

# Experiments on the mechanism of tree and shrub establishment in temperate grassy woodlands: Seedling emergence

PETER J. CLARKE\* AND ELIZABETH A. DAVISON

*Botany, University of New England, Armidale, New South Wales 2351, Australia*  
(Email: pclarke1@metz.une.edu.au)

**Abstract** Field experiments were designed to examine tree and shrub seedling emergence in temperate grassy woodlands on the New England Tablelands. The effects of study sites, intensity of previous grazing, removal of ground cover by fire or clearing, burial of seeds and ant seed theft on seedling emergence were tested in two field experiments. Six tree and seven shrub species were used in the experiments and their cumulative emergence was compared with laboratory germination studies. All species used in field experiments had lower cumulative emergence than those in laboratory germination studies despite prolonged periods of above average rainfall before and after seeds were sown. Eucalypt species emerged faster in the field than the shrub species and generally attained higher cumulative emergence than the shrubs. Spatial effects of sites and patches within sites, and of previous grazing history did not strongly influence patterns of seedling emergence in most species. Ground and litter cover generally did not enhance or suppress the emergence of seedlings, although the removal of cover in recently grazed areas enhanced the emergence of some species. Burning enhanced the emergence of some tree and shrub species where plots had more fuel and intense fires, but this effect was not strong. Compared with other treatments, seedbed manipulations produced the strongest effects. In the absence of both invertebrate and vertebrate predators, seedling emergence was lower for surface-sown seed, compared with seed sown on scarified soil surfaces. Higher seedling emergence of buried seeds in the presence of invertebrate predators probably resulted from the combined effects of predator escape and enhanced moisture status of the germination environment. Some promotion of emergence was achieved for all species in most sown treatments probably as a result of a prolonged above average rainfall. In contrast, the natural recruitment of trees and shrubs was negligible in experimental plots, highlighting the importance of seed supply and dispersal as ultimate determinants of recruitment.

**Key words:** eucalypt woodlands, fire, grazing, myrmecochory, recruitment, savanna, spatial variation.

## INTRODUCTION

Germination and seedling emergence are critical stages in the life history of plants, and have the potential to influence population structure and community composition. In grassy ecosystems, the relative influence of fire, soil disturbance and seed removers on woody plant seedling emergence has rarely been measured (Bond & van Wilgen 1996). Lack of recruitment of trees and shrubs is widely perceived as a major threat to the viability of temperate grassy woodlands in Australia (Yates & Hobbs 1997; Reid & Landsberg 2000). Natural patterns of seedling establishment of shrubs and trees in grassy woodlands are poorly documented but are thought to be related to episodic disturbance events such as fires and seedbed conditions (Semple 1990; Clarke 2000). Seedling establishment of eucalypts in grassy woodlands has been related to

release from competition, escape from grazing and ant predation (Yates & Hobbs 1997; Windsor 2000), all within the constraint of a requirement for above average rainfall and seed supply (Curtis 1989; Yates *et al.* 1996; Yates & Hobbs 1997; Windsor 2000). These models are similar to those proposed for forest eucalypts, where episodic recruitment after a major disturbance has been related to the removal of competitors and predators, and the formation of a seed bed favourable to mass germination (Florence 1996; Gill 1997). Experimental studies using litter (Facelli *et al.* 1999) suggest that seedling emergence can also occur in intervals between fires. Recruitment in the absence of fire and other major disturbances has also been observed in some grassy woodlands (Venning 1985; Ashton & Williams 1989; Curtis 1989).

In contrast to eucalypts, the patterns and mechanisms of shrub recruitment have been rarely examined in temperate grassy woodlands (Clarke 2000). Shrub recruitment has been recorded in dry open forests in both burnt and unburnt forests (Purdie 1977).

\*Corresponding author.

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Enhanced shrub germination was recorded for species in forests and woodlands after fire on the southern and central Tablelands of NSW (Purdie 1977; Leigh & Holgate 1979). In subhumid eucalypt woodlands shrub recruitment has been associated with fire events and seedbed conditions (Hodgkinson 1979, 1991; Noble 1997), as has the recruitment of sclerophyllous shrubs in coastal heath- and shrub-dominated forests (Keith 1996). While fire-related germination cues are well known for shrub species (Keith 1996), the effects of fire on seedbed conditions on seedling emergence are poorly known for common shrub species in sub-humid eucalypt woodlands. Semple (1990) has suggested that seedbed condition may be more significant than either fire or rainfall in shrub recruitment in semi-arid and humid regions as recruitment can occur in the absence of fire (e.g. Kirschbaum & Williams 1991; Semple & Koen 1997).

Seed germination and emergence represent a critical stage in recruitment of species in grassy woodlands and factors influencing this stage may not necessarily operate on later life history stages (Yates & Hobbs 1997). Seedling emergence has been recently examined in field experiments in temperate woodlands but those studies focused on a limited range of species (see Curtis 1989; Yates *et al.* 1996; Semple & Koen 1997; Lawrence *et al.* 1998; Facelli *et al.* 1999).

In the present study we examined the effects of multiple factors that potentially influence seedling recruitment, by manipulating seedbeds from which tree and shrub seeds germinated and seedlings emerged. Seed supply and the survival of seeds in seed-banks ultimately regulate the potential emergence of seedlings. In these experiments we held the supply of seed constant and isolated the influence of seed viability, innate dormancy and vertebrate grazing on the results. By using a sowing experiment in which seeds of known viability and dormancy were dispersed at equal densities, we assessed the relative emergence success of 13 species of woody plants that occur in the grassy woodlands and forests of the New England Tablelands in northern NSW. The effects of five factors on the relative emergence of species were tested in a field experiment: (i) different geological substrates; (ii) intensity of previous grazing; (iii) removal of ground cover by fire; (iv) removal of ground cover by clearing; and (v) burial of seeds. In a second field experiment the effects of seedbeds and ant exclusion on seedling emergence were tested.

**METHODS**

**Study sites**

The three experimental sites were located on rural properties with long histories of grazing on the New

**Table 1.** Characteristics of experimental sites on the New England Tableland in NSW

Study sites	Vegetation type	Grazed	Ground biomass (g m <sup>-2</sup> )	Soil pH (n = 18)	Soil cond. (n = 18)	% Total N (n = 18)	% Total P (n = 12)
Site 1 (Ban Wyong)	Grassy open forest <i>Eucalyptus viminalis</i> on basalt	Gr	43.6	6.1	348	0.55	-
		Un	63.5	6.3	494	0.86	-
Site 2 (Eastlake)	Grassy woodland <i>Eucalyptus caliginosa</i> , <i>Eucalyptus nova-anglica</i> on metasediments	Gr	54.3	5.9	455	0.61	0.05
		Un	81.2	5.9	631	0.68	0.04
Site 3 (Newholme)	Grassy woodland <i>Eucalyptus melliodora</i> , <i>Eucalyptus blakelyi</i> on biotite granite	Gr	45.2	6.7	285	0.24	0.03
		Un	60.6	6.3	241	0.21	0.04

Gr, set stock grazing just prior to experiment; Un, stock grazing excluded for at least 5 years prior to the experiment; cond, conductivity.

