

Emergence and survival of herbaceous seedlings in temperate grassy woodlands: Recruitment limitations and regeneration niche

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Abstract Field experiments examined herbaceous seedling emergence and survival in temperate grassy woodlands on the New England Tablelands of New South Wales. Effects of intensity of previous grazing, removal of ground cover by fire or clearing, burial of seeds, grazing and seed theft by ants on seedling emergence and survival were studied in two field experiments. Thirteen species with a range of traits were used in the experiments and their cumulative emergence was compared with laboratory germination studies. Field emergence correlated to laboratory germination but all species had lower emergence in the field. Little natural emergence of native species was observed in the field in unsown treatments. Short-lived forbs had the highest emergence, followed by perennial grasses; rhizomatous graminoids and perennial forbs had the lowest emergence. Soil surface and cover treatments did not markedly enhance emergence suggesting that intertussock spaces were not prerequisites for forb emergence. No consistent pattern of enhanced emergence was found for any treatment combination across all species. Seedling survival varied among species, with perennial grasses and short-lived forbs having the highest seedling mortality. Low mortality rates in the graminoids and rhizomatous forbs appeared partially to compensate for lower seedling emergence. All perennial grasses and some short-lived forbs showed increased risk of mortality with grazing. Differences in emergence and survival of species were related to ground cover heterogeneity, soil surfaces and, to some extent, herbivory. The complexity of these patterns when superimposed on temporal variability suggests that no generalizations can be made about the regeneration niche of herbaceous species groups. Strong recruitment limitation and partitioning of resources in the regeneration niche may reduce competition among native species and explain the high species richness of the herbaceous layer in the temperate grassy communities of eastern Australia.

Key words: coexistence, field experiments, grasslands, grazing, herbivory, regeneration niche.

INTRODUCTION

Germination, emergence and survival of native herbaceous species in grassy woodlands and forests are key life-history stages that ensure the persistence of plant populations. Ultimately, seedlings must recruit at a rate sufficient to replace deaths, otherwise populations decline. Field observations of recruitment events in temperate eucalypt woodlands are rare and have mainly concentrated on grasses used for livestock production or weeds (Lodge & Whalley 1989) with less attention to native forbs (Trémont & McIntyre 1994). Despite the apparent decline in native perennial herbaceous species in grassy ecosystems, few experimental demographic data are available (see reviews by Lodge & Whalley 1989; Trémont & McIntyre 1994; Yates & Hobbs 1997; Clarke 2000). Recruitment limitation, either through lack of seed banks, lack of appropriate germination cues, or herbivory, may account for declines in native perennial species.

Seed supply and the survival of seeds in seed banks regulate the potential emergence of seedlings, and lack of seed banks has also been attributed to recruitment limitation of perennial forbs in grassy communities (Lunt 1990a,b, 1994; McDougall & Kirkpatrick 1994; Trémont & McIntyre 1994; Morgan 1995; Anderson *et al.* 1996). Low numbers of native perennial herbaceous species in grassland seed banks are a common pattern (McIvor & Gardener 1994; Grant & Macgregor 2001; Lodge 2001) but whether this is a result of lack of seed supply or the removal of seed by ants is not well understood.

Native herbaceous species in temperate, grassy landscapes appear to have short-lived seed banks with limited innate dormancy (Lunt 1990a; Morgan 1995; Clarke 2000). Light-enhanced germination occurs in approximately half the forb species that have been tested on the New England Tablelands (Clarke *et al.* 2000). From these and other observations, it has been suggested that disturbance of buried seed, removal of grass cover, and light gaps could enhance the emergence of forbs in grassy ecosystems (Gilfedder & Kirkpatrick 1994; Trémont & McIntyre 1994; Bosy &

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Reader 1995; Clarke *et al.* 2000). In particular, intertussock gaps are thought to be important for recruitment of forb species because species richness declines in areas where grass tussocks dominate grasslands (Trémont & McIntyre 1994; McIntyre & Martin 2001). Thus, the removal of tussocks either by fire or through grazing is thought to provide appropriate conditions for the recruitment and survival of intertussock herbaceous species.

Mortality of herbaceous seedlings is typically very high, but declines with age if post-emergence disturbance events are rare (Williams 1968; Grice & Barchia 1992; Morgan 1995). Suggested causes of seedling mortality include water stress (Gilfedder & Kirkpatrick 1994; Burrows 1995; Morgan 1995), competition (Harradine & Whalley 1980; Morgan 1995; Hitchmough *et al.* 1996), herbivory (Morgan 1995) or combinations of these. Thus, the successful establishment of herbaceous species in grassy landscapes has been related to intertussock gap formation where there is decreased competition for resources and increased refuge from herbivores (Lodge 1981; Silvertown 1981; Goldberg & Werner 1983; Trémont & McIntyre 1994).

The aim of the present experimental study was to identify factors that might limit recruitment of herba-

ceous species in grassy woodlands. In particular, it examined whether recruitment is limited because (i) seed banks are lacking; (ii) soil disturbances are needed; (iii) ground cover inhibits emergence; or (iv) herbivory is intense. In these experiments, the supply of seed was held constant because of the natural variable rates of seed supply and the lack of perennial seed banks in New England (Grant & Macgregor 2001). Using sowing experiments with seeds of known viability dispersed at similar densities allowed an assessment of the relative emergence and survival success of native grass and forb species that occur in the grassy woodlands and forests of the New England Tablelands.

