

Seed characteristics and soil surface patch type interact to affect germination of semi-arid woodland species

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Abstract Biological soil crusts are common in many arid and semi-arid regions and they can alter micro-environments which are likely to directly and indirectly influence vascular plant establishment. The effect of biological soil crusts on germination is also influenced by the biological characteristics of the seeds themselves but rarely have the effects of both crust type and seed morphology on germination been examined in the same study. In this study, seed of five semi-arid woodland species with contrasting seed morphology were sown on top of patch types that commonly occur in natural woodlands (foliose lichen, short-turf moss, tree leaf litter, disturbed crust) and their emergence was followed. Percent germination varied between patch types and, for the largest-seeded species (*Maireana excavata*), final germination was significantly lower on the biological soil crust and litter patch types because they strongly acted as a physical barrier to seed penetration into the soil. The remaining four species showed no significant differences in final percent germination with patch type because most seeds either completely or partially penetrated the surface layer. Germination time courses, however, showed that biological soil crusts delayed the timing of germination of these species. Hence, soil crusts might differentially affect the spatial patterning of species in semi-arid

woodlands by their subtle influence on seedling emergence that is determined by differences in seed morphology and subsequent positioning within crusts.

Keywords Seedling regeneration · Biological soil crust · Safe site · Litter · Disturbance · Seed morphology

Introduction

Biological soil crusts consisting of lichens, bryophytes, algae, cyanobacteria and fungi are a common and widespread feature of arid and semi-arid landscapes worldwide. In many areas, they are considered to be essential components of healthy ecosystems and several studies have addressed aspects of the influence of crusts on vascular plants (West 1990; Eldridge and Greene 1994; Belnap 2002, Escudero et al. 2007; Su et al. 2007). The available data, however, indicate that biological soil crusts can have either positive (Hawkes 2004; Rivera-Aguilar et al. 2005), inhibitory (Deines et al. 2007; Serpe et al. 2006) or no effect on vascular plant establishment and cover (Prasse and Bornkamm 2000; Belnap et al. 2001).

Positive effects of biological soil crusts on vascular plant establishment are supported in a variety of environments by observational correlations between vascular plant cover and the area occupied by crusts

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(Lesica and Shelly 1992; Eldridge 1993; Bliss and Gold 1999). Experiments under laboratory conditions have also shown positive effects of crusts on germination (e.g. St Clair et al. 1984; Hawkes 2004; Rivera-Aguilar et al. 2005). Hawkes (2004) noted that germination was several fold higher on crusted than on bare soils. Positive effects of the crust on vascular plants may be the result of moisture conditions created by the crust, improved nutrient availability, decreased predation or enhanced seed lodgement (Van Tooren 1988; Van Tooren 1990; Belnap and Harper 1995; Belnap et al. 2001; Su et al. 2007).

Negative correlations between vascular plant cover and the presence of biological soil crusts have also been reported. These correlations have occurred on different types of crust including lichen-dominated, moss-dominated and cyanobacterial crusts (Keizer et al. 1985; Van Tooren 1990; Eldridge et al. 2000; Prasse and Bornkamm 2000; Sedia and Ehrenfeld 2003). Experiments in controlled environments have also shown that the presence of biological soil crusts can inhibit the germination of some species (Zaady et al. 1997; Zamfir 2000; Serpe et al. 2006; Escudero et al. 2007; Deines et al. 2007). Negative effects of the crust on germination could be attributed to competition for water and nitrate, changes in the red/far-red ratio, presence of a physical barrier to root penetration or the presence of inhibitory compounds such as metabolites with allelopathic properties (Van Tooren et al. 1985; Johansen 1993; Belnap et al. 2001; Deines et al. 2007).

The various effects of biological soil crusts on germination are likely to reflect differences in crust composition, seed characteristics and environmental conditions (Prasse and Bornkamm 2000; Zamfir 2000; Serpe et al. 2006; Deines et al. 2007; Su et al. 2007). Differences in crust composition can result in crusts with various morphological, physical and chemical characteristics resulting in different seedbed environments (Eckert et al. 1986; Eldridge and Rosentreter 1999; Belnap et al. 2001; Serpe et al. 2006; Escudero et al. 2007). Furthermore, seeds vary in their requirements for germination and consequently, may respond differently to the conditions created by the crust (Zaady et al. 1997). Evidence is accumulating to suggest that the interaction between crusts and germination of vascular plants is influenced by essential biological characteristics of seeds, such as size, shape and structure (Johansen 1993;

Eldridge and Greene 1994; Zaady et al. 1997; Zamfir 2000; Sedia and Ehrenfeld 2003; Morgan 2006; Deines et al. 2007). For example, biological soil crusts may inhibit germination of seeds that lack burial mechanisms or structures that facilitate soil–seed contact (Van Tooren 1990; Belnap et al. 2001). In addition, the crust may only affect germination under certain environmental conditions such as when germination is limited by water deficits (Keizer et al. 1985; Rokich and Bell 1995; Zamfir 2000; Hawkes and Menges 2003; Hawkes 2004; Li et al. 2005).

