Differential effect of shade, water and soil type on emergence and early survival of three dominant species of the Atacama Desert

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Abstract Understanding the regeneration niche of species may allow us to gain insight into how communities are structured. In deserts, the regeneration niche is usually related to spaces beneath shrubs where shade cast by shrubs creates microenvironments that benefit seedlings and where even small amounts of rain may favour germination and establishment. Shade and water may also interact with different types of soils. However, species may have different requirements for germination and seedling survival. We could expect that shrub species with different drought tolerances exhibit different responses to the combination of these factors. We ask if responses of dominant species of the Atacama Desert to abiotic factors (shade, water and soil type) are related to their drought tolerance, a topic not exhaustively explored in shrubs growing in true deserts. We conducted two factorial experiments. The first one was designed to evaluate how shade (microhabitat) in combination with water may affect germination (emergence) and early survival. In the second experiment, we assessed the influence of shade in relation to soil type. Each species responded distinctively to the three variables under study, but in general, their emergence responses were more influenced by water (more water, greater emergence) than by microhabitat or soil type. Survival was influenced both by microhabitat and by water and was higher under shade and abundant water. Soil type affected only one of our species in terms of emergence. Species responses in general depended on their tolerance to stress. In one species, there was indication of a seed–seedling conflict. Our results show similar species responses to environmental constraints but also more or less unique responses that are related to their tolerance to drought and which may ultimately permit species coexistence. We found that shade may not be important for germination but may be crucial for survival in dry years.

Key words: Atacama Desert, early survival, emergence, germination, shade, shrubs, South America, survival.

INTRODUCTION

Understanding the mechanisms that allow species coexistence is a central issue in the study of biological communities. Several hypotheses have been postulated to explain this coexistence. One of these hypotheses is known as the regeneration niche of the species, understood as the processes involved in the successful invasion of an open space by an individual of a given species (Grubb 1977). Seed germination and establishment are two of the processes involved in the regeneration niche of the species, seed establishment involving seedlings, the most critical stage of the life cycle of a woody species (Harper 1977; Gutterman 1993). In deserts, the regeneration niche of many shrub species is associated with sites beneath shrub canopies, which are known to create improved microclimatic conditions that favour the development of the so-called nurse plant syndrome (Niering *et al.* 1963; Steenbergh & Lowe 1969). The enhanced microclimate frequently results from lower temperatures and higher humidity conditions (as compared with open spaces). These milder conditions are brought about by the shade generated by shrub canopies, which attenuate temperatures during the hottest part of the day and generally produce a more humid atmosphere, both of which benefit the plants in terms of their water relations (Gutiérrez *et al.* 1993; Tracol *et al.* 2011). This microclimate is especially favourable for seedlings.

The presence of these more mesic microenvironments underneath shrub canopies is an important issue in deserts, as it may have an effect on water dynamics. Water is the main factor for plant persistence in desert communities (Noy-Meir 1973). In relation to water, we have gained insight into the characteristics of seed germination in several desert taxa, especially in the case of desert annuals (e.g. Went 1948; Beatley 1974; Gutiérrez & Whitford 1987; Freas & Kemp 1989), one of the most successful life forms of arid regions (Gutterman 1993). Annuals are an important component of desert regions, but so are shrubs (including cacti in American deserts). In some deserts, shrubs are indeed the most important life form as judged by number of species or amount of cover (Ruthsatz 1977; Shmida 1985; López & Beck

2002). Yet, fewer investigations have addressed the problem of the regeneration niche for desert shrubs, especially in South America. It is true that a great deal of research has been conducted in Patagonia (e.g. Aguiar *et al.* 1992; Soriano *et al.* 1994; Schulze *et al.* 1996; Armas *et al.* 2008), which is a cold semi-desert. However, Patagonia shows a very particular vegetation (open spaces and grass rings encircling shrubs), which is not shared by most deserts, and thus, knowledge of its ecology cannot be extended easily to other xeric systems, especially hot deserts. For the latter, the work of López *et al.* (2007, 2013) can be cited for Bolivian/Argentinian summer-rain semi-deserts or that of Barchuk *et al.* (2005) or Tálamo *et al.* (2015) for dry forests. Far less is known in terms of shrub ecology for true deserts, such as the Atacama Desert (e.g. León *et al.* 2011; Martínez-Tillería *et al.* 2012; Carvajal *et al.* 2014). The latter studies show that great amounts of water are needed for establishment, that intermediate levels of shade seem to be better for establishment, that there are important differences among species in their responses to shade and water and that there are no real indications of trade-off between shade and water. Several aspects of the regeneration niche, however, remain vague or unknown. For example, these studies have not assessed the influence of water/shade on germination and how germination and early survival among dominant species correlate. In this sense, they do not allow us to determine, for example, potential seed–seedling conflicts (Schupp 1995), nor have they considered the role of soils on these regeneration niche attributes or how differences in drought tolerance influence species responses to abiotic factors. Understanding the regeneration niche of dominant species may give us insight into how desert communities respond to the influence of the more important abiotic factors in deserts. The two or three dominant species in Atacama Desert ecosystems may represent much more than half the total cover in several of them, hence the importance of understanding their ecology.

