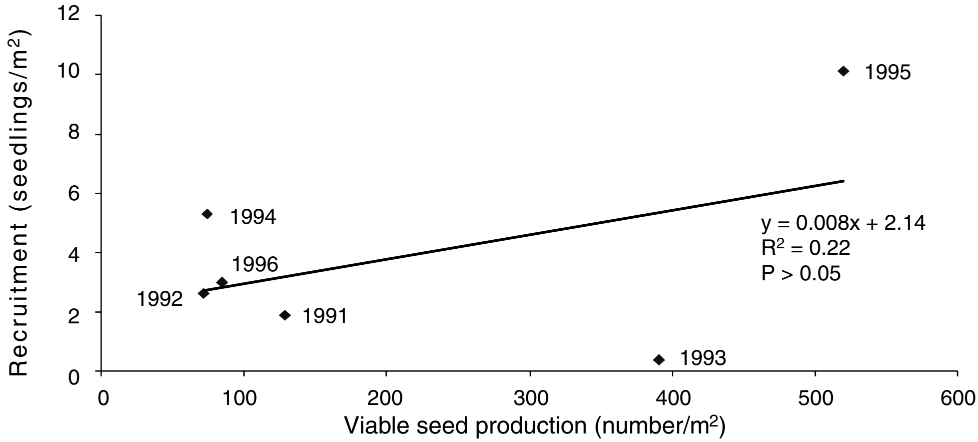

Figure 8. Relationship between seedling recruitment of *H. contortus* in autumn and the soil seed bank in the previous spring (1990–1996) in *H. contortus* pasture in southern Queensland.

that soil seed banks are consistently lower than the amount of seed produced.

Effects of treatments

Both seed production and soil seed banks are influenced by landscape position, reflecting the better fertility/growth conditions in the silver-leaved ironbark compared with the narrow-leaved ironbark land class. This trend was consistent with generally higher plant population parameters for *H. contortus* measured in this study (Orr *et al.* 2004a). Seed production was also influenced by a consistent stocking rate × pasture type interaction, although there is no clear biological explanation for this interaction (Orr *et al*. (2004a).

Seed production was consistently higher at 0.3 beasts/ha than at 0.6 beasts/ha in native pasture but this trend was not evident in oversown pasture.

This stocking rate effect on seed production, at least in native pasture, supports the finding of Wandera (1993) that seed production was the parameter most sensitive to stocking rate. Furthermore, data for the unreplicated 0.9 beasts/ha treatment indicate that very heavy stocking rate impacted on seed production. Both McIvor *et al.* (1996) in northern Queensland and O'Connor and Pickett (1992) in southern Africa reported that increased stocking rate reduced seed production in *H. contortus*. If increasing stocking rate does reduce seed production, as these authors report, then this reduction would be due to the effect of cattle at increasing stocking rate ingesting *H. contortus* tillers that would otherwise produce inflorescences, because Jones and Bunch (1999) reported that cattle do not selectively remove seed of *H. contortus*.

Factors affecting seed production and soil seed banks

Seed production of *H. contortus* ranged from 250 seeds/m^2 (narrow-leaved ironbark in 1991) to 2500 seeds/m^2 (silver-leaved ironbark in 1995). These values are similar to the 2200 seeds/m^2 recorded in exclosures elsewhere at "Glenwood" (Wandera 1993) and slightly below the 3690 seeds/m^2 also recorded in exclosures at another site in southern Queensland (Campbell 1996). These values are also below the 4600 seeds/m^2 recorded in pure stands of *H. contortus* in exclosures in northern Queensland (Howden 1988). However, the values in the current study are higher than the 6 seeds/m^2 recorded in a mixed species pasture at 3 stocking rates during below average rainfall conditions in northern Queensland (McIvor *et al*. 1996). O'Connor and Pickett (1992) reported seed production of 1300–4000 seeds/m^2 for *H. contortus* in southern Africa.

Inflorescence density

Inflorescence density was the major factor influencing seed production in *H. contortus.* The relationship between inflorescence density and rainfall in February (Figure 4) suggests that floral initiation occurs in either late January or early February and that February rainfall influences the development of the floral apex. Similarly, the first seeds of *H. contortus* ripen about 5 weeks after floral initiation in southern Africa (O'Connor and Pickett 1992). Brown (1982) suggested that a similar rapid reproductive development in the Australian native perennial grasses *Aristida armata* and *Thyridolepis mitchelliana* may be a reflection of the unpredictable rainfall environment.

Inflorescence density was also the major determinant of seed production in *H. contortus* in both northern Queensland (McIvor *et al*. 1996) and southern Africa (O'Connor and Pickett 1992). In contrast, while inflorescence density was the major factor influencing seed production in the native perennial grass *Astrebla* spp., variation in both the number of spikelets per inflorescence and seeds per spikelet had a significant impact (Orr and Evenson 1991; Orr 1991).