**Table 2.** Species used in field experiments on the emergence of seedlings. Mean percentage viability and diaspore mass are from the results of Clarke *et al.* (2000)

Species	Growth form	Experiment	Most common habitat	Relative abundance index**	Mean diaspore mass (mg)	Mean percentage viability (mg)
<i>Acacia dealbata</i>	Small tree	I, II	Granite	37	13.83	100
<i>Allocasuarina litoralis</i> *	Tree	II	Metasediment	8	2.59	85
<i>Cassinia quinquefaria</i>	Shrub	I, II	Granite	24	0.07	100
<i>Eucalyptus blakeyi</i> *	Tree	I, II	All	29	0.12	100
<i>Eucalyptus melliodora</i> *	Tree	I	All	54	0.28	100
<i>Eucalyptus viminalis</i> *	Tree	I	Basalt	59	1.06	100
<i>Eucalyptus youmanii</i> *	Tree	I, II	Granite	15	2.23	78
<i>Hakea microcarpa</i> *	Shrub	II	Granite	1	5.21	100
<i>Hovea linearis</i>	Shrub	II	Granite	18	6.44	NA
<i>Indigofera australis</i>	Shrub	II	Metasediment	13	6.14	100
<i>Leptospermum polygalifolium</i> *	Shrub	I	All	10	0.16	48
<i>Lomatia fraseri</i> *	Shrub	I	Granite	8	7.20	100
<i>Xanthorrhoea johnsonii</i> *	Shrub	I	Metasediment	1	18.05	100

\*Canopy-held seed-bank; \*\*summed frequency scores across 77 sample sites; NA, not available.

England Tableland and within 50 km of Armidale, NSW. The average annual rainfall of the area ranges from 850 to 950 mm with a higher proportion falling in summer–autumn. The area is characterized by mild to warm summers and moderately cold winters. The New England Tableland has a range of rock types and each of the three sites was representative of the range of parent materials that support grassy woodlands and forests; these are basalt, metasediments and biotite granite. The plant communities at each site consisted of grassy woodlands and grassy open forests with different dominant species (see Table 1). At each study site there were two paddocks (patches) where stock grazing had been excluded for more than 5 years and an adjacent area set stocked grazed. Standing ground biomass and litter ranged from 44 to 81 g m<sup>-2</sup> dry weight and was consistently lower in grazed plots prior to fencing (Table 1). No consistent trends in soil surface conductivity, pH, total percentage nitrogen and total percentage phosphorus were detected among plots with different grazing histories (Table 1).

### Species

Five shrub and five tree species were used in the first experiment, and four shrub and three tree species in the second experiment. All species used are widely distributed in temperate woodlands on the New England Tablelands, although some are associated with particular geological substrates. Seeds of all species were collected soon after they became available and were stored at room temperature for no more than 6 months prior to sowing. Viability and laboratory germinability of the seeds are from Clarke *et al.* (2000) (Table 2). Dormancy of species with hard seed coats was broken by heat treatment (80°C for 5 min) prior to sowing. The remaining species readily germinate with adequate moisture and have short-lived seed-banks in the soil. Nine of the species used for sowing have canopy-held seed-banks but some are only weakly serotinous (Table 2).

### Experimental designs

#### *Interactive effects of sites, grazing history, ground cover and burial*

The first experiment (experiment I) was arranged at each of the three study sites in four fenced plots measuring 5 m × 5 m on either flat or slightly sloping ground. Fencing excluded rabbits, kangaroos and livestock. Each of the 12 plots had a complete ground cover of grasses and forbs and had a canopy cover of eucalypt trees ranging from 10 to 30% with the nearest tree being no closer than 3 m from the plots.

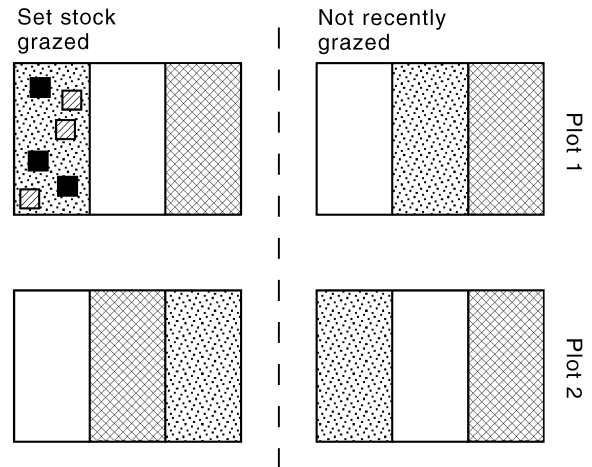
Three species were sown in all plots; the rest were sown in sites with known association with the geological substrate (Table 2).

The experiment had a factorial design involving sites, grazing history, ground cover and seed burial. There were three levels of soil type: (i) high nutrient (Bam Wyong plots); (ii) medium nutrient (Eastlake plots); and (iii) low nutrient (Newholme plots). Note that for those species not sown at all sites (see Table 2) the experiment consisted of grazing history, ground cover and seed burial. At each site, two levels of grazing history were selected; (i) recently grazed by set stock; and (ii) stock grazing excluded for more than 5 years. Stocking rates have varied from 1 to 8 dry sheep equivalent (dse) ha<sup>-1</sup>. 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 12 plots three cover treatments were imposed on a randomly allocated section of the plot by dividing it into three. The three levels of cover were: (i) mechanically cleared of ground herbage and litter > 1 cm above ground; (ii) burned; and (iii) uncleared (Fig. 1). Finally, within each of the three cover treatments a seed burial treatment was applied within a month of clearing and burning. The two levels in this treatment were: (i) seed sown onto a raked soil surface and buried (approximately 1 cm); or (ii) seed sown onto a raked soil surface left open. A raked unsown surface was also created to assess background germination. Each of these treatments were replicated three times and randomised within the cover treatments. Fifty seeds of each of the species listed in Table 1 were sown onto an area of 5 cm × 5 cm for each replicate. Plots were monitored at weekly intervals and seedling emergence and mortality were censused by the use of stainless steel pins. 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.