METHODS

Study sites

The three main study sites were located in grassy woodlands on the New England Tablelands within 50 km of Armidale on rural properties with a long history of grazing. Average rainfall ranged from 850 to

Table 1. Species used in each of the field experiments and their growth forms, habitats, abundance, seed mass and seed viability

Species (Family)	Growth form	Experiment	Frequency in grassy landscapes (%)	Relative abundance index [†]	Mean diaspore mass (mg) [‡]	Mean viability (%) [‡]
<i>Ammobium alatum</i> Asteraceae	Short-lived forb (monocarpic)	1	13.0	46	0.50	99.0
<i>Aristida ramosa</i> Poaceae	Perennial grass (C4)	1	17.0	149	2.33	100.0
<i>Austrostipa scabra</i> Poaceae	Perennial grass (C3)	1	<3.0	18	ND	56.0
<i>Austrodanthonia laevis</i> Poaceae	Perennial grass (C3)	2	9.2	30	ND	ND
<i>Austrodanthonia racemosa</i> Poaceae	Perennial grass (C3)	1	6.7	197	0.36	70.0
<i>Bracteantha bracteata</i> Asteraceae	Short-lived forb (polycarpic?)	1,2	8.3	78	0.39	100.0
<i>Carex inversa</i> Cyperaceae	Perennial graminoid	1	33.0	102	0.69	100.0
<i>Cullen tenax</i> Fabaceae	Forb woody rootstock	1	4.2	45	5.04	100.0
<i>Lomandra longifolia</i> Lomandraceae	Perennial graminoid	1	8.3	69	12.27	50.8
<i>Microseris lanceolata</i> Asteraceae	Perennial forb	2	4.2	<1	3.53	100.0
<i>Microlaena stipoides</i> Poaceae	Perennial grass (C3)	2	25.0	377	0.34	100.0
<i>Mentha saturooides</i> Labiatae	Perennial forb	1	4.2	79	0.18	78.0
<i>Vittadinia muelleri</i> Asteraceae	Short-lived forb (polycarpic)	1	6.7	8	0.56	100.0

[†]Summed frequency scores across 77 sample sites; [‡]mean percentage viability and diaspore mass from the results of Clarke *et al.* (2000). ND, not determined.

950 mm with a high proportion falling in summer–autumn. The area is characterized by cool to warm summers and moderately cold winters. Plant communities at each site consisted of grassy woodland and forest, with different dominant species (Clarke & Davison 2001). Pronounced *Themeda* tussocks were not present at any of the study sites. At each study site there were two paddocks where stock grazing had been excluded for more than 5 years prior to the start of the study and adjacent areas that were set stocked. Above-ground herbaceous biomass ranged from 44 to 81 g m⁻² dry weight and was consistently lower in the grazed plots prior to fencing (Clarke & Davison 2001). No consistent trends in soil surface electrical conductivity, pH, total nitrogen (%) or total phosphorus (%) were detected among plots with different grazing histories (Clarke & Davison 2001).

Species

Thirteen herbaceous species were used in the experiments, representing a range of growth forms, plant families, germination responses and abundances (Table 1). Seeds of all species were collected soon after they became available and stored for no more than 6 months prior to sowing. Viability (Table 1) and laboratory germinability of the seeds (Table 2) were determined by Clarke *et al.* (2000).

Effects of grazing history, ground cover, burial and plots

In experiment 1, four fenced plots (5 m × 5 m) were constructed, two in grazed and two in ungrazed paddocks, on either flat or slightly sloping ground at

each of the three study sites. Each of the 12 plots had a complete ground cover of grasses and forbs and a canopy cover of eucalypt trees ranging from 10 to 30%. Two species were sown in all plots (*Austrodanthonia racemosa* and *Bracteantha bracteata*); the others were sown only in sites with their known soil preferences (Table 1). The experimental plots used in the present experiment were the same as the ones used by Clarke and Davison (2001) for their study on woody species emergence. The design of the experiment in Clarke and Davison (2001) was erroneously reported as a factorial design.

The experimental design was a partially nested or split plot design with grazing history and sites as between-plot factors and ground cover and seed burial as within-plot factors (Fig. 1). At each site, there were two levels of grazing history: recently grazed by stock and grazing excluded for more than 5 years prior to the study. Each of these levels was replicated in two independent fenced plots; thus, there were four fenced plots at each site (Fig. 1). At each of the plots, three cover treatments were imposed on a randomly allocated section of the plot. The three levels of cover were (i) mechanically cleared of ground herbage and litter >1 cm above ground; (ii) burned ground cover; and (iii) cover retained (Fig. 1). Within each of the three cover treatments, a seed burial treatment was applied. The two levels in this treatment were (i) seed sown onto a raked soil surface and buried (at approximately 1 cm); and (ii) seed sown onto a raked soil surface left open. Each of these treatments was replicated three times and randomized within each cover treatment. Fifty seeds of each of the species listed in Table 1 were sown onto an area 5 cm × 5 cm for each replicate; an additional replicate was left unsown. Plots were regularly monitored and seedling emergence and mortality were measured by adding and removing

Table 2. Comparison of laboratory germination and total field emergence of seedlings for surface-sown and buried treatments

Species	Laboratory [†]		Field			
	Diurnal	Dark	Surface treatment experiment		Buried treatment experiment	
			1	2	1	2
<i>Ammobium alatum</i>	93.8	72.4	62.6	–	55.6	–
<i>Aristida ramosa</i>	93.7	93.7	42.3	–	47.1	–
<i>Austrostipa scabra</i>	28.8	30.4	10.7	–	11.1	–
<i>Austrodanthonia laevis</i>	–	–	–	32.3	–	41.9
<i>Austrodanthonia racemosa</i>	70.0	63.7	41.7	–	40.7	–
<i>Bracteantha bracteata</i>	53.8	37.1	18.8	4.4	24.9	8.9
<i>Carex inversa</i>	49.7	10.0	2.4	–	1.9	–
<i>Cullen tenax</i>	5.0	6.0	5.1	–	4.1	–
<i>Lomandra longifolia</i>	0.0	3.7	2.8	–	8.1	–
<i>Microseris lanceolata</i>	47.5	34.5	–	12.8	–	28.2
<i>Microlaena stipoides</i>	100.0	100.0	–	36.7	–	58.8
<i>Mentha saturoides</i>	51.2	3.1	4.1	–	1.1	–
<i>Vittadinia muelleri</i>	55.0	9.4	23.6	–	23.1	–

[†]Data from Clarke *et al.* (2000). –, no data.

stainless steel pins. Supplementary watering of plots to above average rainfall was envisaged for the experiments, but fortuitously, above average rainfall fell following seed sowing. At each site, between 200 and 250 mm of rainfall fell in the month of seed sowing, approximately twice the monthly summer average rainfall for the region.

