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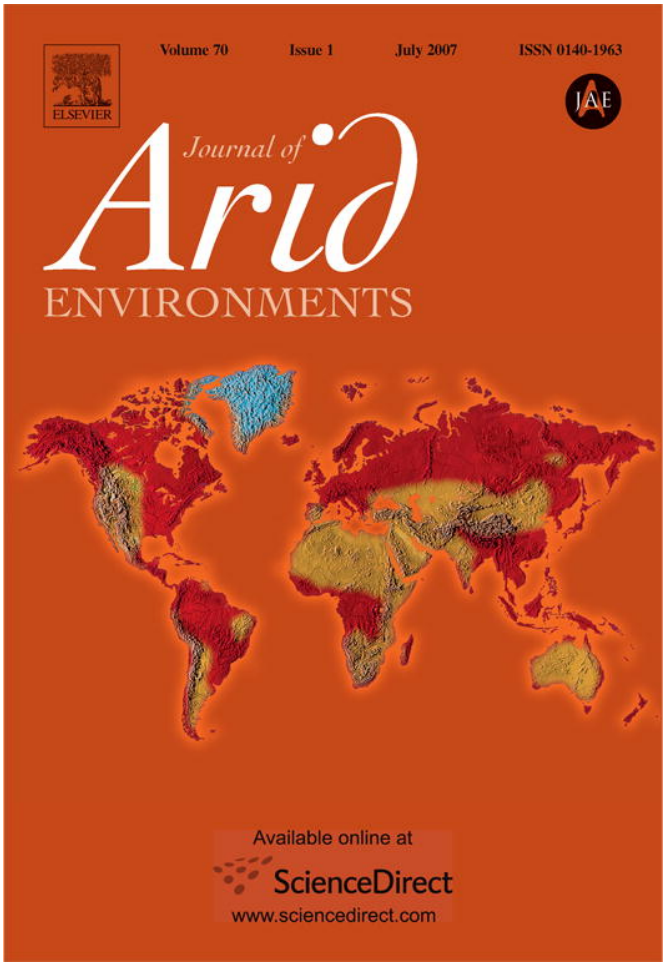

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Journal of Arid Environments 70 (2007) 18–28

Journal of Arid Environments

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Soil lichens have species-specific effects on the seedling emergence of three gypsophile plant species

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Received 7 March 2006; received in revised form 25 October 2006; accepted 15 December 2006
Available online 20 February 2007

Abstract

Despite advancements in our knowledge on the importance of biological soil crusts (BSC) in arid and semiarid environments, little is known on the effects of specific crust organisms on vascular plant seed emergence. We conducted a growth chamber experiment to evaluate the effects of two BSC-forming lichens (*Squamarina lentigera* and *Diploschistes diacapsis*) on the emergence of three specialist vascular plants from gypsum Mediterranean habitats (*Campanula fastigiata*, *Reseda stricta* and *Helianthemum squamatum*). The design of the experiment included three disturbance levels (intact, disturbed and removed) and two sterilization levels (live vs. autoclaved) of BSC-forming lichens. Specifically, we evaluated three hypotheses: (i) lichens will reduce the emergence of vascular plants, (ii) the magnitude of the negative effect of lichens on emergence will be species-specific, and (iii) the two species of lichens evaluated will exert differential effects on seed emergence. Emergence in the presence of lichens was lower than that obtained in tests conducted under optimum lab conditions (reduction of 50%). The effects of crust disturbance and sterilization on seed emergence were species-specific, and also varied with the lichen species serving as substrate. When germinated with *Squamarina*, a disturbance × sterilization interaction was found in *Campanula*. Disturbance increased and reduced the emergence of this species when the lichen was dead and alive, respectively. When *Helianthemum* was sown on *Squamarina* and *Diploschistes*, disturbance reduced and increased, respectively, the emergence of this species. The emergence of *Reseda* was not affected by any treatment when sown on *Diploschistes*, but disturbance reduced it when shown on *Squamarina*. Our