*Interactive effects of ground surfaces and ant exclusion frames*

A second experiment (experiment II) was arranged at each of two study sites in woodland areas where stock grazing had been excluded. In each site seven species



**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 area where stock grazing had ceased for at least 5 years. Six treatment combinations of manipulated factors of ground cover (burnt, cut, natural) and seed burial (surface-sown or buried) were assigned randomly within the plots. Three replicates (25 cm × 25 cm) were located within the cover treatment. Each species was assigned randomly within each replicate in each treatment combination. (⊠), Ground cover cleared; (⊡), ground cover burnt; (□), ground cover retained; (⊞), surface-sown seed; (■), buried seed.

**Table 3.** Comparison of laboratory germination (% of viable seed; Clarke *et al.* 2000) and total field emergence (% of viable seed sown) of seedlings surface-sown and buried

Species	Growth form	Field experiments					
		Laboratory		Surface		Buried	
		Light	Dark	I	II	I	II
<i>Acacia dealbata</i>	Small tree	4.1 (16.5*)	2.6	10.5	0.9	14.9	2.4
<i>Allocasuarina littoralis</i>	Tree	82.0	62.7	–	15.1	–	21.1
<i>Cassinia quinquefaria</i>	Shrub	63.2	33.0	1.4	0	1.7	0
<i>Eucalyptus blakelyi</i>	Tree	99.3	46.1	14.6	2.4	17.9	6.2
<i>Eucalyptus melliodora</i>	Tree	86.8	90.7	10.6	–	14.9	–
<i>Eucalyptus viminalis</i>	Tree	96.1	95.5	11.4	–	20.4	–
<i>Eucalyptus youmanii</i>	Tree	22.9	55.1	7.4	6.1	15.1	13.2
<i>Hakea microcarpa</i>	Shrub	67.5	17.5	–	4.2	–	3.9
<i>Hovea linearis</i>	Shrub	2.5 (23.5*)	2.5	–	0.4	–	0.8
<i>Indigofera australis</i>	Shrub	17.5 (45.0*)	6.9	13.4	–	13.5	–
<i>Leptospermum polygalifolium</i>	Shrub	100.0	15.4	7.3	–	10.2	–
<i>Lomatia fraseri</i>	Shrub	88.7	80.0	10.0	–	13.4	–
<i>Xanthorrhoea johnsonii</i>	Shrub	20.0	53.7	8.0	–	16.4	–

\*Heat pretreatment; I, experiment I; II, experiment II.

were sown into areas where soil surfaces and ant presence had been manipulated. The experiment had a factorial design involving sites, soil sowing surface and ant exclusion. Three soil surface treatments were: (i) raked soil surface and buried (approximately 1 cm); (ii) seed sown onto a raked soil surface left open; and (iii) seed sown onto an undisturbed soil surface. Ants were excluded using galvanized sheet metal frames (50 cm × 50 cm × 10 cm) with an eave painted with Fluon™. Each combination of treatments was replicated four times and randomised within the two areas. Fifty seeds of each species listed in Table 2 were sown onto an area of 5 cm × 5 cm for each replicate. Seedling emergence was monitored at regular intervals. Four replicate sham exclusions, using an open-ended frame, were also applied at one site to test for confounding effects of the frame.

**Statistical analyses**

Data from seeds sown at all sites in experiment I were analysed with a five-factor ANOVA. Site, grazing history,

ground cover and seed burial were treated as fixed factors, whereas the two replicate plots were a nested factor. The data from seeds sown in single sites in experiment I were analysed with a four-factor ANOVA. Grazing history, ground cover and seed burial were treated as fixed factors, whereas the two replicate plots were a nested factor. Where plot effects were not evident ( $P > 0.25$ ) they were pooled with replicates. The data from seeds sown in experiment II were analysed with a three-factor ANOVA. Site, seed burial and ant exclusion were treated as fixed factors. All emergence data were adjusted to the proportion of viable seed sown and an angular transformation was used (arc sine square root). A single-factor ANOVA compared the sham frames with intact frames. Post-hoc comparisons were undertaken using the Bonferroni test. For each species, homogeneity of variances was tested by using Cochran's test. 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.

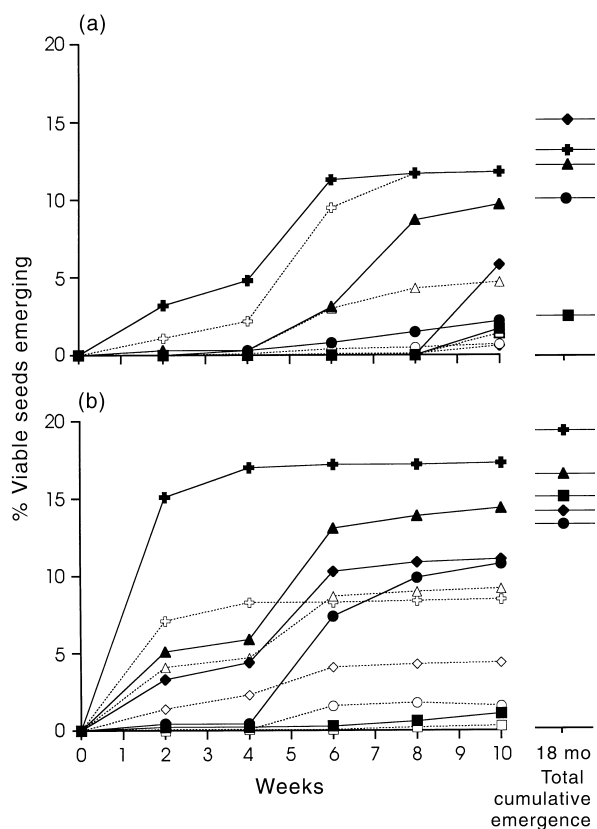
**RESULTS**

**Field emergence and laboratory germination comparisons**

Negligible emergence of seedlings was observed for unsown surfaces in all plots. The overall results of cumulative field emergence from sown plots and laboratory germination of the same seeds showed lower seedling emergence in the field experiments (Table 3). There was a weak positive correlation between germination in the laboratory under dark conditions and seedling emergence after burial in the field ( $r = 0.59, P < 0.05$ ). However, there was no strong correlation between laboratory germination and emergence of surface-sown seeds ( $r = 0.38, P > 0.05$ ). Seed mass was negatively correlated with germination in the laboratory ( $r = -0.69, P < 0.05$ ) but not with seedling emergence in the field ( $P > 0.1$ ).

Species with a diurnal light preference in the laboratory experiments showed no enhanced emergence in the field when surface-sown. The two species that had preferential dark germination in the laboratory (*Xanthorrhoea johnsonii*, *Eucalyptus youmanii*) had better emergence when buried than surface-sown in the field, as did most other species (Table 3).