South American deserts are particularly interesting in ecological/biogeographical terms. Among other things, they are unique in several aspects. For example, beside the aforementioned importance of woody vegetation, South American deserts are part of the Neotropics, the most diverse region in the world. On the other hand, in South American deserts, extratropical influences seem to extend up to very low latitudes; this is reflected in climate patterns reminiscent of more temperate latitudes below 20° and also in the biology of certain taxa, such as cacti, which show reproductive biologies more akin to extratropical counterparts (e.g. Badano & Schlumpberger 2005; Larrea-Alcázar & López 2011). Another interesting characteristic of these deserts is that a different granivorous community has evolved in them (Vásquez *et al.* 1995; Marone *et al.* 2000), so that ants and birds are the most important granivorous guilds (whereas rodents play that role elsewhere). South American deserts are strongly influenced by the Andes, the longest mountain range in the world, and this influence may explain some of the 'anomalies' present in these deserts. Thus, the study of South American deserts should give us greater insight into desert ecology in general.

This study addresses the influence of water, shade and soil on both plant germination (emergence) and early survival of dominant species of the Atacama Desert. This is an important issue not only because the seed/seedling phases are particularly sensitive to environmental variables but also because, frequently, the microsites that are suitable for seeds are not so for seedlings, creating a seed–seedling conflict (Schupp 1995) that must be taken into consideration in order to understand the ecology of species and interpret distribution patterns correctly. The study is also designed to understand how species with different drought tolerances behave in relation to important environmental factors. It is part of a larger study that addresses plant–plant interactions in the Atacama Desert and that also focuses on seedling establishment in field conditions.

Specifically, we asked (i) how does shade affect germination and early seedling survival of three species from the Chilean coastal desert (*Encelia canescens*, *Flourensia thurifera* and *Pleocarphus revolutus*) and if its influence depends on precipitation or soil type; (ii) is the response related to drought tolerance of these species; and (iii) is there any indication of seed–seedling conflicts? To answer these questions, we set up two factorial experiments involving these three species, which differ in their tolerance to water stress. We predicted that the species less tolerant to stress will be more dependent on water and/or shade, and its early survival in low irrigation should be the lowest. The more water-stress-resistant species should have the opposite response, while a third intermediate species should show an intermediate response.

METHODS

Study site

The study was conducted in the common garden of the Biology Department, University of La Serena, Chile (29°54′S, 71° 15′W). This zone is located in the southern extreme of the coastal desert. Seeds were collected from the Quebrada El Romeral (29°43′S, 71°14′W, 300 m), 20 km north of La Serena. Average annual precipitation for the last decades was 83 mm (Squeo *et al.* 2006); most of it falls in winter, but in El Niño years, rainfall may exceed 200 mm; average temperature was 11.4 °C (Squeo *et al.* 2006). Vegetation was characterized

by Gajardo (1994) as coastal steppe shrubland. The species used in the experiments were *E. canescens*, *F. thurifera* and *P. revolutus*, all from the Asteraceae family. These are three dominant species in many plant communities of the southern coastal desert, which frequently co-occur. *E. canescens* is a small deciduous shrub or subshrub of 1 m or less in height, which has superficial roots; its yellow flowers may be seen from October to December; it is distributed from southern Peru to northern-central Chile, from sea level to 3000 m. *F. thurifera* is a 1- to 2-m-tall, deciduous shrub with a dimorphic (superficial and deep) root system; it has big yellow flowers that are present between August and December; it is distributed in the north-central regions of Chile, between sea level and 1000 m. *P. revolutus* is an evergreen shrub with a dimorphic root system and yellow flowers with a conspicuous white pappus, which are seen mainly between February and April; it is distributed in north and central Chile and from sea level to 3000 m. Propagules of these species are small and provided with pappi and thus are wind dispersed and can be transported far from their parents to different microhabitats.