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0140-1963/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jaridenv.2006.12.019

results highlight the importance of species-specific interactions between vascular plants and BSC-forming soil lichens. The potential mechanisms underlying these interactions are discussed.
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Keywords: Biological soil crusts; Facilitation; Seed germination; Specific interactions; Spain

1. Introduction

Biological soil crusts (BSC) composed of bacteria, cyanobacteria, algae, mosses, liverworts, fungi, and lichens are a common feature of soil surfaces in arid and semiarid areas throughout the world (West, 1990). They exert a great influence on ecosystem functioning by affecting soil nutrient cycling, stability, and infiltration, by influencing the establishment and performance of vascular plants, and by serving as habitats for a large number of arthropods and microorganisms (Belnap and Lange, 2001). Given their ubiquity and importance, BSC have been the subject of a large number of studies, and many of them have focused on the interactions between BSC and vascular plants. Empirical evidence of the effects of BSC on vascular plants is contradictory, and range from negative (Hawkes and Menges, 2003; Prasse and Bornkamm, 2000) to neutral (Anderson et al., 1982; Jeffries and Klopatek, 1987; Kleiner and Harper, 1977) and positive (DeFalco et al., 2001; Graetz and Tongway, 1986; Lesica and Shelly, 1992). Positive effects have been related to the ability of BSC to minimize soil erosion (Belnap and Gillette, 1997), to favor infiltration and water retention (Maestre et al., 2002), to fix atmospheric nitrogen (Harper and Belnap, 2001), to retain sediments and seeds (West, 1990), and to provide safe sites for seeds and seedlings (Eckert et al., 1986). Contrarily, negative effects are related to specific exudates from BSC (West, 1990), to the creation of physical barriers (Romão and Escudero, 2005), and to competition for resources during the early stages of seedling development (Belnap et al., 2001).

Part of this controversy may be accounted for the experimental and observational approaches followed in most studies, which have usually considered both BSC and the vascular plant guild as a whole. As is often the case with plant–plant interactions (Maestre et al., 2005), plant–BSC interactions are likely to be highly species specific (Maestre, 2003). However, and despite important advances in our knowledge of the ecology of BSC achieved in recent years, only a reduced set of papers have explored species-specific responses of vascular plants to BSC as a whole (e.g., Hawkes, 2004; Hawkes and Menges, 2003; Zaady et al., 1997) or to different types of BSC (Rivera-Aguilar et al., 2005). These studies have found that the BSC effects on vascular plants are dependent on the plant species considered, and that affect especially the emergence and the performance of seedlings.

'In a recent study, Serpe et al. (2006) evaluated the effect of two different types of moss-dominated BSC (one composed predominantly by the tall moss *Tortula ruralis* Hedw. and the other dominated by the short moss *Bryum argenteum* Hedw.) on the germination of four grasses from the Great Basin of North America. However, and to our knowledge, no previous study has evaluated the effect of different BSC-forming lichen species on the emergence and establishment of different plant species. Soil lichens are an important constituent of BSC in arid and semiarid environments throughout the globe, and usually represent a later stage on its development (Belnap and Lange, 2001). Furthermore, it is

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unknown whether potential species-specific effects of these lichens on vascular plants are due to their morphological attributes (Eldridge and Rosentreter, 1999) or to the exudates produced by these species. With the aim to fill this gap, we conducted a growth chamber experiment to evaluate the physical and chemical (mediated by exudates and other soil compounds) effects of two BSC-forming lichens (*Squamarina lentigera* [Weber] Poelt. and *Diploschistes diacapsis* [Ach.]) on the emergence of three specialist vascular plants from gypsum habitats, two annuals (*Campanula fastigiata* Dufour, and *Reseda stricta* Pers.) and a shrub (*Helianthemum squamatum* (L.) Dum. Cours). The lichen and plant species studied are dominant components of the BSC and the vegetation, respectively, in gypsum outcrops from semiarid areas of Spain (Escudero et al., 1999; Martínez et al., 2006). These habitats are the home of an interesting bryo-lichenic and vascular plant flora characterized by a high degree of species diversity and rarity (Guerra et al., 1995), and rank among the most threatened ecosystems in Europe (Gómez-Campo, 1984). We tested the following hypotheses:

(i) Seed emergence will be reduced by lichens. We expect this to occur because the two lichen species evaluated firmly adhere to the substrate to form a very hard crust, which cannot be easily trespassed by recently emerged seedlings (Romão and Escudero, 2005).
(ii) The magnitude of the negative effect of BSC on seed emergence will be species-specific. All the plant species evaluated produce small seeds, albeit the seeds they produce differ in size (0.4×0.15 mm in *Campanula*, 1×0.9 mm in *Reseda*, and 1.25×1 mm in *Helianthemum*) and other traits (*Helianthemum* has mucilaginous seed coats whereas two other species do not).
(iii) The two species of lichens evaluated will exert differential effects on the emergence of seeds. We expect this to occur because of differences in their morphology (*Diploschistes* has a crustose thick thallus, continuous and smooth to verrucose, while *Squamarina* has a foliose and lobate thin thallus), and because of the presence of species-specific lichen exudates (lecanoric, orselinic, and diploschistesic acids in *Diploschistes*, and usnic and psoromic acids in *Squamarina*; Purvis et al., 1982).

2. Materials and methods

2.1. Lichen and seed collection

BSC and seeds were collected in gypsum outcrops located next to Belmonte de Tajo (3°18′23″W, 40°06′36″N, 686 m), in Central Spain. Seeds were collected from mature fruits from a minimum of 30 individuals in July 2004. They were kept at ambient temperature in the laboratory until March 2005, when the experiments were carried out. Individual lichens were carefully collected with a thin layer of soil beneath them (4 mm thick) in December 2004, and were kept at ambient temperature in the laboratory until the beginning of the experiment (lichens were watered every week).

2.2. Experimental design

We conducted a factorial experiment in the facilities of the Universidad Rey Juan Carlos from March to April of 2005. The design of the experiment consisted of two lichen species

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levels (*Diploschistes* and *Squamarina*), three disturbance levels (intact, disturbed and removed crust), two sterilization levels (live vs. autoclaved crust), and three vascular plants (*Campanula*, *Reseda*, and *Helianthemum*), resulting in 36 treatment combinations. In the intact disturbance level, the lichen was left intact; in the disturbed level, the lichen was crushed and thoroughly mixed with the soil beneath; in the removed level, the lichen was removed with a knife, leaving the soil uncovered and crushed. These disturbance levels cover a complete array of ecological scenarios: from undisturbed to a severe grazing and, finally, to a complete destruction (like those which occur in gypsum quarries, which are abundant in the seed and lichen collection area). Petri dishes (9 mm in diameter, 12 mm height) were carefully filled with all these sowing substrates. With the intact treatment we can detect chemical and physical effects, whereas with the disturbed treatment we can detect only chemical effects (physical effects are removed). Finally, with the removed treatment we eliminate both chemical and physical effects. For every disturbance level, half of the Petri dishes were autoclaved at 121 °C for 20 min. This treatment aimed to evaluate the effect of living lichens on germination. If chemical effects are relevant, they should be more apparent in alive than in dead soil lichens. Six replicates of each experimental combination were sown with 20 seeds, except for *Helianthemun*, for which we only sowed four replicates because of lack of seeds. The position of the seeds sown was controlled by means of a transparent sheet, where each sowing point on top of the lichen surface was marked with indelible ink. The number of naturally emerging seedlings (seedlings emerging outside the sowing points) was really low, and were clipped regularly.

In addition, we conducted standard laboratory tests on filter paper to determine, under the best possible conditions, the highest germination in each species, and to have a baseline for comparison (Escudero et al., 1997). These tests were carried out with different temperatures (15, 20, and 25 °C), and with different treatments (no treatment, physical scarification with sand paper, watering with giberelic acid—200 mg/l, and both last treatments together). As *Campanula* showed a very low percentage of germination under these conditions, we ran a battery of dry-heat treatments varying the temperature, but setting the heat timing very short because of the small size of their seeds. The most suitable temperature in all the evaluated species was 20 °C. The highest germination was achieved using light dry-heat pretreatment (1 min at 100 °C) for *Campanula*, and mechanical scarification for *Reseda* and *Helianthemum* (Pérez-García et al., 1995). Four replicates of 25 seeds were used per treatment.