Effects of ground surfaces and ant exclusion

Experiment 2 was at two plots in woodland areas where stock grazing had been excluded. At each plot, four species (*Bracteantha bracteata*, *Austrodanthonia laevis*, *Microlaena stipoides* and *Microseris lanceolata*) were

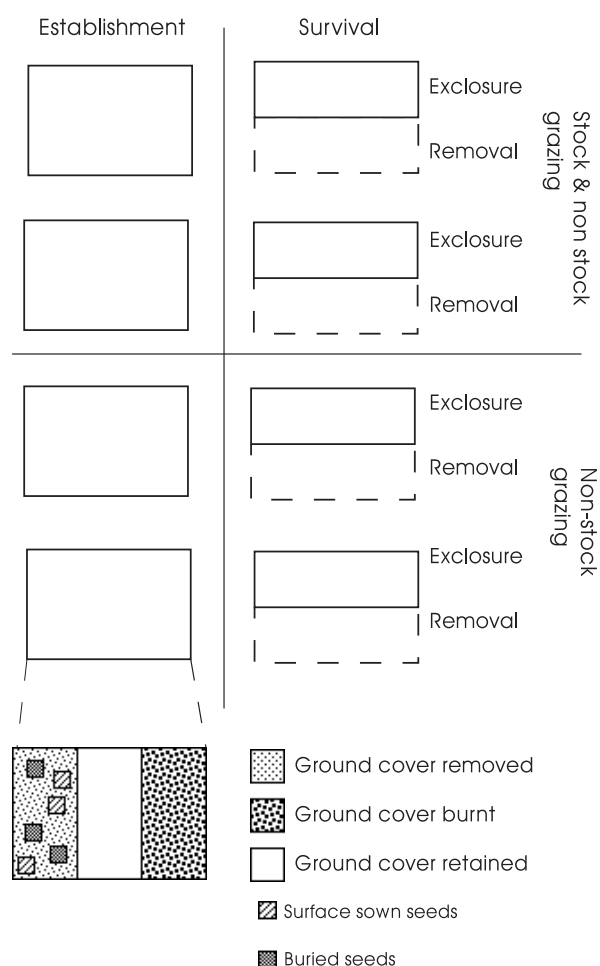


Fig. 1. Schematic arrangement of fenced plots within a study site. Within each study site, two plots were placed in areas that were currently grazed and two in areas where grazing had been excluded for at least 5 years. Six treatment combinations of two manipulated factors of ground cover (burnt, cut, background) and seed burial (open or buried) were assigned randomly within the plots. Three replicate burial areas (25 cm × 25 cm) were located within the cover treatment. Each species was assigned randomly within each replicate in each treatment combination.

sown into areas where the soil surface and ant presence were manipulated. These species are known to be removed by ants when placed on bare ground (Davison, pers. comm.). The experiment had a factorial design involving sites, soil sowing surface and ant exclusion. Soil sowing surfaces were (i) a raked soil surface with seed buried (at approximately 1 cm); (ii) a raked soil surface left with seed unburied; and (iii) an undisturbed soil surface. Ants were excluded using galvanized sheet metal frames (50 cm × 50 cm × 10 cm) with eaves painted with an ant-proof surface (Fluon). Each combination of treatments was replicated four times and randomized within the two areas. Fifty seeds of each species were sown onto an area 5 cm × 5 cm in each replicate (Table 1). Seedling emergence was monitored at regular intervals. At one site, an open-ended frame was also applied to test for any confounding effects of the frame.

Survival and grazing factors

At each plot in experiment 1, two levels of grazing were imposed after approximately 6 months of seedling growth. In plots where stock grazing had been excluded, half the replicates were exposed to grazing by kangaroos and rabbits by removal of fences (Fig. 1). In plots where stock grazing had occurred prior to the erection of fences, half the replicates were exposed to grazing by cattle, sheep, kangaroos and rabbits by removal of fences. Stocking rates varied in space and time, but ranged from 1 to 8 dry sheep equivalent per ha. Seedlings were monitored 2, 4, 8, 12 and 21 months after emergence.

Statistical analyses

Emergence

Data from seeds sown at all sites in experiment 1 were analysed in a partly nested ANOVA with two between-plot factors (grazing history and sites) with two plots for each combination. Within-plot factors were ground cover and seed burial. The response variable was percentage seedling emergence after 10 weeks, which was arcsine transformed. The data from seeds sown in experiment 2 were analysed in a three-factor ANOVA with ground cover and ant exclusion as fixed orthogonal factors and sites as a nested factor. For comparative purposes, all emergence data were expressed as a proportion of viable non-dormant seed sown. A matrix of Pearson correlation coefficients was calculated among field germination, laboratory germination, seed mass and relative abundance of species in the field. Probability levels were calculated using Fisher's r to z transformation.