Because biological soil crusts may favour the establishment of some plants over others, their presence is likely to influence the distribution of vascular plants (Belnap 2003). Biological soil crusts, though important, do not completely dominate the ground layer in all crust associated ecosystems (Martinez et al. 2006; Thompson et al. 2006). Litter can also be an important ground cover component (Facelli and Pickett 1991), as are localised animal diggings that disrupt soil crusts and litter (Pyrke 1994). Therefore, whilst it is useful to study the interaction of biological soil crusts and vascular plants alone, it is likely to be more beneficial to also consider the role of litter and disturbance in generating soil patch-type heterogeneity and how plants, via seed germination, respond to such patchiness.

In semi-arid woodlands, crusts are common components (Eldridge 1996; Belnap 2003) but their ecological role in Australia has rarely been examined. Previously, we identified the diversity and distribution of crust components across a topography/community gradient in a semi-arid environment (Briggs and Morgan 2008) and we now ask: do these crusts affect the potential distribution of vascular plant species by affecting germination? In this study, the effects of biological soil crusts (intact and disturbed) and litter on germination of five species (covering a range of seed characteristics) from semi-arid woodlands in southern Australia were examined in a laboratory experiment.

Methods

Study area

Soil samples for this experiment were collected from Terrick Terrick National Park (TTNP), 225 km

northwest of Melbourne, Victoria, Australia. TTNP is situated within the Patho Plains, a sub-section of the Victorian Northern Plains Bioregion, and includes the Terrick Terrick Range and adjacent plain. Average annual precipitation for the Patho plains is ~400 mm, with winter months weakly dominating the rainfall patterns. Seasonal average maximum temperatures range from 30°C in summer to 15°C in winter. Seasonal average minimums range from 15°C in summer to 3°C in winter. The vegetation is a semi-arid *Callitris* grassy woodland typical of the rocky outcrops and outwash slopes at TTNP.

Study species

Five species common in semi-arid woodlands at TTNP and covering a range of seed sizes, shapes and germinability were selected for study: ^a*Salvia verbenaca* (Lamiaceae), *Austrodanthonia* sp. (Poaceae), *Maireana excavata* (Chenopodiaceae), *Leptorhynchos scaber* (Asteraceae) and *Vittadinia gracilis* (Asteraceae). Table 1 and Fig. 1 provide a description of the habit, seed morphology and mass and germinability of these species. [^a denotes exotic species].

Effect of patch type on germination

This experiment was designed to compare germination on different patch types amongst species. Seeds were collected from TTNP as they matured (September–October 2006) and stored dry at room temperature. At the beginning of November 2006, 48 naturally occurring soil ‘patch type’ samples were excavated from *Callitris*-dominated woodlands. Twelve patches (5 cm deep × 17 cm wide × 25 cm long) each of foliose lichen-dominated (*Xanthoparmelia* sp.), mixed-species short turf moss-dominated, *Callitris* leaf litter-dominated (average depth 7 mm) and disturbed soil crust (raked with a hoe to break up crust and surface soil) were removed whilst the soil was moist, placed in plastic trays and transported to La Trobe University where they were allowed to dry at room temperature for 7 weeks prior to commencement of the experiment. The minimum cover of foliose lichen and moss on a sample was approximately 50% and 60%, respectively. A thin cyanobacterial crust was present underneath the moss and lichen dominated patch samples.

In late December 2006, 15 seeds each of *S. verbenaca*, *Austrodanthonia* sp., *L. scaber*, *V. gracilis* and, due to their larger size, 10 seeds of *M. excavata*, were placed onto the surface of patch types, giving 12 replicates per treatment for each species. For foliose lichen and moss samples not covering 100% of the surface, seeds were specifically placed on top of the particular soil crust component. All seeds were placed on the surface rather than being buried, with the aim of mimicking initial positions of seeds after wind dispersal. The trays were then placed into two Zankel germination chambers (six replicates of each treatment in each chamber) set at 12 h light/12 h dark and 20/10°C diurnal light and temperature cycles, respectively. On day one of the experiment, each soil surface replicate was sprayed with 200 ml of distilled water reflecting a 12 mm rainfall event. Replicates were then watered to soil saturation (approximately 300 ml) on day five and this 5-day-watering regime was maintained for the duration of the experiment (60 days). This regime allowed drying out of soil surface between watering. Every five days, treatments were sprayed with distilled water, trays re-randomized within the germination chambers, and seeds checked for germination. Seeds were considered germinated on emergence of the radicle, or appearance of the cotyledon.

Seed fate

To determine if differences in germination were related to seed position within the ground cover layer, at the conclusion of the experiment the positional fate of every seed (germinated and un-germinated) on each patch type was assessed and placed into one of three categories: (1) no penetration (NP)—no part of the seed was below the surface layer of the patch type in question; (2) partial penetration (PP)—some part of the seed was below the surface layer, and; (3) complete penetration (CP)—the whole seed was below the surface layer.