It must be noted that, to test our first hypothesis properly, it would have been desirable to evaluate the emergence of seeds shown in unmanipulated soil surfaces not colonized by lichens. However, we did not added such a treatment in our experiment because in our study area, non-disturbed gypsum outcrops are well-covered by BSC. As this crust is primarily absent in our study area because of disturbances such as grazing and trampling, we believe that our experimental design is a reasonable approach to test this hypothesis.

Tests were carried out simultaneously in a germination chamber (Selecta Hotcold GL, Barcelona, Spain) equipped with 6 cool-white fluorescent light tubes (Philips 18 W 'TL'D standard type, wavelength 400–650 nm) that provide a photon flux density of approximately 19 $\mu mol\, m^{-2}\, s^{-1}$. Emergence conditions were set at 20 °C with a photoperiod of 16/8 h (see Escudero et al., 1997). The Petri dishes were sprayed with water once a day and watered every 3–4 days. The location of the Petri dishes in the chamber was regularly changed (each 3–4 days). Seeds with cotyledons were counted and thereafter removed from the Petri dishes. Usually, positive results in standard germination

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tests are considered immediately after radicle elongation. However, in our experiment this was only feasible after cotyledon growth. Although this usually implies an important development of seed roots before counts, we have preferred to focus our work on emergence instead of germination because radicle elongation was difficult to monitor. For this reason, we have maintained a differentiation between germination in the standard laboratory experiments on filter paper whereas emergence when lichens and gypsum soil was used. Experiments were maintained for 45 days.

2.3. Statistical analysis

The data were analyzed separately for each plant and lichen species using Generalized Linear Models (GLMs; McCullagh and Nelder, 1989). Emergence data follow a binomial distribution (probability ranging from 0 to 1), so the best way to achieve linearity is the use of a GLM with logit link function and binomial error distribution, setting the variance to 'mean (1−mean)' (Venables and Riplay, 1998). Because the data are overdispersed, we used the quasilikelihood approach to overcome possible difficulties (Guisan et al., 2002). Consequently, F ratio tests were conducted to evaluate whether selected predictors explained a significant fraction of the deviance, which is an estimator of the total variation in the modeled variable (Guisan et al., 2002). Statistical analysis was performed using the S-Plus 2000 statistical package (MathSoft, Seattle, WA, USA).

3. Results

Standard tests on filter paper revealed that the germination of dry-heated *Campanula* and scarified *Helianthemun* seeds was very high, 94% ± 1.9 (mean ± SE) and 100% ± 0, respectively. Scarified *Reseda* seeds showed a lower emergence, 38% ± 2.9 (mean ± SE). When shown on lichens, the emergence of the three species was lower than that obtained in these standard tests (Figs. 1(A)–(C)). The effects of disturbance and sterilization on seed emergence varied between plant species, and varied also with the lichen species used as a sowing substrate. When sown on *Squamarina*, a disturbance × sterilization interaction was found in *Campanula* (Table 1). When the lichen was dead and alive, disturbance increased and reduced the emergence of this species, respectively (Fig. 1(A)). The removal of the lichen crust increased the emergence of *Campanula* seeds when sown on *Diploschistes*, especially when the lichen was alive.

Helianthemum showed the highest emergence of the three evaluated species. The effect of disturbance on its emergence varied with the identity of the lichen used as substrate (Table 1). When this species was sown on *Squamarina* and *Diploschistes*, disturbance treatments reduced and increased, respectively, its emergence (Fig. 1(B)). Sterilization also increased the emergence rate of this species, but only when the seeds were sown on *Diploschistes*.

Reseda showed the lowest emergence of the three species evaluated (Fig. 1(C)). When its seeds were sown over *Diploschistes*, their emergence was below 10%, and was not affected by any of the treatments evaluated. This percentage increased when the seeds were sown on *Squamarina*. In this case, disturbance reduced the emergence of *Reseda* seeds.