Survival

All survival data were adjusted to a proportion of seedlings that had emerged after 3 months. Cumulative survival data were then analysed using 3-month emer-

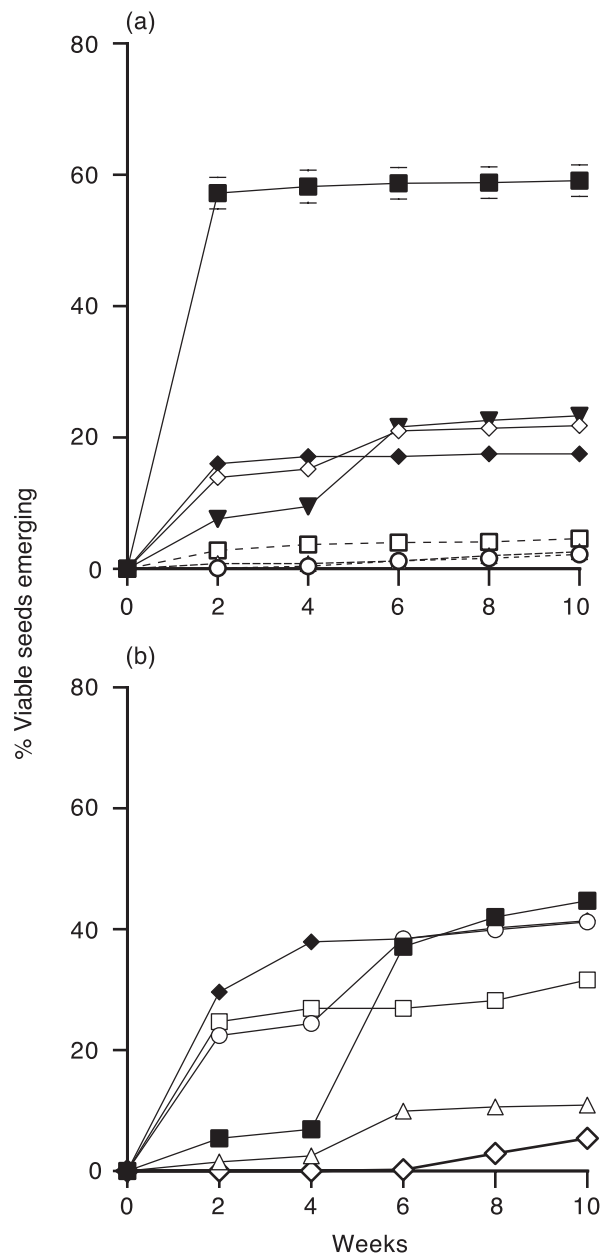


Fig. 2. Mean cumulative emergence of seedlings over 10 weeks for (a) forbs and *Carex inversa* and (b) perennial grasses and *Lomandra longifolia*. Six treatment combinations of two manipulated factors of ground cover (burnt, cut, background) and seed burial (open or buried) were assigned randomly within the study plots. Values are averaged across all factorial treatments of burial and cover. (a) ■, *Ammobium*; ▼, *Vittadinia*; ◇, *Bracteantha*; ◆, *Microseris*; □, *Psoralea*; ○, *Carex*; △, *Mentha*. (b) ■, *Aristida*; ○, *Austrodanthonia r.*; ◆, *Microseris*; □, *Austrodanthonia l.*; △, *Austrostipa*; ◇, *Lomandra*

gence as a starting point rather than the absolute time since seeds had been sown. Data were plotted at 2, 4 (exclosures removed), 8, 12 and 21 months after maximum seedling emergence (3 months).

Survival analyses were also performed on right-censored data using a proportional hazard regression model (Cox & Oakes 1984). In survival analysis, time to event (death) is the variable of interest and regression models can be used (Cox & Oakes 1984). When an experiment 'ends' before all events have occurred, then data for non-events are right censored. Although comparisons of survival functions are useful, the number of census points in the present study precluded detailed parametric analyses of survival functions. However, differences in survival patterns among treatments (strata) can be undertaken where the underlying hazard functions are proportional (Cox & Oakes 1984). Initial plots of log-cumulative hazard and time for different treatment pairs (stock and exclosure; other herbivores and exclosure; recently grazed and less grazed) were generally parallel, indicating proportionality. The likelihood ratio test was used to evaluate whether the levels of covariates made a significant contribution to the global model. Chi-squared tests were used to test for each level of covariates in expanded models after the hazard functions were examined for proportionality. The exponents of the regression coefficient (e^{β}) give the relative risk of mortality for a seedling subjected to a hazard (grazing or grazed landscapes) compared with a seedling in an exclosure that has not been recently grazed. The relative hazard of treatments was compared with initial densities of seedlings to determine if it correlated to density.

RESULTS

Field emergence of sown seed and laboratory germination

The cumulative field emergence of sown seed ranged from 59.1% in *Ammobium* sp. to 2.2% in *Mentha* sp. and was consistently lower than laboratory germination for the same species (Table 2). There was a positive correlation between germination in the laboratory, either diurnal or dark, and seedling emergence in the field ($r = 0.89$, $P < 0.001$). Seed weight did not significantly correlate to seedling emergence in the field.

The three species of forbs (*Bracteantha*, *Mentha* and *Vittadinia*) with a diurnal light preference in the laboratory experiments did not have enhanced emergence in the field when surface sown. One species that had preferential dark germination in the laboratory (*Lomandra*) often had higher emergence when buried in the field (Table 2).