Laboratory germination was mostly complete within 14 days once innate dormancy was broken. In the field, emergence was more staggered and corresponded to periods after heavy rainfall. Most eucalypt species responded faster to early rainfall events than the shrub



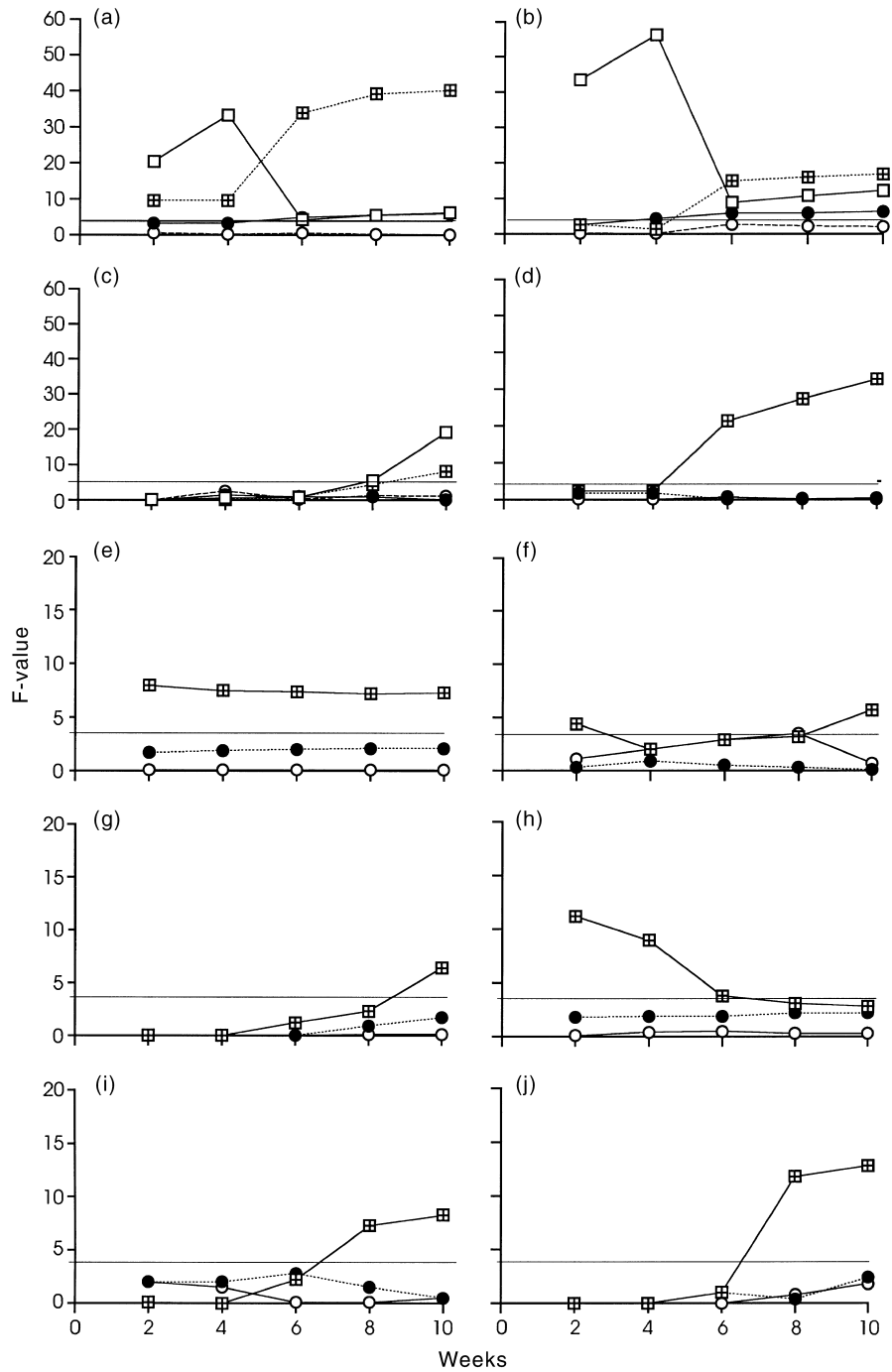
**Fig. 2.** Plots of mean cumulative emergence of surface-sown (open) and buried (solid) seeds for (a) shrubs and (b) trees in experiment I. Total cumulative emergence data over 18 months are shown to the right of the 10-week emergence data. (a) (◆), *Xanthorrhoea*; (+), *Indigofera*; (▲), *Lomatia*; (●), *Leptospermum*; (■), *Cassinia*; (b) (+), *Eucalyptus viminalis*; (▲), *Eucalyptus blakelyi*; (■), *Acacia*; (◆), *Eucalyptus melliodora*; (●), *Eucalyptus youmanii*.

species and attained higher cumulative emergence (Fig. 2). *Xanthorrhoea* showed a strong dormancy effect when sown in the field and few seedlings emerged until approximately 10 weeks after sowing. Seedlings continued to emerge up to 18 months after sowing but late emergence generally did not change the relative patterns of emergence at 10 weeks (Fig. 2). The exceptions were *Xanthorrhoea johnsonii*, which had the highest cumulative emergence of shrub species after 18 months, and *Acacia dealbata*. Both species

have innate dormancy that was not adequately broken by heat pretreatment.

**Interactive effects of sites, grazing history, ground cover and burial**

The effects of treatments on the emergence of seedlings changed through time as shown by plots of variance ratios (*F* values) for the main treatment



**Fig. 3.** Plots of variance ratios (*F* values) analysed at five time intervals for each of the main effects in experiment I. Significant effects at  $P < 0.05$  are shown approximately by a thin horizontal line at the appropriate *F* values. (a) *Eucalyptus meliiodora*; (b) *Eucalyptus blakelyi*; (c) *Leptospermum polygalifolium*; (d) *Eucalyptus youmanii*; (e) *Eucalyptus viminalis*; (f) *Acacia dealbata*; (g) *Cassinia quinquefaria*; (h) *Indigofera australis*; (i) *Lomatia fraseri*; (j) *Xanthorrhoea johnsonii*. (□), site effects; (⊠), burial effects; (●), cover effects; (○), grazing effects.

effects (Fig. 3). Site effects were initially very strong for two eucalypt species but the site effect decreased over time. Seven species showed an increasing effect of seed burial over time, whereas one shrub (*Indigofera*) decreased and one eucalypt (*E. viminalis*) remained constant. In general, the effect of cover treatments and grazing history did not change over time (Fig. 3).