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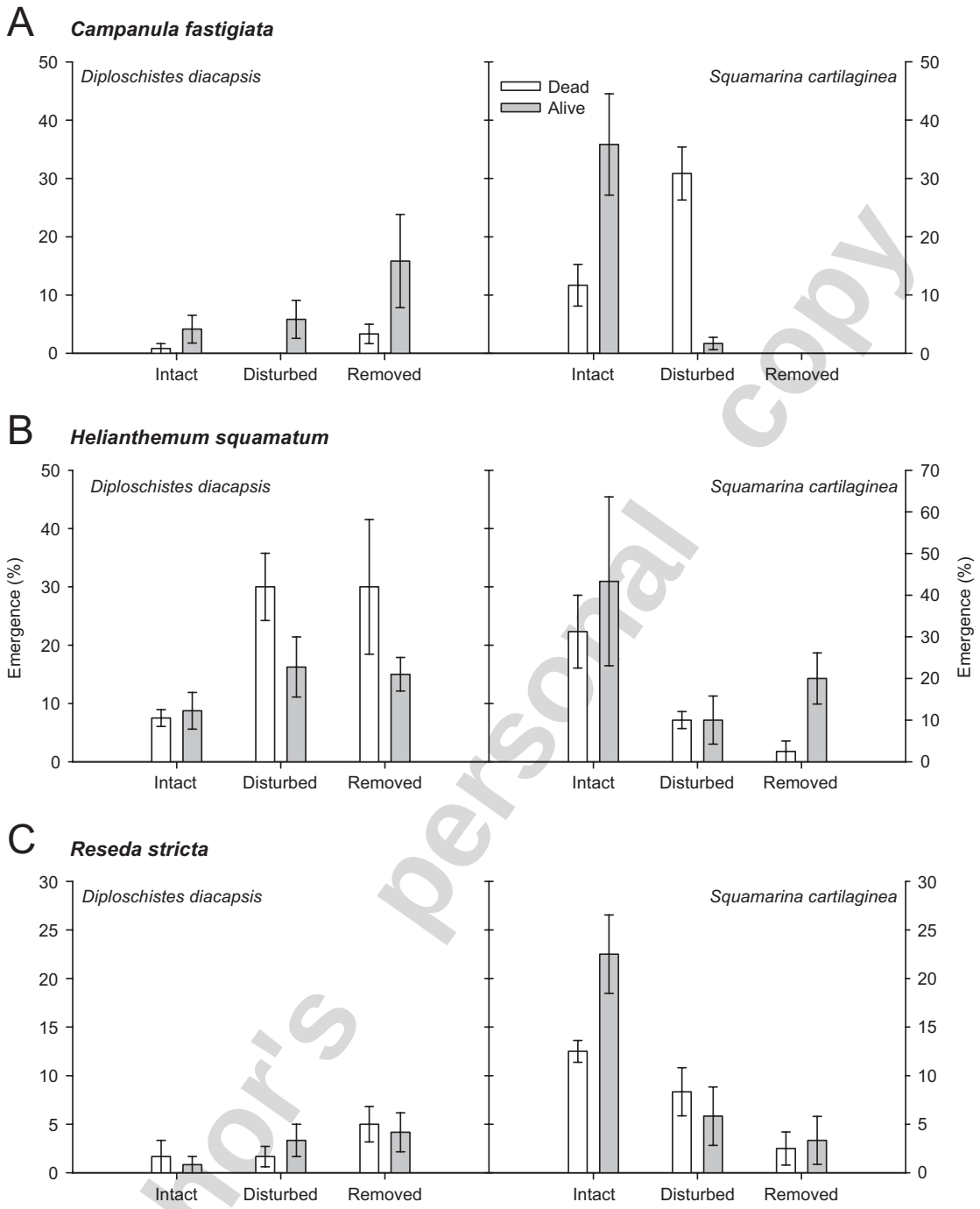

Fig. 1. Emergence of *Campanula fastigiata* (A), *Helianthemun squamatum* (B), and *Reseda stricta* (C) compared among sterilization (dead vs. alive), disturbance (intact, disturbed and removed), and lichen serving as substrate (*Diploschistes* vs. *Squamarina*) levels. Data represent means ± SE ($n = 6$, 4 and 6 for *Campanula*, *Helianthemun*, and *Reseda*, respectively).