Data analysis

Germination lag time (LAG) was recorded as the time from start of experiment until germination commenced. Germination speed (T_{50}) was calculated as the time taken from commencement of germination until 50% of the final percent germination was

Table 1 Plant life form, mean seed mass, and germination attributes in response to different patch types for five northern plains grassland species

Species	Life form	Seed mass (g)			G success (%)			df	Test statistic	P	LAG (days)			T ₅₀ (days)		
		D	L	F	D	L	M				D	L	M	D	L	M
^a <i>Salvia verbenaca</i>	PH	0.134	22.22 ± 6.58	18.89 ± 4.84	20.00 ± 6.82	35.56 ± 8.46	3	1.35 [^]	NS	10–15	10–15	20–25	15–20	5–10	20–25	30–35
<i>Austrodanthonia</i> sp.	PG	0.097	16.11 ± 2.52	15.56 ± 6.16	12.78 ± 4.22	6.11 ± 2.90	3	5.60*	NS	10–15	25–30	30–35	45–50	20–25	15–20	20–25
<i>Maireana excavata</i>	PSS	0.848	35.83 ± 5.83a	2.50 ± 1.67b	0.00 ± 0.00b	3.33 ± 1.88b	3	31.75*	<0.001	20–25	50–55	NA	50–55	20–25	5–10	NA
<i>Leptorhynchos scaber</i>	AH	0.005	1.67 ± 0.74	0.00 ± 0.00	2.78 ± 1.53	2.78 ± 2.24	NA	NA	NA	10–15	NA	20–25	50–55	30–35	NA	25–30
<i>Vitadimia gracilis</i>	PSS	0.060	12.22 ± 2.28	10.56 ± 5.35	10.00 ± 4.89	13.33 ± 4.99	3	0.15 [^]	NS	10–15	25–30	30–35	20–25	15–20	20–25	30–35

Life form: PH perennial herb, AH annual herb, PG perennial grass, PSS perennial sub-shrub. Seed mass = mean of 50 seeds. G success = final % germination ($n = 12$ replicates \times 15 seeds (NB: *M. excavata* = 10 seeds) for each patch type), D disturbed soil crust, L *Callitris glaucophylla* leaf litter, F foliose lichen dominated, M short turf moss dominated. P significance of statistical test, NS not significant ($P > 0.05$). LAG time taken from beginning of experiment until commencement of germination. T₅₀ time taken from commencement of germination until 50% of total observed germination reached. ^a Denotes exotic species

* Denotes H statistic from Kruskal–Wallis test

[^] Denotes F statistic from ANOVA

Different alphabets above mean indicate significant differences in final percent germination ($P < 0.05$)



Fig. 1 Seed size, shape and structure of the five species used in the experiment. From left to right: *Maireana excavata*, *Vittadinia gracilis*, *Austroanthonia* sp., *Leptorhynchus scaber* and ^a*Salvia verbenaca*

reached. The influence of patch type treatment and germination chamber effects on final percent germination were tested for each species using a Nested ANOVA, with germination chambers nested within treatments. Bonferroni post-hoc comparisons were used when significant treatment effects ($P < 0.05$) were detected. Normality was visually assessed using histograms and Levene's test was used to check homogeneity of variances. If the Levene's test proved significant, data were transformed (arcsine, square root and fourth root). If the test remained significant after transformation, the non-parametric Kruskal–Wallis test was utilised with post-hoc comparisons made using Mann–Whitney U -tests.

The Kaplan–Meier method was used to assess differences in germination rates (Pyke and Thompson 1986). This method (traditionally used in survival analysis) allows the use of germination data consisting of elapsed time from the beginning of the experiment to seed germination (non-censored data), but also right-censored data (i.e. seeds that did not germinate before the end of the experiment). Pairwise shape comparisons for modelled germination curves were tested using Mantel's Log Rank test (Pyke and Thompson 1986).

Seed fate was analysed using one way analysis of variance and Bonferroni post-hoc comparisons, using the NP (no penetration) data which, intuitively, represents evidence for soil crusts acting as a physical barrier to germination. All three seed fate categories were not subject to statistical testing because they experience an inverse relationship. Normality and homogeneity of variances were assessed as above for final percent germination, and the Kruskal–Wallis test was applied to appropriate data.

Effect sizes of moss, foliose lichen and litter treatments were calculated relative to the disturbed (bare soil) treatment which acted as the control for this analysis (Quinn and Keough 2002). Effect sizes can be interpreted by comparing percent of non-overlap of the treated group's scores with those of the untreated group (Cohen 1988). An effect size of 0.0 indicates that the distribution of scores for the treated group overlaps completely with the distribution of scores for the untreated group, i.e. there is 0% of non-overlap. An effect size of 0.8 indicates a non-overlap of 47.4%, and an effect size of 1.7 specifies a non-overlap of 75.4% in the two distributions (Cohen 1988).