Table 3. Summary results of partly nested ANOVA for cumulative seedling emergence 10 weeks after seeds were sown in experiment 1

	<i>Ammobium alatum</i>	<i>Aristida ramosa</i>	<i>Austrodanthonia racemosa</i>	<i>Austrostipa scabra</i>	<i>Bracteantha bracteata</i>	<i>Carex inversa</i>	<i>Lomandra longifolia</i>	<i>Mentha saturoides</i>	<i>Cullen tenax</i>	<i>Vitadina muelleri</i>
Between subjects (<i>F</i> -values)										
S	—	—	7.6*	—	0.3 (NS)	—	—	—	—	—
G	<0.1 (NS)	1.8 (NS)	4.8 (NS)	1.0 (NS)	7.5*	9.9 (NS)	0.4 (NS)	1.1 (NS)	4.1 (NS)	0.4 (NS)
S × G	—	—	0.2 (NS)	—	0.3 (NS)	—	—	—	—	—
P(S × G) or P(G)	6.6**	7.0**	6.2***	0.8 (NS)	4.7***	3.0 (NS)	6.5**	3.7*	1.7 (NS)	0.3 (NS)
Within subjects (<i>F</i> -values)										
C	2.8 (NS)	1.4 (NS)	4.6*	1.5 (NS)	3.9*	7.1*	1.7 (NS)	3.0 (NS)	1.1 (NS)	0.2 (NS)
Cover interactions	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
D	0.6 (NS)	3.0 (NS)	0.1 (NS)	0.5 (NS)	22.6***	6.5 (NS)	47.3**	21.6*	0.6 (NS)	0.5 (NS)
Sowing interactions	9.8 (C × D)*	NS	NS	NS	7.1 (S × D)*	NS	NS	NS	NS	8.6 (G × C × D)*

*, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001. C, cover; D, sowing; G, grazing history; NS, not significant; P, plots; S, sites; —, no data.

Laboratory germinations were mostly complete within 14 days once innate dormancy was overcome (Clarke *et al.* 2000). In the field, however, emergence was more intermittent, corresponding to periods after heavy rainfall. Five species showed flushes of emergence between weeks four and six (Fig. 2). Most germination and emergence of short-lived forbs and grasses occurred within 2 months of sowing. However, the longer-lived species (*Carex*, *Mentha* and *Lomandra*) had delayed emergence (Fig. 2). This late emergence did not produce major changes in treatment effects through time.

Effects of grazing history, ground cover, burial and plots

No natural recruitment of any of the forb species used in the experiment was observed in the unsown treatments. Very low numbers of native perennial grasses (< 100) were observed to emerge in unsown treatments, but these could not be identified to species because none survived longer than a few months. Observations within the entire area of the plots also revealed very low native herbaceous seedling recruitment. In contrast, annual exotic forbs readily emerged from disturbed sites but no attempt was made to census these seedlings.

For the sown species, all treatments had some species that showed significant effects, but the only relatively consistent trend was variation among plots (Table 3). The site effect was also significant for the two species (*Bracteantha* and *Austrodanthonia*) sown in all sites, both of which had high emergence on basalt-derived soils. Enhanced emergence also occurred on long-since-grazed plots for *Austrodanthonia* spp. Neither sites nor plots had interactive effects with any treatments (Table 3).

Five species showed significant within-plot effects of either ground cover manipulation or sowing, but there were no consistent patterns among levels of the treatment (Table 4). Two species (*Bracteantha* and *Austrodanthonia*) showed some enhanced emergence after burning; none responded to clearing; and two emerged best under natural cover (*Carex* and *Mentha*) (Table 4). Seed burial enhanced emergence of *Bracteantha* spp. and *Lomandra* spp., but mostly inhibited emergence of *Mentha* spp. (Table 4). In summary, there were no consistent patterns of treatments that either enhanced or suppressed seedling emergence; instead, each species responded differently to the combination of treatments (Table 4).

Effects of ground surface and ant exclusion frames

Variable patterns of emergence were also found among treatments in the second experiment (Table 5). Signifi-

Table 4. Proportion of viable seed sown that emerged after 10 weeks for each combination of treatments in experiment 1 (mean values pooled among plots and sites for each treatment)

Species	Surface-sown seed						Buried seed						Total
	Recently grazed			Long-since-grazed			Recently grazed			Long-since-grazed			
	Burnt	Clear	Intact	Burnt	Clear	Intact	Burnt	Clear	Intact	Burnt	Clear	Intact	
<i>Ammobium alatum</i>	64.6 [†]	59.6	64.3	62.6	62.9	61.3	62.6	50.2	50.2	62.3	60.3	48.1 [‡]	59.1
<i>Aristida ramosa</i>	43.0	35.3	26.0 [‡]	53.3	50.3	46.0	38.7	46.7	43.3	53.5	55.0 [†]	50.3	44.7
<i>Austrostipa scabra</i>	11.7	15.0 [†]	13.7	9.0	11.7	3.3 [‡]	8.0	11.3	10.3	4.0	14.3	8.7	10.9
<i>Austrodanthonia racemosa</i>	41.8	35.7	27.8 [‡]	51.3 [†]	47.2	46.6	38.3	34.9	32.3	50.7	43.3	44.5	41.2
<i>Bracteantha bracteata</i>	15.8	19.8	15.0 [‡]	26.0	16.1	20.0	31.5 [†]	26.2	21.3	28.3	23.4	18.8	21.8
<i>Carex inversa</i>	0.0 [‡]	0.7	0.3	1.0	4.7	8.0 [†]	0.0 [‡]	0.7	0.7	3.3	0.6	6.0	2.2
<i>Cullen tenax</i>	2.3	6.0	2.7	7.7 [†]	6.0	6.0	1.3 [‡]	5.3	5.0	4.7	4.0	4.0	4.6
<i>Lomandra longifolia</i>	4.0	7.7	0.3 [‡]	4.0	1.7	2.8	2.7	19.1 [†]	5.3	5.0	16.4	12.4	6.8
<i>Mentha satureoides</i>	0.0 [‡]	3.8	4.7	4.7	1.7	9.4 [†]	0.0 [‡]	0.8	1.3	0.0 [‡]	2.1	2.6	2.6
<i>Vittadinia muelleri</i>	20.0	20.0	19.3	29.0	45.0 [†]	8.0 [‡]	17.7	28.3	15.0	28.0	33.7	15.7	23.3

[†]Highest values; [‡]lowest values.