The three species sown at all sites showed differences in emergence among sites, burial treatment and cover (Table 4), but no effect of plots within each of the sites ( $P < 0.1$ ). The Newholme site consistently had the highest emergence where sown seed was buried.

Burial of sown seed generally had the strongest effects of any treatment (Tables 3–5), resulting in enhanced germination of most species (Figs 3,4). The effects of burial rarely interacted with grazing history or cover treatments (Tables 4,5). Plots that had a history of grazing showed no general trend of suppressed or enhanced emergence of seedlings when cover was retained. However, there was a pattern of interaction between grazing history and ground cover treatments in *E. blakelyi* (Table 4). Plots that had a recent history of grazing showed enhanced emergence when ground cover was removed (Fig. 4a). In contrast, long-since grazed plots that had been burnt had enhanced seedling emergence (Fig. 4a). Similar trends of enhanced emergence with removal of cover are suggested in two eucalypts (*E. viminalis*, *E. youmanii*) (Fig. 4c,d) and three shrub species (*Cassinia*, *Lomatia*, *Xanthorrhoea*) when seeds were buried (Fig. 5b,e,f). Effects of the fire treatment were not consistent across species (Figs 4,5). In three species (*Cassinia*,

*E. blakelyi*, *E. melliodora*), enhanced emergence occurred in ungrazed plots where there was more fuel (litter and biomass) and fires were more intense (Table 1).

#### Interactive effects of ground surface and ant exclusion frames

Of the seven species used, one (*Cassinia*) did not germinate in sufficient numbers to be analysed. Significant effects of different types of sown surfaces were detected in four species, whereas two species had significant effects associated with the enclosure treatment (Table 6). The use of the ant exclusion frame significantly enhanced seedling emergence for two species (*Allocasuarina littoralis* and *Eucalyptus blakelyi*) across sowing treatments and similar trends were detected for other species (Fig. 6). Burial of sown seed also enhanced seedling emergence, as did sowing seed on scarified soil surfaces relative to sowing on an undisturbed surface (Fig. 6). Within-site comparisons of sham exclusion frames with complete frames revealed no detectable differences (Table 6), although the power of the test was very low.

## DISCUSSION

### Field emergence and laboratory germination

The times taken for seedlings to emerge in the field were slower than those observed for seedling

**Table 4.** Analysis of variance of percentage of viable seeds emerging for the three species sown at all sites 10 weeks after sowing in experiment I

Source	d.f.	<i>Eucalyptus blakelyi</i>		<i>Eucalyptus melliodora</i>		<i>Leptospermum polygalifolium</i>	
		MS	F	MS	F	MS	F
S	2	1559.8	12.2***	630.0	6.2**	636.8	19.2***
B	1	2145.8	16.8***	4113.2	40.2***	267.0	8.1**
C	2	808.1	6.3**	599.7	5.9**	3.7	0.1
G	1	259.1	2.0	8.5	0.1	37.9	1.1
S × B	2	488.1	3.8*	558.8	5.5**	400.5	12.1***
S × C	4	384.2	3.0*	153.7	1.5	16.4	0.5
S × G	2	330.3	2.6	51.5	0.5	100.7	3.0
B × C	2	79.8	0.6	217.6	2.1	13.6	0.4
B × G	1	185.7	1.5	176.1	1.7	5.2	0.2
C × G	2	1136.0	8.9***	226.9	2.2	49.4	1.5
S × B × C	4	94.6	0.7	54.9	0.5	19.6	0.6
S × B × G	2	258.1	2.0	545.1	5.3**	8.4	0.3
S × C × G	4	302.9	2.4	86.0	0.8	12.3	0.4
B × C × G	2	27.7	0.2	47.7	0.5	14.4	0.4
S × B × C × G	4	91.3	0.7	115.3	1.1	16.8	0.5

S, site; B, burial; C, cover; G, grazing. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

germination in the laboratory. Most seedlings had emerged by 10 weeks in the field compared with 14–21 days under laboratory conditions. This difference may be attributed to the colder conditions at night in the field. At each of the experimental sites, above-average rainfall fell before and after sowing seed and this appeared to provide optimal conditions for germination of the species used. Despite these ideal conditions total seedling emergence in the field was generally less than germination in the laboratory and negligible background emergence was observed. It is unlikely that seedling emergence was missed in the field as weekly censuses were undertaken, although some seed may have germinated in the buried treatments and not emerged. Studies of eucalypts have shown that woodland species can emerge from shallow burial (< 5 mm; Curtis 1989; Yates *et al.* 1996) and deeper burial may have inhibited some species from emerging. However, it is likely that reduced emergence in the field was related to seedbed conditions (to be discussed further on).

Overall there was no relationship between seed size and seedling emergence in the field, although seed size and laboratory germination were negatively correlated. Several studies have shown that seed mass and relative growth rates are negatively correlated for shrubs and trees (Jurado & Westoby 1992; Wright & Westoby 1999) but it appears that the ability of seedlings to emerge in the present study was unrelated to seed size.

**Rainfall**

Initial seedling emergence of eucalypt species varied among sites but these differences decreased over time. This changing spatial effect was probably due to initial rainfall differences among sites that evened out over the first few months of emergence. Over all sites the total rainfall was more than double the long-term summer average of 95 mm per month. Such events have only occurred on the New England Tablelands seven times in the past 50 years and extreme events where rainfall reaches 250 mm per month, as they did in January 1996, have only occurred a few times. Whalley and Curtis (1991) suggested that successful seedling establishment of eucalypts was associated with these events. The lack of dry weather precluded us from testing these ideas by supplementary watering through both emergence and early survival life stages. All large tree species (eucalypts and *Allocasuarina*) emerged faster than the shrub species and generally attained higher cumulative emergence than the shrubs in the field. This suggests that field emergence of shrub species is more dependent on rare rainfall events than that of tree species in grassy woodlands.