The Kaplan–Meier method was performed using the software package Systat version 10. All other statistical analysis was undertaken in SPSS version 14.0

Results

Effect of patch type on germination

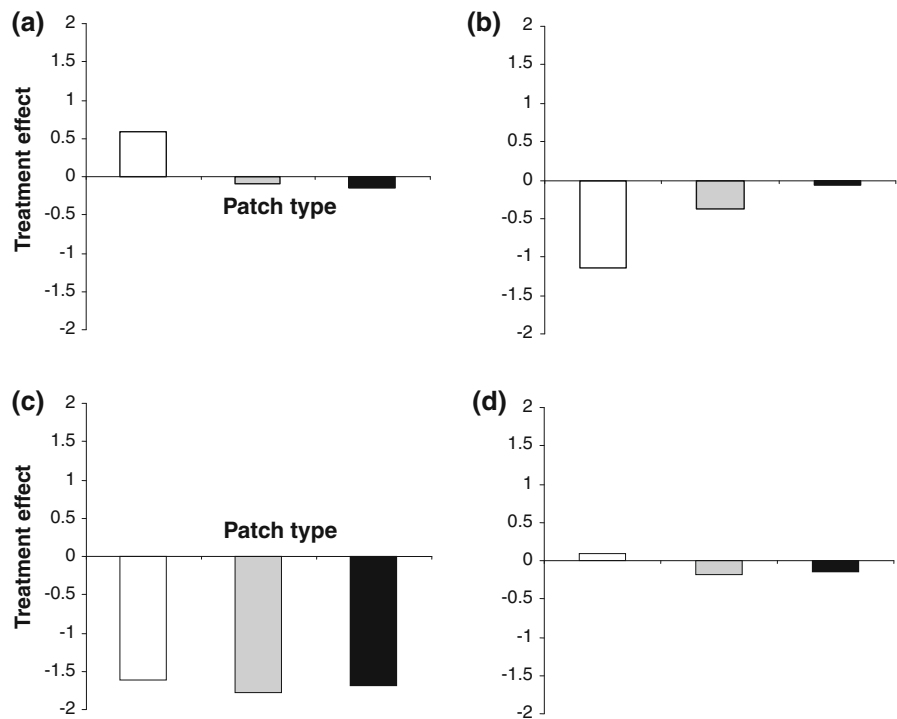
Germination chamber effects

No significant effect of germination chamber or germination chamber \times treatment interaction was detected in any of the analyses ($P > 0.05$ for all species). Therefore, differences observed were attributed to the patch type treatment and those effects are reported below.

Germination success

Final percent germination varied both amongst and within species across patch types (Table 1). ^a*Salvia verbenaca* had the highest percent germination on all patch types (except disturbed, on which *M. excavata* exhibited the highest germination) (Table 1). Germination of *L. scaber* was generally low on all substrates (<3%) (Table 1) and hence, was excluded from all statistical analysis. Final percent germination of *M. excavata* was significantly higher, by an order of magnitude, on disturbed soil than on litter, moss and foliose lichen patches (Table 1). *V. gracilis* germination was not significantly affected by patch type ($P > 0.05$), and small effect sizes support this result (Fig. 2d). Final percent germination of

Fig. 2 Relative treatment effect size of moss (white bars), foliose lichen (grey bars) and leaf litter (black bars) on **a** *Salvia verbenaca*, **b** *Austrodranthonia* sp., **c** *Maireana excavata* and **d** *Vittadinia gracilis*. A positive treatment effect indicates increased final percent germination relative to the control (disturbed). A negative treatment effect indicates decreased final percent germination relative to the control



S. verbenaca and *Austrodranthonia* sp. was not significantly different amongst patch types (Table 1). However, moss inhibited germination of *Austrodranthonia* sp. by an effect size of -1.14 (relative to disturbed control, Fig. 2b) and facilitated germination of *S. verbenaca* by an effect size of 0.58 (Fig. 2a).