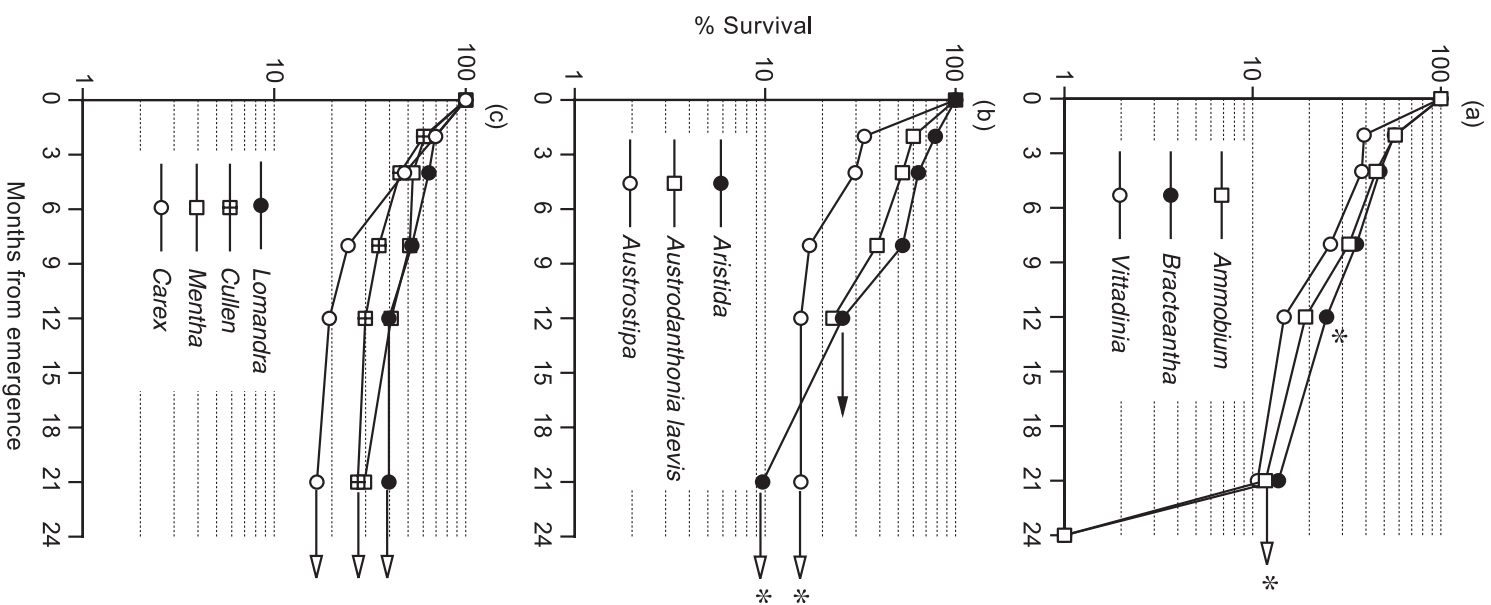


Fig. 3. Mean survival of (a) short-lived herbs, (b) perennial grasses and (c) rhizomatous forbs and graminoids over 2 years since initial emergence flush. (*) Flowering observed. Arrows indicate plants present after 3 years of observations at approximately similar densities to the 21-month census.

cant sowing effects were found in two species (*Austrodanthonia* and *Microlaena*; Table 5), with burial of sown seed enhancing seedling emergence (Table 6). The use

of the exclusion frame significantly enhanced seedling emergence in only one species (*Bracteantha*; Table 6).

Within-site comparisons of sham exclusion frames with complete frames showed no detectable difference

Table 5. Summary results for experiment 2, ANOVA of cumulative seedling emergence 10 weeks after seeds were sown

	<i>Bracteantha bracteata</i>	<i>Austrodanthonia laevis</i>	<i>Microlaena stipoides</i>	<i>Microseris lanceolata</i>
Source (<i>F</i> -values)				
F	5.2*	1.2 (NS)	4.0 (NS)	1.2 (NS)
S	1.6 (NS)	3.9*	7.7*	1.1 (NS)
F × S	0.7 (NS)	0.6 (NS)	0.2 (NS)	0.1 (NS)
P(F × S)	0.7 (NS)	2.2*	1.9 (NS)	4.2**

*, *P* < 0.05; **, *P* < 0.01. F, fence; NS, not significant; P, plots; S, sowing.

Table 6. Frequency of cumulative seedling emergence 10 weeks after seeds were sown for each combination of treatments in experiment 2 (variation among plots pooled for each treatment)

Species	Total	Ants excluded			Sham frame			Ants present		
		Buried	Raked	Surface	Buried	Raked	Surface	Buried	Raked	Surface
<i>Bracteantha bracteata</i>	6.2	10.5	6.0	7.7	16.0	1.0	0.0	5.5	3.7	4.3
<i>Austrodanthonia laevis</i>	31.6	45.0	39.5	24.5	33.0	23.0	25.0	31.0	27.5	15.2
<i>Microlaena stipoides</i>	41.4	61.7	44.5	36.5	64.0	29.0	33.0	54.5	30.7	19.8
<i>Microseris lanceolata</i>	19.0	32.2	19.8	18.5	18.0	0.0	12.0	26.8	9.0	14.8

Table 7. Summary of mean species emergence and survival for all treatments

Species	Seed sown	Emergence	Time since emergence (months)				
			2	4	8	12	21
<i>Ammobium alatum</i>	3384	2257	1293	1022	735	432 [†]	264 [‡]
<i>Aristida ramosa</i>	3384	1878	1470	1199	989	480	183 [†]
<i>Austrostipa scabra</i>	1037	467	155	139	80	72	72 [†]
<i>Austrodanthonia racemosa</i>	7560	4735	2845	2490	1831	1079	ND
<i>Bracteantha bracteata</i>	5810	2622	1487	1243	934	649 [†]	359 [‡]
<i>Carex inversa</i>	1789	144	100	69	35	28	24 [†]
<i>Cullen tenax</i>	3492	227	137	103	80	68	62 [†]
<i>Lomandra longifolia</i>	1828	340	235	235	178	135	135
<i>Mentha saturooides</i>	1843	98	60	52	50	40 [†]	27
<i>Vittadinia muelleri</i>	1980	920	360	350	239	136 [†]	98 [‡]

[†]Flowering and seed-set; [‡]subsequently, all individual died before 36 months. ND, not determined.