**Table 5.** Analysis of variance of percentage of viable seeds emerging for species sown at single sites 10 weeks after sowing in experiment I

Source	d.f.	<i>Acacia dealbata</i>		<i>Cassinia quinquefaria</i>		<i>Eucalyptus viminalis</i>		<i>Eucalyptus youmanii</i>		<i>Indigofera australis</i>		<i>Lomaria fraseri</i>		<i>Xanthorrhoea johnsonii</i>	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
B	1	104.2	5.7*	19.5	0.5	1127.1	7.3**	2963.8	32.8***	221.6	2.8	810.9	8.3**	938.0	11.8***
C	2	1.8	<0.1	247.8	6.4**	318.7	2.1	0.1	<0.1	172.8	2.2	45.1	0.5	33.4	0.4
G	1	12.4	0.7	64.2	1.7	8.5	<0.1	38.5	0.4	23.8	0.3	4.5	<0.1	60.1	0.8
B × C	2	4.7	0.3	3.1	0.1	52.7	0.3	136.9	1.5	3.4	<0.1	3.6	1.0	3.8	<0.1
B × G	1	36.7	2.0	34.7	0.9	351.9	2.3	41.3	0.5	1.1	<0.1	167.2	1.7	4.7	<0.1
C × G	2	2.2	0.1	34.5	0.9	128.5	0.8	10.6	0.1	49.1	0.6	37.8	0.4	218.4	2.7
B × C × G	2	3.2	0.2	36.3	0.9	113.8	0.7	28.3	0.3	10.8	0.1	87.2	0.9	217.7	2.7

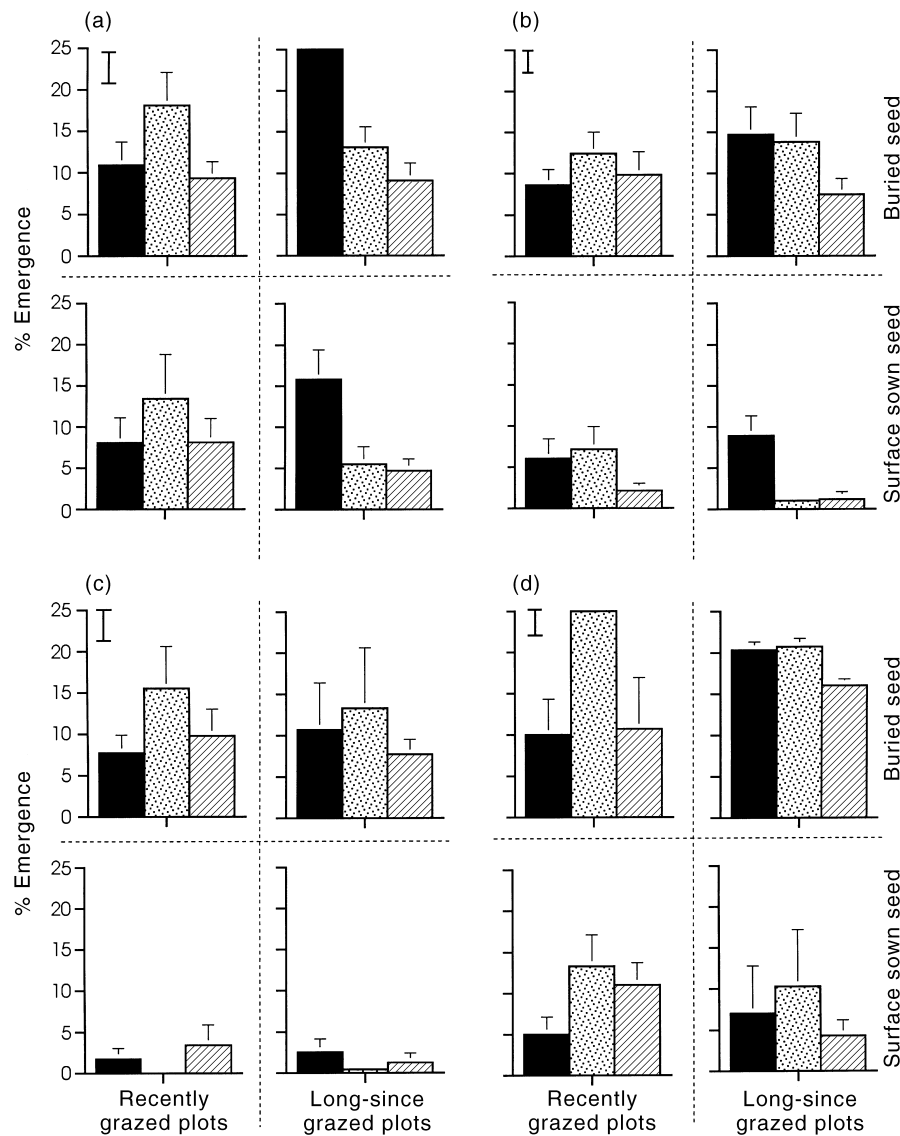
B, burial; C, cover; G, grazing. \**P* < 0.05; \*\**P* < 0.01; \*\*\**P* < 0.001.

**Factors that enhanced seedling emergence:  
Grazing history and fire**

Grazing history is thought to inhibit the regeneration of woody plants indirectly in woodlands by modification of the soil through increasing soil compaction and changed nutrient status (Windsor 2000). Analyses of soils at our sites showed little difference between sites that were recently grazed and those in adjacent areas where grazing had been excluded for many years, so we cannot speculate about these effects on seedling emergence. Ground layer and litter biomass were enhanced in plots long-since grazed by stock (Table 1). Enhanced ground biomass in these plots appeared to have little effect on seedling emergence when cover was maintained. Similarly, removal of ground cover in high biomass plots had little effect on seedling emergence. This contrasts

with many forest eucalypt studies, where either removal of the litter layer enhanced emergence in the absence of herbivores (see Stoneman & Dell 1994), or the presence of litter enhanced emergence (Facelli *et al.* 1999). The lack of cover effects in long-since grazed plots probably reflects the favourable moisture conditions during emergence. However, some competitive effects may have occurred in recently grazed pastures as we found that removal of ground cover enhanced the seedling emergence of several species.

Interactive effects of burning and grazing history were found in two eucalypts (*E. blakelyi*, *E. melliodora*) and similar trends were apparent for two shrub species (*Cassinia*, *Xanthorrhoea*). In these species, enhanced seedling emergence often occurred if long-since grazed plots were burnt. This effect probably resulted from the higher biomass that