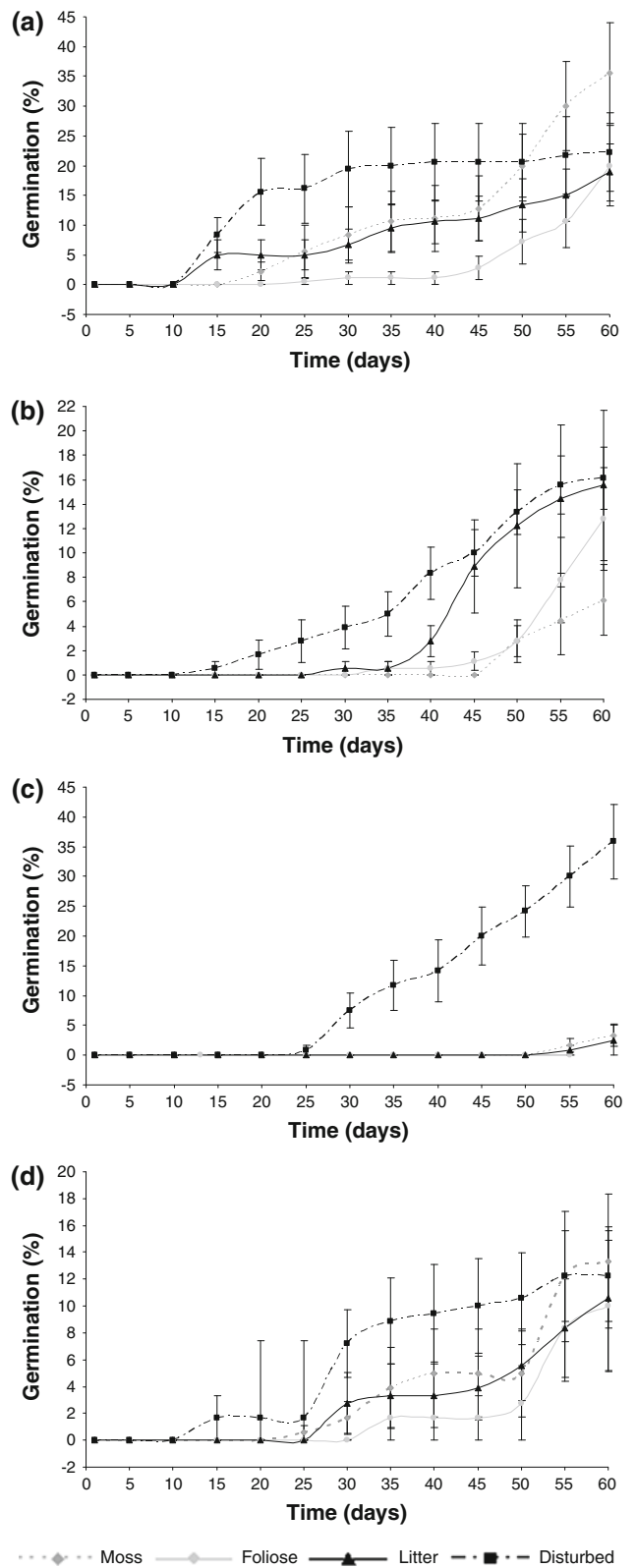
Germination lag and speed

Patch type affected lag time and germination speed (T_{50}) of all species (Table 1). All species experienced the shortest lag time on the disturbed soil crust, with *S. verbenaca*, *Austrodranthonia* sp. and *V. gracilis* commencing germination within 10–15 days, and *M. excavata* commencing within 20–25 days (Table 1). *S. verbenaca* and *V. gracilis* exhibited delayed germination on the foliose lichen patch type (20–25 and 30–35 days, respectively), whilst moss patches incurred the longest lag time of *Austrodranthonia* sp. and *M. excavata* (45–50 and 50–55 days, respectively) (Table 1). *S. verbenaca* and *V. gracilis* exhibited the shortest T_{50} on disturbed soil crust and longest on moss and foliose lichen (Table 1). T_{50} was shortest on moss for *Austrodranthonia* sp. and *M. excavata*.

Germination time courses

Germination time courses varied between patch types for each species (Fig. 3). Germination curves obtained via the Kaplan–Meier method were significantly different amongst patch types for *S. verbenaca* (Mantel $\chi^2 = 16.22$, $df = 3$, $P = 0.001$), *Austrodranthonia* sp. (Mantel $\chi^2 = 11.08$, $df = 3$, $P = 0.011$) and *M. excavata* (Mantel $\chi^2 = 129.10$, $df = 3$, $P < 0.001$). The *S. verbenaca* germination curve obtained on the moss patch type differed significantly from curves obtained on the disturbed (Mantel $\chi^2 = 4.70$, $df = 1$, $P = 0.030$), litter (Mantel $\chi^2 = 10.95$, $df = 1$, $P = 0.001$) and foliose lichen patch types (Mantel $\chi^2 = 12.67$, $df = 1$, $P < 0.001$). This was also the case for *Austrodranthonia* sp. with the curve from moss differing significantly to the curves from disturbed (Mantel $\chi^2 = 9.72$, $df = 1$, $P = 0.002$), litter (Mantel $\chi^2 = 8.64$, $df = 1$, $P = 0.003$) and foliose lichen (Mantel $\chi^2 = 4.49$, $df = 1$, $P = 0.034$). The disturbed patch type significantly altered the germination curve of *M. excavata* relative to litter (Mantel $\chi^2 = 46.38$, $df = 1$, $P < 0.001$), moss (Mantel $\chi^2 = 43.85$, $df = 1$, $P < 0.001$) and foliose lichen (Mantel $\chi^2 = 54.83$, $df = 1$, $P < 0.001$). *Maireana excavata* germination

Fig. 3 Germination time courses of **a** *Salvia verbenaca*, **b** *Austroanthonia* sp., **c** *Maireana excavata* and **d** *Vittadinia gracilis* on four different patch types. Germination based on mean (\pm standard error) accumulative percent recorded every 5 days ($n = 12$ for each patch type). Short turf moss dominated (moss), foliose lichen dominated (foliose), leaf litter (litter) and disturbed biological soil crust (disturbed)