Experiments

Two experiments were conducted in the winter and early spring 2012. Experiment 1 (winter) was designed to evaluate how shade may affect germination (indeed, what we recorded was emergence) and early survival of the study species and also to assess how it may modulate the influence of water on emergence. For each species, the treatments were irrigation (high/low) and microhabitat (shade/open). The main influence of shrubs in terms of microhabitat relates to the provision of shade. Shade has a positive effect on plants in terms of a reduction of excessive heat and light extremes, which in deserts attain very high/low values in open spaces. That is why shade and open may be seen as the two most important microhabitats for seeds and seedlings. As for water, it is the most limiting factor in deserts, and while assessment of the species responses to different water levels is recommended, comparisons of two markedly different irrigation treatments are sufficient to give us insight into how water may limit species performance. This is the more feasible alternative when logistic reasons (as happened in our case) do not allow for greater differentiation of the levels of a given factor.

Seeds were sown in pots 10 cm in diameter and 8 cm tall, filled with 250 cm^3 of sandy soil coming from the Quebrada El Romeral, which had been sterilized for 5–6 h at 120 °C to kill shrub seeds. Quebrada El Romeral is located near the city of La Serena, at about 30° south, at 150 m. Its vegetation is formed by a semi-desert shrubland placed on an old fluvial terrace. Shrub cover is around 50%. Dominant floristic elements are *Haplopappus parvifolius*, *F. thurifera*, *E. canescens*, *P. revolutus* and *Proustia cuneifolia*, among the most important ones, and *Senna cumingii*, *Bahia ambrosioides* and *Balbisia peduncularis* are among other less

important floristic elements. Seeds were taken from 30 or more individuals in February and April 2012 also from Quebrada El Romeral. The irrigation treatment was gradually provided over several days, keeping the soils near field capacity. By day 9, we stopped adding water to the low irrigation treatment (when 18 mm had been added) but continued to do so for the high treatment (until we reached 33 mm on day 31). However, on days 21 and 22, a natural rain of 15 mm increased the low irrigation treatment to 33 mm and the high irrigation treatment to 48 mm. Treatments for assessing microhabitat effects were open full light and deep shade (15% photosynthetically active radiation (PAR) reaching open sites, which is a value usually recorded near the shrub's base). Each treatment was replicated five times (one replicate of the combination high irrigation/shade for *E. canescens* was lost). For each replicate of *E. canescens* and *F. turifera*, 30 seeds were sown, while for *P. revolutus*, we planted 20 seeds/replicate. The pots were arranged in a completely randomized block design. Observations for emergence and survival were recorded daily and ended on day 37, when no more plant emergences were detected. Survival evaluation could not proceed further because of the shallow nature of the pots, which could not allow root development. Data were arcsin transformed in order to meet assumptions of normality and heteroscedasticity.

Based on the results of León *et al.* (2011), which assessed survival of coastal desert species, personal observations and expert opinion from local botanists, we established a ranking of tolerance to stress for the three species. From less to more tolerant, we arrived at the following order: *P. revolutus* < *E. canescens* < *F. thurifera*. Differences between *E. canescens* and *F. thurifera* may be small, but both are clearly more drought resistant than *P. revolutus*.

In experiment 2 (conducted in spring), we assessed the influence of shade in relation to soil type. Five shrub species were initially considered here (*E. canescens*, *F. thurifera*, *H. parvifolius*, *P. revolutus* and *P. cuneifolia*), but two of them (*H. parvifolius* and *P. cuneifolia*) had a very low emergence fraction; *P. revolutus* emergence was not as low, but it did not generate enough seedlings for survival to be evaluated. As before, two microhabitats were established: beneath shade and open. Soil type also had two levels: soils from beneath shrubs and soils from the open. Soils from beneath shrubs are known to contain more nutrients, and we could expect that this should have a positive influence on species performance. For the first case, soils were collected from beneath several individuals of dominant species at the Quebrada El Romeral. The soil samples from the open were also taken from multiple spots from the same site. Soils were thoroughly mixed before being placed in the 15-cm-deep, 12-cm-wide pots. A split-plot design was used in this case. Ten blocks were arranged in two columns and five rows. Five blocks were shaded, and five were kept in the open. Shading was less intense in this experiment, reaching 50% PAR of that in open sites; this is common in spaces

beneath shrubs not far from the canopy perimeter, and so this represented moderate shade. With this, we wanted to evaluate if moderate differences in shading were able to trigger different responses. Blocks were randomly assigned to a given position inside the arrangement. Inside each block, four pots were installed, one pair containing soils from shrub underneath canopies and the others from the open. Each pot contained 20 seeds of the different species. Data were arcsin transformed in order to meet assumptions of normality and heteroscedasticity. Observations for emergence were carried out weekly over 6 weeks, when practically no more emergences were observed. Evaluation of survival ended 3 months after the experiment began, when it was clear that the pots were too dry to sustain the seedlings. The analysis was performed with SPSS v.18.