Table 8. Summary results of survival analyses

	Likelihood ratio [†]			Stock versus enclosure			Herbivores versus enclosure			Grazed versus less grazed		
	d.f.	e ^{β‡}	<i>P</i>	d.f.	e ^{β‡}	<i>P</i>	d.f.	e ^{β‡}	<i>P</i>	d.f.	e ^{β‡}	<i>P</i>
<i>Ammobium alatum</i>	3	–	***	1	1.56	***	1	1.40	***	1	1.01	NS
<i>Aristida ramosa</i>	3	–	***	1	1.23	***	1	1.00	NS	1	0.90	NS
<i>Austrostipa scabra</i>	3	–	*	1	1.50	*	1	1.70	**	1	1.32	NS
<i>Austrodanthonia racemosa</i>	3	–	***	1	1.17	***	1	1.02	NS	1	0.87	**
<i>Bracteantha bracteata</i>	3	–	*	1	1.00	NS	1	1.00	NS	1	0.91	NS
<i>Carex inversa</i>	3	–	NS	1	1.55	NS	1	1.48	NS	1	1.05	NS
<i>Cullen tenax</i>	3	–	NS	1	1.07	NS	1	1.16	NS	1	1.11	NS
<i>Lomandra longifolia</i>	3	–	NS	1	1.02	NS	1	0.97	NS	1	0.97	NS
<i>Mentha saturooides</i>	3	–	NS	1	1.16	NS	1	1.11	NS	1	1.10	NS
<i>Vittadinia muelleri</i>	3	–	NS	1	1.05	NS	1	1.00	NS	1	0.93	NS

[†]Global model shown as the likelihood ratio column; [‡]coefficients greater than 1 indicate increasing risk of mortality; –, no data; *, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001; d.f., degrees of freedom; e^β, relative hazard which is assumed to be constant over time; NS, not significant.

between them, although the power of these tests was low. As in experiment 1, there were no consistent patterns of treatments that either enhanced or suppressed seedling emergence (Table 6).

Effects of spatial variation and grazing on survival

Mean survival of seedlings for all treatments ranged from 10 to 40% with most mortality occurring in the first 12 months (Fig. 3; Table 7). Three broad patterns were apparent for all treatments: (i) short-lived forbs with more than 10% of plants surviving to flowering (Fig. 3a); (ii) perennial grasses with less than 10% mortality flowering after 2 years of growth (Fig. 3b); and (iii) rhizomatous forbs and graminoids with greater than 20% survival but no flowering after 2 years (Fig. 3c).

Survival analyses were performed on each species using censored data up to 21 months after initial recruitment (Table 8). For the purpose of these analyses, only the effects of treatment on the relative hazard of mortality are given as the plot effects were not tested. The likelihood ratio test, used to evaluate the contribution of covariates to the global model, was significant in four of the nine species tested (Table 8). Four species (*Ammobium*, *Aristida*, *Austrostipa* and *Austrodanthonia*) had significant regression coefficients indicating increased risk of mortality as a result of the introduction of stock (Table 8). Two species (*Ammobium* and *Austrostipa*) also had significant regression coefficients reflecting increased mortality as a result of the introduction of other herbivores, whereas no species had regression coefficients associated with increased mortality as a result of the effects of grazing prior to seedling emergence. Correlations of increasing relative hazard of stock grazing and the abundance of species in the landscape produced no significant effect. Field observation of 'lawns' around exclosures indicated that sheep and cattle grazed the plots to 'lawn' within 2 weeks of the fences being removed.

DISCUSSION

Are seed banks limiting?

At each of the experimental sites, above average rainfall fell before and after sowing, providing optimal moisture conditions for germination and emergence as soils were moist in the weeks following sowing (Lodge & Whalley 1981; Watt 1982; Maze *et al.* 1993; Clarke *et al.* 2000). Despite these conditions, there was no native perennial forb and little perennial grass emergence in unsown areas indicating either a lack of a large soil-stored seed bank or the requirement for a stronger

germination cue. The seed bank explanation is consistent with previous experiments on the longevity of seed in the soil (Lunt 1990a; Morgan 1995) and patterns of longevity from laboratory storage of seed (Clarke *et al.* 2000). However, this idea is not consistent with seed bank studies where large numbers of perennial exotic forbs and sedges have been recorded from soil on the New England Tablelands (Grant & Macgregor 2001). Nevertheless, these seed banks did not have many native perennial grasses, perennial forbs or shrub species, indicating that seed supply of perennial native species is generally limiting in these systems.

Where seeds were sown in the field, seedling emergence was less than germination under laboratory conditions indicating either mortality of germinable seed prior to emergence or a secondary dormancy effect. In a related experiment on woody species, Clarke and Davison (2001) found the relative difference between laboratory germination and field emergence was much greater than the herbaceous species used in the present study. This suggests that herbaceous species have less pre-emergence attrition and dormancy than woody species under the same environmental conditions.

Are emergence and survival related to growth form?