Seeds per inflorescence

There was little variation in the number of seeds per inflorescence across either years or treatments with a range of 10.6–12.7. These data are similar to the 8.5–10.6 for *H. contortus* in southern Africa (O'Connor and Pickett 1992) and 11.7 for *H. contortus* in India (Parihar *et al*. 1999).

Seed viability

The relationship between seed viability of *H. contortus* and March rainfall (Figure 5) probably reflects a direct effect of rainfall in that month on seed maturation. Similarly, O'Connor and Pickett (1992) recorded seed viability of *H. contortus* ranging from 33–77% in southern Africa and attributed this variation to differences in both total rainfall and its seasonal distribution. In the current study, many *H. contortus* plants flowered in January in 1996 following a prolonged wet period (504 mm October–January; Decile 5 rainfall 333 mm) rather than in March suggesting that, in at least some years, flowering may be related more to growth stage than to photoperiod. However, viability of this 1996 seed was <1% and many seeds contained no caryopsis while others contained an immature caryopsis reflecting unfavourable rainfall conditions during seed development (10 mm February–March; Decile 5 rainfall 160 mm) (J.M. Hopkinson, personal communication). Similarly, O'Connor and Pickett (1992) reported that greater than 90% of non-viable seeds failed to contain an embryo. For *Astrebla* spp., which can flower at almost any time of the year, Orr (1991) suggested that seed viability was affected by both seasonal rainfall and ambient temperature at the time of seed maturation.

Soil seed banks

Soil seed banks of *H. contortus* were extremely variable ranging from 40–670 seeds/m^2 in the narrow-leaved (1993) and silver-leaved ironbark (1994) land classes, respectively, but were unaffected by stocking rate or pasture type. These values were lower than the maximum of 1500 seeds/m^2 recorded elsewhere at "Glenwood" (Wandera 1993) and 1700 seeds/m^2 recorded at another site in southern Queensland (Campbell 1996) although both those values were recorded in exclosures. However, the values from the current study exceeded the 0–100 seeds/m^2 recorded under moderate grazing (2–5 ha/beast) in central Queensland (Orr and Paton 1993) and the 0–60 seeds/m^2 for a range of exclosed and grazed situations in northern Queensland (McIvor 1987; McIvor and Gardener 1994). Seed banks measured in the current study were similar to that measured in South Africa under a range of grazing and seasonal conditions (O'Connor and Pickett 1992). In the persistence of these pastures, the high variability in seed production of *H. contortus* is likely to be further compounded by the transient nature of the seed in the soil seed bank (Tothill 1977; O'Connor and Pickett 1992; Orr 1999).

Relationships between seed production, seed banks and seedling recruitment

This study highlights but fails to explain the large discrepancy between the production of viable *H. contortus* seed in autumn and the size of the soil seed bank in the following spring. Wandera (1993) also recorded a poor relationship between total seed production and the subsequent soil seed bank elsewhere at "Glenwood". Howden (1988) measured total seed production of 4600 seeds/m^2 in autumn and a germinable soil seed bank of only 38 seeds/m^2 in spring in northern Queensland. A similar discrepancy between seed production and soil seed bank has been recorded for many other grasses including the undesirable perennial grass *Sporobolus indicus* (Andrews *et al.* 1996).

Studies of seed removal by ants during winter (Howden 1988) and of the diet selected by cattle (Jones and Bunch 1999) indicate that neither ants nor cattle selectively remove seed of *H. contortus.* One possible explanation may be seed damage by insects, as examination of seed produced in autumn 1994 and 1996 in the current study revealed parasitisation levels of 23.7% and 14.4%, respectively. In addition, some dead dipterous fly larvae were detected inside the glume while some seed exhibited a larva exit hole (J. M. Hopkinson, personal communication). In the high rainfall environment of Hawaii, Goergen and Daehler (2001) reported that most seed and ovule loss in *H. contortus* was caused by the smut fungus *Sporisorium caledonicum*.

The poor relationship between the soil seed bank in spring and new plants recruited in the subsequent autumn (Figure 8) is consistent with similar relationships developed elsewhere at "Glenwood" by Wandera (1993). One reason for this poor relationship is the overriding influence of summer rainfall and this is highlighted by the generally poor seedling recruitment recorded in this study because of severe drought.

This study indicates that *H. contortus* has the potential to produce relatively large amounts of seed and, in terms of persistence of this species, it is important for much of this seed to germinate and establish and so contribute to overall plant density (Orr *et al*. 2004a). However, this study also indicates that the seasonal pattern of rainfall plays a major role in achieving this potential seed production as it does in seedling recruitment (Orr *et al*. 2004a).

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