RESULTS

Experiment 1

Emergence

Emergence of *F. thurifera* (66%), *P. revolutus* (50%) and *E. canescens* (36%) was relatively high, especially in the high precipitation treatment (Fig. 1). The first emergences began on day 7 in *F. thurifera* and *P. revolutus*, with only 12 mm of simulated rain. The first emergences in *E. canescens* occurred on day 9, with 15 mm of irrigation, after which few seedlings emerged daily (generally less than five). In *F. thurifera*, multiple emergences were recorded from day 9 to day 17, and for *P. revolutus*, the corresponding values were between days 9 and 15. In *E. canescens*, mult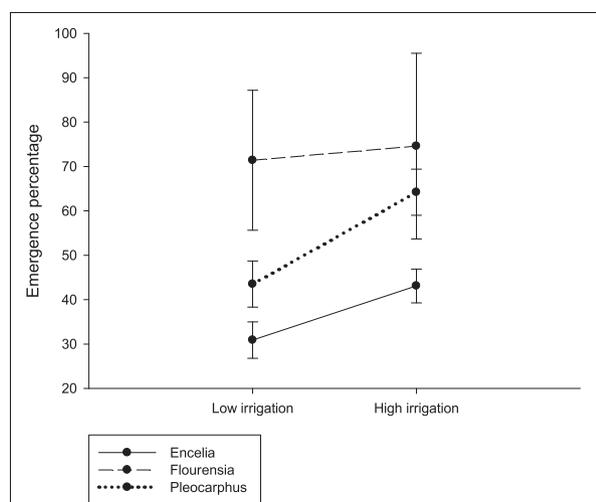iple emergences were recorded from day 11 to day 20. *P. revolutus* and *E. canescens* showed higher emergence with increased irrigation (from 43% to 64% in *P. revolutus* and from 31% to 43% in *E. canescens*), even though for this last species, differences were only marginally significant ($F_{1,11} = 4.672$, $P = 0.054$ for *Encelia* and $F_{1,12} = 7.789$, $P = 0.016$ for *Pleocarphus*; Fig. 1; see also Appendix). Seed emergence in shade and in open microhabitats was similar for the three species, but before the rain on day 22, *E. canescens* showed higher emergence in open ground (not shown). A high percentage of seeds emerged on day 21, that is, 1 day before the natural rain. For *E. canescens* from a final emergence fraction of 36%, 29% had already germinated on day 21; the corresponding fractions for *F. thurifera* and *P. revolutus* were 66/63% and 50/48%, respectively.

Seedlings survival

All three species had high survival rates with high irrigation (almost 100% survival for *E. canescens* and *F. thurifera* and over 80% for *P. revolutus*) and shade (>90% for *E. canescens* and *F. thurifera*). Our results showed that the increase in irrigation and the presence of shade had a positive effect on survival of all three species (for irrigation, *Encelia*: $F_{1,11} = 42.694$, $P < 0.01$; *Flourensia*: $F_{1,12} = 28.918$, $P < 0.01$; *Pleocarphus*: $F_{1,12} = 5.888$, $P = 0.032$; for microhabitat, *Encelia*: $F_{1,11} = 22.66$, $P = 0.001$; *Flourensia*: $F_{1,12} = 9.352$, $P = 0.01$; *Pleocarphus*: $F_{1,12} = 3.46$, $P = 0.088$; Fig. 2). However, in *E. canescens* and *F. thurifera* (also in *P. revolutus*, although results were only marginally significant), there was an interaction effect (precipitation by microhabitat interaction; *Encelia*: $F_{1,11} = 33.49$, $P < 0.001$; *Flourensia*: $F_{1,12} = 7.462$, $P = 0.018$; *Pleocarphus*: $F_{1,12} = 3.681$, $P = 0.079$; Fig. 3), indicating that seedlings may not survive in the open with low irrigation (plants with low irrigation in shade had only slightly diminished early survival as compared with those with high irrigation).