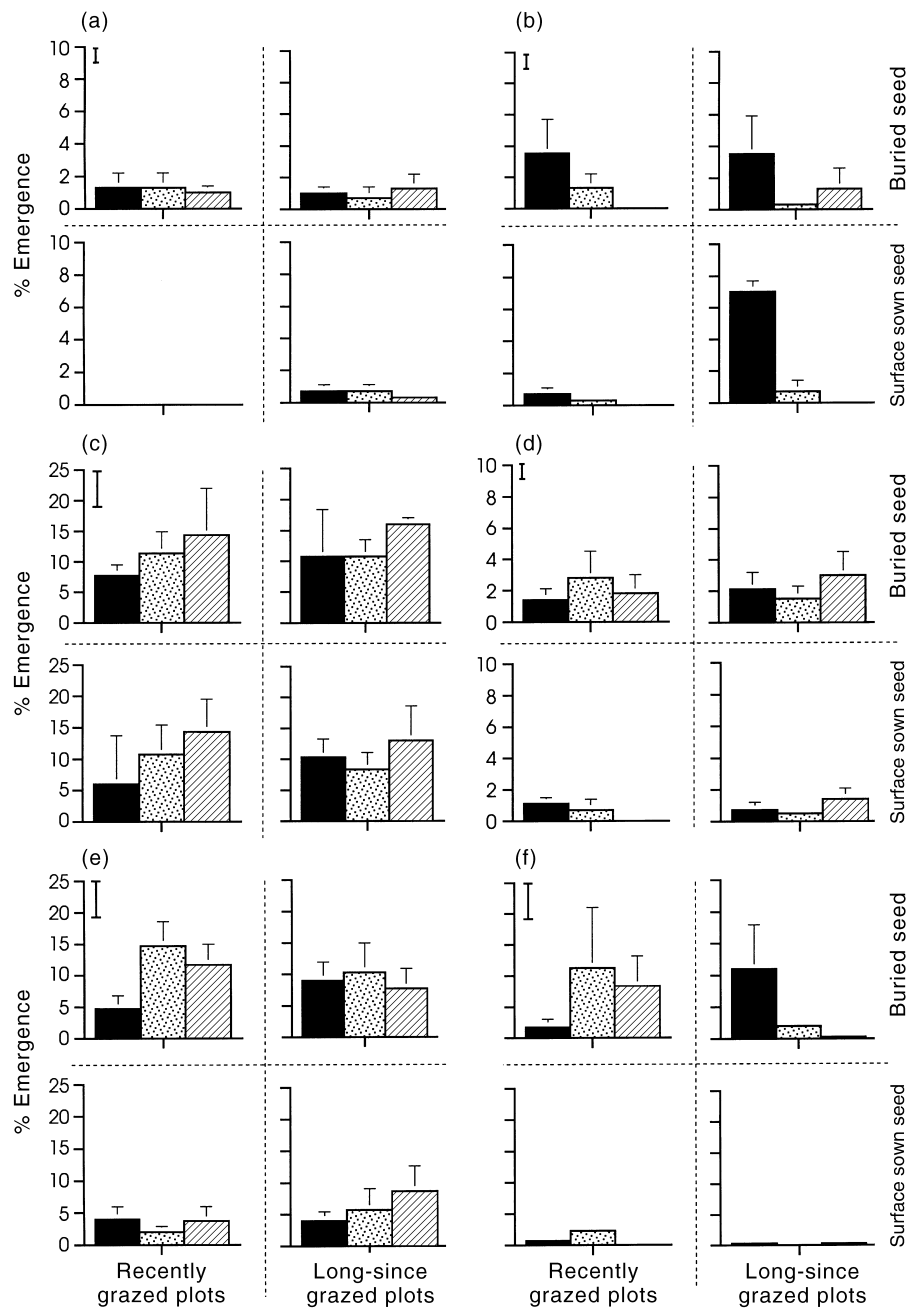


**Fig. 4.** Mean (+ SE) cumulative emergence of eucalypt seedlings 10 weeks after sowing in recently grazed and long-since grazed plots with ground cover treatments and sowing treatments. *Post hoc* significant difference ( $P < 0.05$ ) is shown as a bar. (a) *Eucalyptus blakelyi*; (b) *Eucalyptus melliodora*; (c) *Eucalyptus youmanii*; (d) *Eucalyptus viminalis*. (■), Burnt; (◻), cleared; (▨), intact.

produced more intense heat and ash. Similar ash-bed effects have been noted for temperate woodland species, in which fire is unrelated to breaking seed dormancy (Yates *et al.* 1996; Semple & Koen 1997). It should be noted that the hard-seeded species used in our experiments were heat pretreated before sowing and did not show any ash-bed effects. We therefore think that intense fire could not only break dormancy for hard-seeded species (see Clarke *et al.* 2000), but also provide seedbed conditions for the recruitment of selected trees and shrubs.

**Factors that enhanced seedling emergence:  
Soil and seedbed conditions**

Soil surface treatments had the strongest effects in both experiments. Buried seed generally had higher seedling emergence than surface-sown treatments. Enhanced emergence where seed is buried has been reported for both eucalypt (e.g. Stoneman & Dell 1994; Semple & Koen 1997) and shrub species (e.g. Clarke *et al.* 1996; Semple & Koen 1997). This may be attributed to: (i) innate physiological preference for germination in the



**Fig. 5.** Mean (+ SE) cumulative emergence of shrub seedlings 10 weeks after sowing in recently grazed and long-since grazed plots with ground cover treatments and sowing treatments. Post hoc significant difference ( $P < 0.05$ ) shown as a bar. (a) *Acacia dealbata*; (b) *Cassinia quinquefaria*; (c) *Indigofera australis*; (d) *Leptospermum polygalifolium*; (e) *Lomatia fraseri*; (f) *Xanthorrhoea johnsonii*. (■), Burnt; (▨), cleared; (▩), intact.

**Table 6.** Analysis of variance of percentage of seedling emergence for experiment II

Source	d.f.	<i>Acacia dealbata</i>		<i>Allocasuarina littoralis</i>		<i>Eucalyptus blakeyi</i>		<i>Eucalyptus youmanii</i>		<i>Hakea microcarpa</i>		<i>Hovea linearis</i>	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
S	1	37.8	2.6	100.4	0.9	114.2	2.3	432.4	3.4	393.9	5.7*	38.3	2.2
E	1	51.5	3.5	942.4	8.2**	314.8	6.2*	409.9	3.2	5.7	0.1	30.7	1.7
B	2	145.6	9.8***	921.2	8.0**	214.2	4.2*	599.8	4.7*	145.3	2.1	1.9	0.1
S × F	1	21.2	1.4	7.9	0.1	40.0	0.8	263.6	2.1	4.3	<0.1	10.5	0.6
S × B	2	63.5	4.3*	290.6	2.5	38.1	0.7	298.1	2.3	55.1	0.8	8.0	0.5
F × B	2	59.5	4.0*	164.3	1.4	87.8	1.7	163.4	1.3	60.1	0.9	26.1	1.5
S × F × B	2	34.8	2.3	361.2	3.1	2.2	<0.1	79.3	0.6	29.2	0.4	28.1	1.6
Sham contrast	1	3.9	0.1	238	0.9	45.0	0.6	342.0	1.7	222.0	2.5	27.8	1.7