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4. Discussion

Seedling emergence was reduced by the presence of BSC in all cases (when compared to standard germination conditions). However, responses to the treatments evaluated (disturbance and sterilization) were both plant and lichen species-specific. Therefore, our three hypotheses were supported by our results. Overall, emergence of the three plant

Table 1
Deviance analysis for the effects of *Squamarina lentigera* and *Diploschistes diacapsis* on the emergence of the three plant species evaluated

Lichen	Plant		df	Deviance	Residual df	Residual deviance	F	*P*
Squamarina lentigera	*Campanula fastigiata*	NULL			35	9.71		
		D	2	4.47	33	5.25	36.12	**<0.001**
		S	1	0.02	32	5.22	0.38	0.541
		D × S	2	3.20	30	2.02	25.90	**<0.001**
	Helianthemum squamatum	NULL			21	5.24		
		D	2	1.95	19	3.29	6.80	**0.007**
		S	1	0.41	18	2.88	2.89	0.109
		D × S	2	0.38	16	2.50	1.34	0.290
	Reseda stricta	NULL			35	3.94		
		D	2	1.63	33	2.31	12.45	**<0.001**
		S	1	0.09	32	2.22	1.34	0.26
		D × S	2	0.16	30	2.06	1.21	0.31
Diploschistes diacapsis	*Campanula fastigiata*	NULL			35	5.23		
		D	2	0.74	33	4.48	3.76	**0.035**
		S	1	1.12	32	3.37	11.31	**0.002**
		D × S	2	0.11	30	3.26	0.56	0.577
	Helianthemum squamatum	NULL			21	2.27		
		D	2	0.75	19	1.52	6.15	**0.010**
		S	1	0.30	18	1.22	4.89	**0.042**
		D × S	2	0.12	16	1.10	0.99	0.392
	Reseda stricta	NULL			35	2.07		
		D	2	0.26	33	1.81	2.22	0.126
		S	1	<0.01	32	1.81	<0.01	0.999
		D × S	2	0.06	30	1.75	0.49	0.615

P values lower than 0.05 are in bold. D = Disturbance, S = Sterilization.

species was higher on intact *Squamarina* thalli, especially when this species was alive. There are two potential mechanisms underlying our results: (i) morphological differences between *Squamarina* and *Diploschistes*, and (ii) differences in the secretion of allelochemical compounds among these two lichens.

The morphology of BSC components largely determines their ecological function relative to water infiltration, erosion, water retention and resiliency to disturbances (Eldridge and Rosentreter, 1999). Increased soil surface roughness by BSC may increase soil moisture and nutrient availability (Belnap et al., 2001; Elmarsdottir et al., 2003), and this mechanism has been advocated to explain enhanced plant emergence on BSC under field conditions (Harper and St. Clair, 1985). Morphological differences among lichens may contribute to explain our findings, as the morphology of *Squamarina*—with a large number of lobules—provides many hollows that can trap seeds and accumulate water and nutrients. It has been suggested that even subtle differences in substrate texture may lead to high differences in germination (Zamfir, 2000). Nevertheless, this affirmation should be taken with caution because moist conditions in germination chambers, which aim to simulate field conditions during the emergence season, are never limiting at this early stage

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(Escudero et al., 1999, 2000). On the other hand, intact *Diploschistes* thalli produced a significant reduction in the emergence of both *Campanula* and *Helianthemum*. This suggests a significant physical constraint. As suggested by Meyer (1986), and experimentally shown by Romão and Escudero (2005), most of the competitive ability of gypsophytes is related to the ability to penetrate extremely hard physical crusts during emergence. Furthermore, we have found that seedling emergence under field conditions can take place in microsites with high soil compaction values (Escudero et al., 1999). This implies that intact thick thalli of *Diplochistes* are very resistant to penetrating roots.