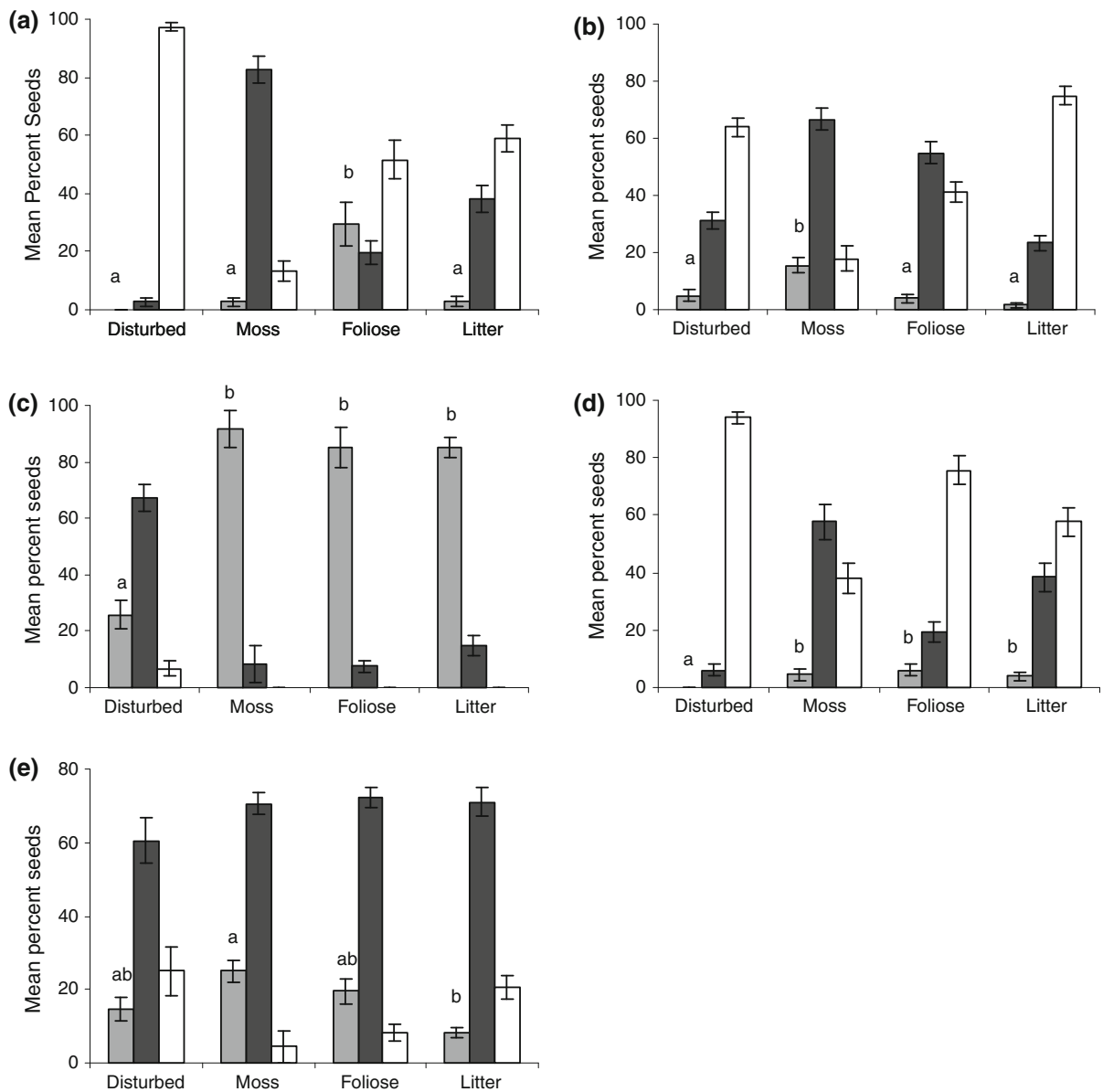


Fig. 4 Mean percent of seeds (\pm se) of **a** *Salvia verbenaca*, **b** *Austrodanthonia sp.*, **c** *Maireana excavata*, **d** *Leptorhynchos scaber* and **e** *Vittadinia gracilis* in different positional fates on each patch type at the conclusion of germination experiment ($n = 12$ for each patch type). NP no penetration of surface

layer, PP partial penetration of surface layer, CP complete penetration of surface layer. Different letters represent significant differences ($P < 0.05$) in patch types. grey bars NP, black bars PP, white bars CP

curves from the moss and foliose lichen patch types also differed significantly (Mantel $\chi^2 = 4.06$, $df = 1$, $P = 0.044$), though the effect was weak. *Vittadinia gracilis* showed no significant difference between germination curves from different patch types (Mantel $\chi^2 = 1.39$, $df = 3$, $P = 0.709$).