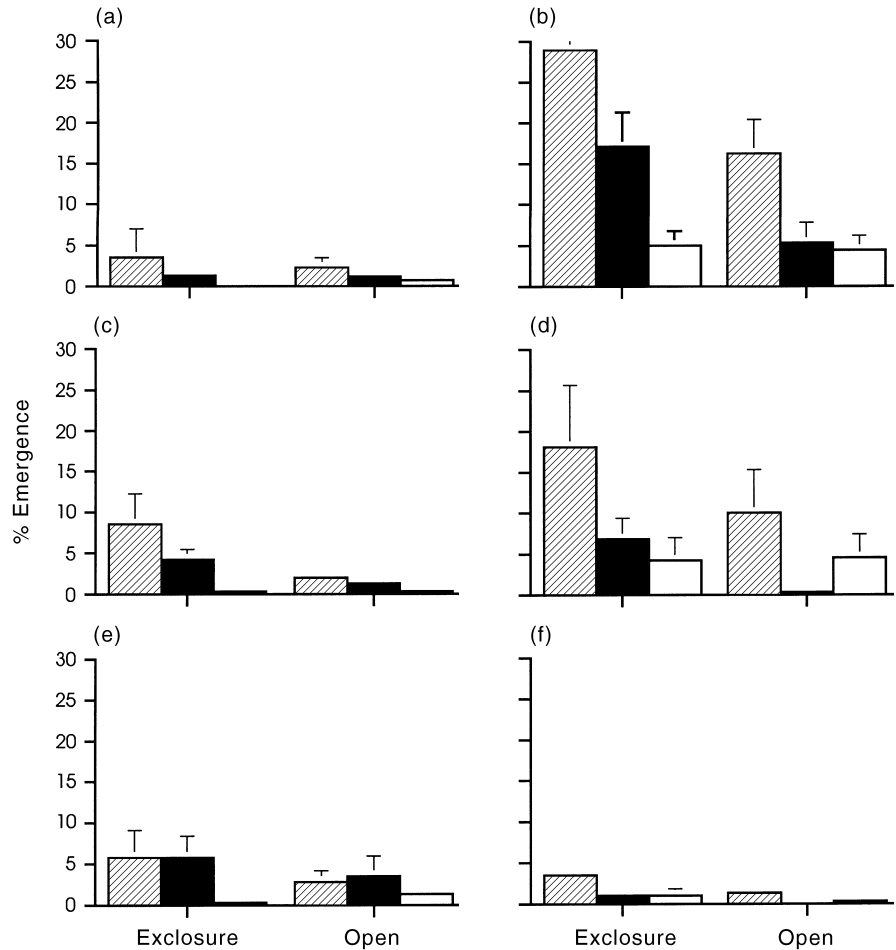
S, site; E, exclosure; B, burial. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

dark or depth; (ii) better soil contact with seed, which enhances humidity and imbibition; (iii) escape from seed removers; or combinations of these effects.

There was some evidence for preferential dark germination, because species with a preference for dark germination in the laboratory (*E. youmanii*, *Xanthorrhoea johnsonii*) showed substantially enhanced germination compared with other species when buried. However, those species that showed preferential germination under diurnal light cycles in the laboratory showed no emergence inhibition when buried. The large number of *E. viminalis* seedlings emerging from buried seed in the present study may be related to the ability of this species to emerge better from depth than *E. blakeyi* and *E. melliodora* are able to do (Curtis 1989).

Comparisons among seedbed treatments in experiment II highlight the importance of microsites in seedling emergence when the effects of ant removal are isolated. Within the confines of ant exclosures, all surface-sown seed had better emergence when soil surfaces were scarified compared with unscarified soil. On unscarified soil surfaces, large-seeded species (*Acacia*, *Hovea*, *Hakea*) had less emergence than the smaller-seeded species. This effect was similar to the results found in a laboratory study of nine species by Campbell and Nicol (1996) where large-seeded species did not germinate well when surface-sown. Open soil surfaces will have greater water deficits for large-seeded species and have been shown to reduce the germination and emergence of several forest eucalypt species (Bachelard 1985; Gibson & Bachelard 1986). The positive effect of litter on enhanced seedling emergence in some eucalypts has also been attributed to reduced water deficits by enhancement of humidity (Facelli *et al.* 1999). However, in experiment I the retention of natural cover and litter rarely enhanced seedling emergence.

Reduced emergence from surface-sown seeds of species in experiment I may have been the result of seed removal by ants or other invertebrates. Ants are significant predators of eucalypt seeds and have been shown to remove seeds of a range of woodland eucalypts (Andersen 1989; Clayton-Greene & Ashton 1990; Stoneman & Dell 1994; Yates *et al.* 1995) and other temperate woodland species (Clarke 2000). A comparison of caged and uncaged treatments in experiment II suggested that seed removal by invertebrates reduced seedling emergence. This was supported by the observation that ants removed 50–90% of seeds when presented with seeds of woody species (Clarke 2000). However, comparison of sham cages and intact cages showed no significant differences, which means that the effect of cages in excluding ants and other predators was potentially confounded by the enhanced shelter provided by the cages. Hence the results of the exclusion experiment must be treated cautiously. The effects



**Fig. 6.** Mean (+ SE) cumulative emergence of seedlings 20 weeks after sowing in three levels of ground cover treatments with and without ground invertebrate exclosures. (a) *Acacia dealbata*; (b) *Allocasuarina littoralis*; (c) *Eucalyptus blakelyi*; (d) *Eucalyptus youmanii*; (e) *Hakea microcarpa*; (f) *Hovea linearis*. (▨), Buried seed scarified surface; (■), surface-sown scarified surface; (□), surface-sown not scarified.

of burial in experiment I were equivocal; they may be a result of better water relations and/or the effects of reduced seed theft by invertebrates.

Models for the recruitment of trees in eucalypt forest ecosystems highlight the importance of disturbance in wet forests with decreasing reliance on disturbance in drier forests (Florence 1996). Recent studies of subhumid woodlands (Semple & Koen 1997; Yates & Hobbs 1997) support our findings that the creation of microsites by ground disturbance is also important for initial recruitment of eucalypts in drier forests when seed rain and rainfall coincide. Nevertheless, eucalypt species appear to be better at emerging in low-disturbance treatments than shrub species, possibly as a result of their smaller seed size and lack of innate dormancy. Much less attention has been paid to models of the recruitment of shrub seedlings in grassy woodlands and forests. Germination experiments highlight the effects of fire in breaking the dormancy of many shrub species (Clarke *et al.* 2000). Our field experiments also suggest that ground disturbance, ashbeds and seed burial, either for escape from predation or enhanced water relations, enhance the seedling

emergence of shrub species when above-average rainfall occurs. In our experiments we were able to promote some emergence of all species in most sown treatments, probably as a result of a prolonged above-average rainfall. In contrast, natural recruitment of trees and shrubs was absent from our plots, highlighting the importance of seed supply and dispersal as ultimate determinants of recruitment.

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