Pronounced differences in total emergence and patterns of emergence through time were apparent among groups of species and these were unrelated to seed size. The short-lived forbs (*Ammobium*, *Bracteantha* and *Vittadinia*) had a high proportion of germinable seed emerge, as did the perennial grasses (*Aristida*, *Austrostipa* and *Austrodanthonia*). Most grasses tended to emerge before the forbs, but emergence of *Austrostipa scabra* was slow and may have been temperature limited (Hagon & Groves 1977). The slowest and least successful group were the longer-lived rhizomatous graminoids and forbs (*Carex*, *Lomandra*, *Cullen* and *Mentha*), which generally had less than 20% emergence, the majority of which occurred several months after sowing. These patterns are consistent with the generalization that short-lived species can rapidly establish themselves in disturbed sites and longer-lived forbs are slower to recruit even where adequate seed banks exist.

Patterns of seedling survival varied among species and to a lesser extent among treatments. The short-lived forbs had similar survival patterns to the perennial grasses for the first year, but most individuals died before the second year of growth, resulting in a typical annual type I survival curve. The perennial grasses showed a very similar initial pattern of survival to the short-lived forbs, but did not reproduce until the second year. The perennial grasses all had type II

survival curves that differed from the type III curves for similar species but in more variable environments and seasons (Williams 1968; Lodge 1981). Lodge (1981) followed the survival of 2387 seedlings across six species of native perennial grasses, of which approximately 2% survived over several years. Most of the survivors emerged in intertussock spaces where survival was enhanced by a light cover of litter. As the ground cover treatments were not maintained during the survival phase, the effects of cover on survival are unknown.

Does disturbance enhance emergence?

No one disturbance treatment produced consistent enhancement of seedling emergence across the 13 species used in the experiments in the present study. The most intense combination of disturbance treatments (seed buried in recently grazed burnt areas) showed little difference in seedling emergence from the least-disturbed treatment (surface-sown seed in long-since-grazed sites with a natural herbaceous cover). This contrasts with the woody species used in a concurrent experiment where seed burial generally enhanced emergence (Clarke & Davison 2001). Although disturbance (seed burial, fire and cover removal) enhanced the establishment of several species, the size of the effect was not as pronounced as might have been expected for gap-recruiting species (Gilfedder & Kirkpatrick 1994; McIntyre *et al.* 1994; Trémont & McIntyre 1994; Boser & Reader 1995; Morgan 1995; Hitchmough *et al.* 1996). In particular, the expectation that light-demanding forbs would emerge prolifically in open disturbed spaces was not supported by the results.

Burning of the ground prior to sowing also failed to enhance emergence despite the strong effects of heat and smoke on soil-stored seed banks of herbaceous species in grassy forests (Read *et al.* 2000). Fire effects at the scale of this experiment should be treated cautiously because at a landscape scale fires can burn more intensely. The burn treatments, however, promoted the recruitment of weedy annuals into the surface-disturbed sites. These weeds might have subsequently competed for soil moisture and reduced the emergence of perennial species (see Harradine & Whalley 1980).

Herbivores and survival

Despite the apparent palatability of the broad-leaved forbs (*Ammobium* and *Bracteantha*), only *Ammobium* showed an increased risk associated with herbivory. All perennial grasses suffered an increased risk of seedling mortality as a result of the introduction of stock and, in

one species (*Austrostipa*), there was an increased risk associated with other herbivores. This corresponds with the grazing response in natural pastures where *Aristida ramosa* and *Austrostipa scabra* decrease with set stock grazing (Lodge & Whalley 1981). Field observations showed that seedling mortality resulted from herbivory rather than trampling, as seedlings did not become resistant to defoliation until multiple tillers had developed. In contrast, the rhizomatous species (*Carex* and *Mentha*) had no increased risk of mortality associated with introducing herbivores, resulting in the lowest rate of mortality among all herbaceous species. These low rates of mortality after initial emergence are similar to the few examples of survival curves for perennial forbs (Burrows 1995; Morgan 1995) and could compensate for low emergence.

The effect of grazing on perennial grasses and non-clonal forb survival suggests that intense stocking at times of herbaceous emergence when herbage is sparse could result in recruitment failure. This is likely to occur after a dry winter when bare ground becomes more common followed by patchy summer rainfall. This factor, combined with adult senescence, could have led to the shift in composition of tableland grasslands toward communities dominated by exotic annuals (Lodge & Whalley 1981; Lunt 1991; McIntyre & Lavorel 1994; Clarke 2003).

The regeneration niche

The paradigm that intertussock gaps provide sites for the recruitment of forbs was not supported by our results. Both the removal of grass tussocks by clipping and burning had little effect on emergence and survival, possibly because of increased competition from exotic annuals. Another possible explanation is that our unclipped and unburnt control areas did not have large tussock structures often found in temperate *Themeda* grasslands. Thicker swards of grass and litter might have inhibited the recruitment of herbaceous species, because gap size and litter have been shown to reduce the survival of herbaceous species (Lodge 1981; Boser & Reader 1995; Morgan 1995; Hitchmough *et al.* 1996). The relative difference in emergence among species did, however, correlate to laboratory germination in the present study. This suggests that intrinsic seed factors, rather than partitioning of resources, controlled emergence patterns in these experiments.

In contrast to results for woody species, soil disturbance did not consistently enhance recruitment through seed burial (Clarke & Davison 2001; Clarke 2002). This difference might be related to the smaller seed size of the herbaceous species allowing them to germinate across a wide range of soil microsites. Given the number of herbaceous species found in grassy woodlands, the range of seed sizes, their shapes and

habitat differences, further research on the regeneration niche should be carried out to test the tussock gap paradigm and partitioning of the regeneration niche. Lack of natural species saturation in seed banks, limited recruitment and the stochastic nature of recruitment events (rainfall and soil disturbance) suggest that niche partitioning may not be occurring in space but could occur in time.

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