Seed fate

Seed fates on each patch type varied amongst species (Fig. 4). The percent of seeds not penetrating the surface differed significantly between patch types for all species (*S. verbenaca* $H = 31.64$, $P < 0.001$;

Austrodanthonia sp. $H = 21.80$, $P < 0.001$; *M. excavata* $F = 27.93$, $P < 0.001$; *L. scaber* $H = 8.57$, $P = 0.036$; *V. gracilis* $F = 6.05$, $P = 0.002$) ($df = 3$ for all species). Moss, litter and foliose lichen inhibited penetration of *M. excavata*. Significantly more seeds did not penetrate these patch types than did not penetrate disturbed soil (Fig. 4c). In other words, a greater percentage of *M. excavata* seeds penetrated (partially or completely) disturbed soil. For *Austrodanthonia* sp., complete penetration was greatest on disturbed soil and litter (64% and 75%, respectively), whilst the percentage of seeds not penetrating moss was significantly greater than the percentage of seeds not penetrating the other patch types (Fig. 4b). ^a*Salvia verbenaca* and *L. scaber* seeds all penetrated disturbed soil to some extent (Fig. 4a, d), and in the case of the latter species, this resulted in a significant difference between the percent of seeds not penetrating disturbed soil and the three other patch types. However, overall percentages were low (<7%) in that seed fate category. The majority of *V. gracilis* seeds partially penetrated all patch type surfaces (Fig. 4e), but the percentage of seeds not penetrating the moss surface was significantly greater ($P < 0.05$) compared to the litter surface.

Discussion

The results of this study indicate that patch type can differentially influence germination of plants found in semi-arid woodlands. However, outcomes of patch type vary and may reflect differences in seed size and structure, and the germinability of the species. Overall germination was highest for ^a*S. verbenaca* and *Austrodanthonia* sp., the two species with mechanisms for enhancing seed–soil (moisture) contact. The round seeds of ^a*S. verbenaca* develop a thick mucilage which increases seed–water contact, whilst *Austrodanthonia* sp. possess a hygroscopic awn which enhances the seed's ability to penetrate the surface layer. Moreover, biological soil crusts may have more influence on germination time courses than on final percent germination.

Germination of all species occurred first on disturbed patches, probably because seeds in close contact with the soil typically have a greater and more reliable supply of moisture than seeds on the soil surface (Rokich and Bell 1995). Hence, water uptake and

germination are faster (Oomes and Elberse 1976). The effects were especially pronounced for the large disc-shaped seeds of *M. excavata* (Fig. 1), which showed significantly higher final percent germination on disturbed patches compared to biological soil crust and litter patches. *M. excavata* has a high germinability and is likely limited by moisture availability. Although moss patches can enhance moisture availability (Van Tooren et al. 1985), seeds of *M. excavata* did not benefit because their large size prevented them from penetrating the moss layer. By contrast, the smaller seeds of ^a*S. verbenaca* were able to penetrate the surface and germination was promoted, most likely as a result of increased moisture. This suggests that due to the seed size and structure of *M. excavata*, foliose lichen, litter and moss patch types indirectly prevented germination by acting as a physical barrier to the soil or to microsites where conditions may be more favourable. Morgan (2006) also showed that large-seeded species did not germinate on top of soil crusts whereas small-seeded species germinated in small quantities. The regeneration niche for species such as *M. excavata* may be promoted by the soil disturbances created by native digging animals (Pyrke 1994).

Short-turf moss delayed and decreased germination of the grass *Austrodanthonia* sp. relative to the disturbed treatment (though the difference was not significant, the effect size was great). Serpe et al. (2006) found similar results on short moss-dominated crust relative to bare soil for four grass species in the Great Basin, USA. Seeds of *Austrodanthonia* sp. possess a hygroscopic awn and, upon wetting can essentially 'drill' their way into cracks and depressions. Although germination on foliose lichen and litter patch types was initially reduced, once seeds were positioned within or beneath the surface, they were more likely in a moister microenvironment, and this process may explain the delayed germination. This theory is supported by seed fate data which show similar percentages of seeds penetrated litter, foliose lichen and disturbed soil patches, whilst the percent penetrating short-turf moss patches was significantly lower than these patch types.

^a*Salvia verbenaca* germination on disturbed soil crust peaked at around 20% by day 30, with little germination after this time. Almost 100% of ^a*S. verbenaca* seeds completely penetrated the surface of disturbed soil and observations suggest burial into the soil occurred quite rapidly (i.e. in the first 25 days of

the experiment). Seeds generally have optimal burial depths, and increased or decreased burial can prevent germination (Baskin and Baskin 1998). Therefore, it is possible further germination was not seen on this patch type because seeds eventually became buried too deeply, hampering gas exchange and blocking light. The percentage of *S. verbenaca* seeds which partially penetrated the surface was highest on moss patches, suggesting this position is most favourable for germination. In chalk grasslands, the presence of a bryophyte layer enhances water availability at the soil surface (Van Tooren et al. 1985); similarly, mosses in the present study are likely to create a moister microenvironment than that of disturbed soil and *S. verbenaca* seeds can further optimise conditions through their mucilage layer. Partial penetration of moss combines advantages of increased moisture availability with maintenance of full (or close to full) exposure to light which may be a requirement for germination of this species.