Exudates produced by lichens could have some inhibitory or enhancing effects on seed emergence and seedling growth (West, 1990). In a laboratory experiment, Hawkes (2004) found that germination in autoclaved crusts was dramatically reduced in comparison with living crusts in three out of four plant species from central Florida. Since water uptake and loss in lichens is purely a physical process, differences between dead and living intact thalli may be a consequence of the lack of some thermolabile compounds or the occurrence of new of them (Kershaw and Rouse, 1971; Rundel, 1978). The germination of *Helianthemum* when emerging on *Diplochistes* was not affected by the sterilization treatment. Emergence of *Campanula* was improved on alive *Diplochistes* thalli. When this plant species was sown on *Squamarina*, its emergence was enhanced when the thalli was intact and alive. However, when sown on crushed lichens, this response was significantly higher when the lichens were dead, suggesting that some link exists between the morphology of the lichen and the presence of specific chemical compounds. Further experiments should be conducted to demonstrate whether allelopathy is an operating mechanism in the observed plant–lichen interaction. These experiments could include, in a full factorial design, two artificial lichen morphologies and additions of exudates from each lichen species. Alternatively, these experiments could include multiple lichen species of each growth form and with different chemical compositions.

The differential effect of *S. lentigera* and *D. diacapsis* on the emergence of the species evaluated could have important implications for the composition and dynamic of plant communities in semiarid gypsum outcrops, as the recovery of vegetation in these areas may be associated to the presence of certain lichens. In the study area, *Squamarina* and *Diplochistes* are associated to late- and early-successional stages of the development of BSC in gypsum outcrops (Martínez et al., 2006). Our results would not support Eldridge and Greene (1994), who suggest that BSC may facilitate vascular plants in semiarid habitats mostly during the early stages of BSC and vegetation development. However, our findings are in agreement with those of St. Clair et al. (1984) and Elmarsdottir et al. (2003). These authors found a significantly higher seedling density on BSC after 5–11 years from disturbance, suggesting that seedling emergence and survival is higher in soils with non-pioneer crusts. Nevertheless, these lag times should be considered with caution because colonization times vary widely for mid- and late-successional crust species, and depend on factors such as the type, severity, and extent of disturbance, the structure of the vascular plant community, the type of substrate and the climatic conditions (Belnap and Eldridge, 2001).

Our experimental approach has some limitations that need to be acknowledged. The experiments were performed in Petri dishes under controlled conditions. Petri dishes prevent diffusion or leaching of chemicals, in contrast to the soil surface in the field. In addition, standardized climatic conditions (i.e., light, temperature, humidity, and water supply) in the growth chamber may amplify emergence responses to the treatments

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evaluated over those that may be observed in the field. The latter limitation is extensible to many controlled-environment studies and, when taken together with the first limitation, it is clear that extrapolation of our results to the natural world should be done with caution.

Previous studies evaluating the effects of BSC on the germination and emergence of vascular plants have found contradictory results, with studies showing positive or negative effects. Interestingly, most of these studies have considered both the plant and BSC communities as a whole, without taking into consideration the species involved. Our results highlight the importance of species-specific interactions between vascular plants and BSC-forming soil lichens. They also suggest that these effects should be explored separating, for each plant species studied, each of the BSC components. Albeit not definitive, observed differences between co-occurring gypsophytes probably are related to their variation in seed size and other seed traits. *Helianthemum* has mucilaginous seeds that favor its attachment to the substrate, decreasing the probability of being transported by wind or water. Studies on plant species coexistence should take into consideration not only plant–plant interactions, but also specific interactions with other organisms. Future studies are needed to explore the generality of the responses observed, and to test whether the responses observed in our experiment are also found under field conditions.

Acknowledgements

We thank the owners of La Encomienda estate for allowing us to work on their property, and Damian A. Ravetta and two anonymous referees for proposing multiple comments that substantially improved the manuscript. This research was supported by the Spanish Ministry of Education and Science (MEC; project number REN 2003-03366), and by the Community of Madrid projects GR/AMB/0932/2004 and REMEDINAL (S-0505/AMB/0335). ADLC was supported by a collaboration grant from MEC. FTM was supported by a Ramón y Cajal contract from MEC, and by an Early Career Project Grant (ECPG 231/607) from the British Ecological Society.

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