Vittadinia gracilis is abundant across the study area. This species germinated equally well under all patch type treatments and germination time courses were not significantly different. Seed fate of this species was similar across patch types with only moss and litter differing significantly in the number of seeds not penetrating the surface. The majority of seeds partially penetrated all surfaces and this result was likely to be influenced by the shape and size of the seed. The seeds are narrow, linear-wedge shaped and 4–7 mm long with a crown of numerous bristles as long as or longer than the seed. It was observed that the narrow, heavier end of the seed penetrated surfaces whilst the crown of bristles stopped at the surface and prevented the rest of the seed from penetrating further. This may indicate that for *V. gracilis* partial penetration is the most beneficial position for germination. Combined with its high germinability, all the above mentioned factors probably facilitate its broad distribution and suggest it is a generalist species with few small scale habitat preferences. Hawkes (2004) reported similar findings in which germination of an abundant herb species from xeric Florida shrublands was not influenced by different crust treatments (intact cyanobacterial crust, disturbed cyanobacterial crust, no crust).

Leptorhynchus scaber seeds (the smallest in the study) had high penetration on all patch types (>90%) which may be expected to enhance germination due to positioning in moister microsites. However,

germination was extremely low in all treatments suggesting light and temperature conditions were not optimal, or perhaps this species has a more complex germination ecology. If germination of a species is triggered by fire or extreme temperature events, small differentiations in moisture and light availabilities on different patch types are not likely to influence germination in the absence of such triggers. Therefore, the influence of biological soil crusts in these cases is likely to be of secondary importance. Conversely, it is likely that species with high germinability but which are limited by moisture requirements will show stronger differentiation amongst patch types (due to differences in micro-environments) than those species with complex germination ecologies.

Lag times were increased on crust patches for all species, and germination time courses varied amongst patch types. Germination speed and lag, as well as the uniformity of germination, are often of more ecological significance than final percent germination (Oomes and Elberse 1976; Fowler 1988; Jurado and Westoby 1992; Kader 2005). Species that can germinate quickly in water-limited environments are likely to benefit through a competitive advantage over slower germinating seeds (Ross 1976) by taking advantage of infrequent rainfall events. However, a site suitable for seed germination is not always suitable for successful seedling establishment and growth (Schupp 1995; Li et al. 2005). Although moss and foliose lichen crusts may delay or slow rates of germination (seen in four of the five species in the present study), they could enhance survival of established seedlings relative to disturbed soil. This is particularly true for late-successional species and where abiotic stress is high (Bowker 2007). Therefore, the benefits of germinating early in the season on disturbed soil could be equalled or outweighed by enhancement of seedling survival on soil crusts. In other areas, researchers have found that once plants become established, the effect of biological soil crusts on survival and biomass appears universally positive (Li et al. 2005).

In the present study, the effect of short-turf moss, foliose lichen, litter and disturbed soil crust on germination was studied and related to seed position within the surface layer because it likely influences moisture and light conditions (Van Tooren 1990; Facelli and Pickett 1991; Serpe et al. 2006). However, effects of biological soil crusts can also be mediated by chemical factors (Zaady et al. 1997;

Sedia and Ehrenfeld 2003; Hawkes 2004). Lichens in particular, have been shown to reduce germination through the synthesis of secondary compounds with allelopathic properties (Rundel 1978, although see Deines et al. 2007), and the litter of some plant species can do the same (Facelli and Pickett 1991). With respect to mosses, the effects of chemical factors on seed germination are poorly understood (van Tooren 1990). Some experiments suggest, however, that mosses do not affect germination through chemical compounds. Sedia and Ehrenfeld (2003) applied moss extracts to seeds, but this treatment did not have any effect on germination. It is also likely that variations in chemical characteristics exist between different moss species. Whether chemical factors were partly responsible for the reduction of *Austrodanthonia* sp. germination on short-turf moss remains unknown. The reduced penetration on this patch type suggests, however, a physical effect relating to seed water status. The fact that moss, litter and foliose lichen patches generally only delayed germination, rather than prevented it all together, suggests differences are a result of physical factors and subsequent changes to moisture and light conditions in the microsites surrounding seeds as they move through the surface layers, rather than inhibitory chemical compounds. Moreover, final percent germination and germination time courses were not significantly different between litter and foliose lichen patches for any species, suggesting they have similar ecological roles and act merely as a physical barrier to large seeded species.

In summary, this study showed that patch types differentially influence germination, and that initially, biological soil crusts may act as physical barrier to microsites more suitable for germination. Distinct differences in surface morphology of the patch types result in different seedbed environments, explaining why differences in germination exist within species. In addition, the result also appears to be influenced by biological characteristics of the seeds such as size, structure and germinability. The present study investigated effects in an artificial environment with consistent water applications. Under natural conditions, germination on the different patch types is likely to be effected by factors not considered here. In the study area, evaporation exceeds rainfall in all months except June and July (Skene and Harford 1964). As a result, moisture availability for plant

growth is frequently low, particularly in warmer months. Consequently, germination is almost certainly lower than under the germination chamber conditions. Moreover, this reduction in germination in the field may be more pronounced in certain patch types. Similarly, seed predation rates may be different on bare soil than on litter or crusts (Van Tooren 1988) which could affect seed density, distribution and germination. We show, however, that the outcomes of biological soil crusts on plant germination depend on both seed characteristics and soil patch type and it is likely that these interactions have important effects on patterns of local species coexistence.

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