Experiment 2

Neither *F. thurifera* nor *E. canescens* responded differentially to microhabitat or soil type levels, either in terms of emergence or in terms of early survival (Fig. 4; see also Appendix). However, for *E. canescens*, there was a marginally significant effect of microhabitat (tendency to higher emergence in the open, as in the first experiment; $F_{1,32} = 3.281$. $P = 0.081$). *F. thurifera* had an emergence fraction almost identical to that from the first experiment (67 *vs.* 66, respectively), but for *E. canescens*, emergence was lower (23%). *F. thurifera* and *E. canescens* had high survival rates (around 80% and 84%). *P. revolutus* emergence, on the contrary, responded to both, having higher emergence in shade and in soils from open spaces
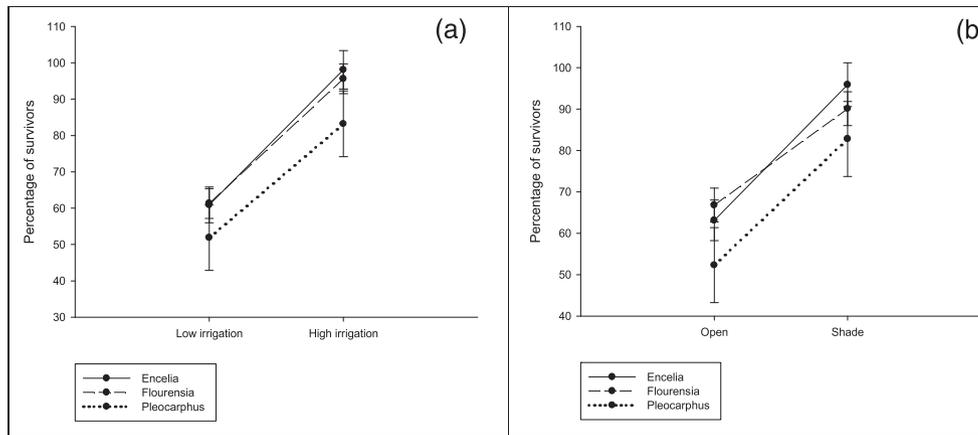

Fig. 1. Emergence fractions of the three shrub species employed in this experiment as a function of irrigation levels. Bars indicate standard deviations.

Fig. 2. Percentage of the emerged individuals of the three experimental species surviving to the end of the experiment as a function of (a) irrigation levels and (b) type of microhabitat. Bars indicate standard deviations.

($F_{1,32} = 4.901$, $P = 0.034$ for shade; $F_{1,32} = 5.681$, $P = 0.023$ for soil type; Figs 4 and 5). Its emergence was, however, much lower than that in the first experiment (only 8%).

DISCUSSION

The aims of this study were to determine the effects of irrigation, shade and soil type on two of the more crucial stages in the life history (emergence and, especially, early survival) of dominant shrub species of the South American coastal desert and if responses are related to drought tolerance of the species.

The effect of shade, water and soil type on emergence and early survival of dominant Atacama Desert shrubs

One first conclusion from this study is that all three species may survive only if there is significant rainfall. This is common in desert species (Beatley 1974). Emergence also was, in general, positively influenced by water. The effects of shade and soil were less important, but the response was species specific; thus, we consider this in the following sections. Other performance parameters in plant ecology are related to physiological and/or growth measurements or flower/fruit production, but this study was designed to evaluate survival only, which can be considered as the most important performance parameter. A qualitative evaluation of general plant appearance, however, allowed us to see that survivors in shaded condition in both sets of experiments were markedly bigger, had much larger leaves and these lasted longer than their counterparts from the open.

Was the response to the abiotic factors dependent on drought tolerance of the species?

Our results showed great interspecific variability in the response of these desert species. We found differences in the behaviour of the three shrub species. Emergence from our most stress-tolerant (*F. thurifera*) did not respond differentially to the treatments in terms of emergence (seeds exhibited an all or none response; Freas & Kemp 1989; Vidiella & Armesto 1989; Armesto *et al.* 1993). Nevertheless, in this case, there were two water levels only. The two less tolerant species increased their emergence fraction with higher irrigation water, showing a sort of predictive response (Venable & Lawlor 1980). A predictive response avoids the unnecessary loss of seeds. These results support the hypothesis of a greater response to water by the species less tolerant to water stress (especially *Pleocarphus revolutis*).

The study species had a fast response to increased irrigation, especially *F. thurifera* and *P. revoluta*; emergences were already observed on the seventh day after the experiments were initiated and with only 12 mm of irrigation (the emergence or germination threshold). *E. canescens* responded only a little later (day 9, 15 mm of irrigation), and its peak emergence period also ended after that of the other two species (day 20). Low emergence thresholds (usually below 25 mm) have also been observed in shrubs of other world deserts (e.g. Shalaby & Youssef 1967; Hammouda & Bakr 1969; Beatley 1974; Bowers 1994). Shrub emergence thresholds are usually lower than those reported for annuals, which range between 15 and 40 mm (e.g. Mott 1972; Beatley 1974; Vidiella & Armesto 1989). This may confer an advantage to shrubs over annuals in years when an initial, low precipitation pulse triggering germination in these shrub species is followed by further rains that permit shrub seedlings to be established earlier.
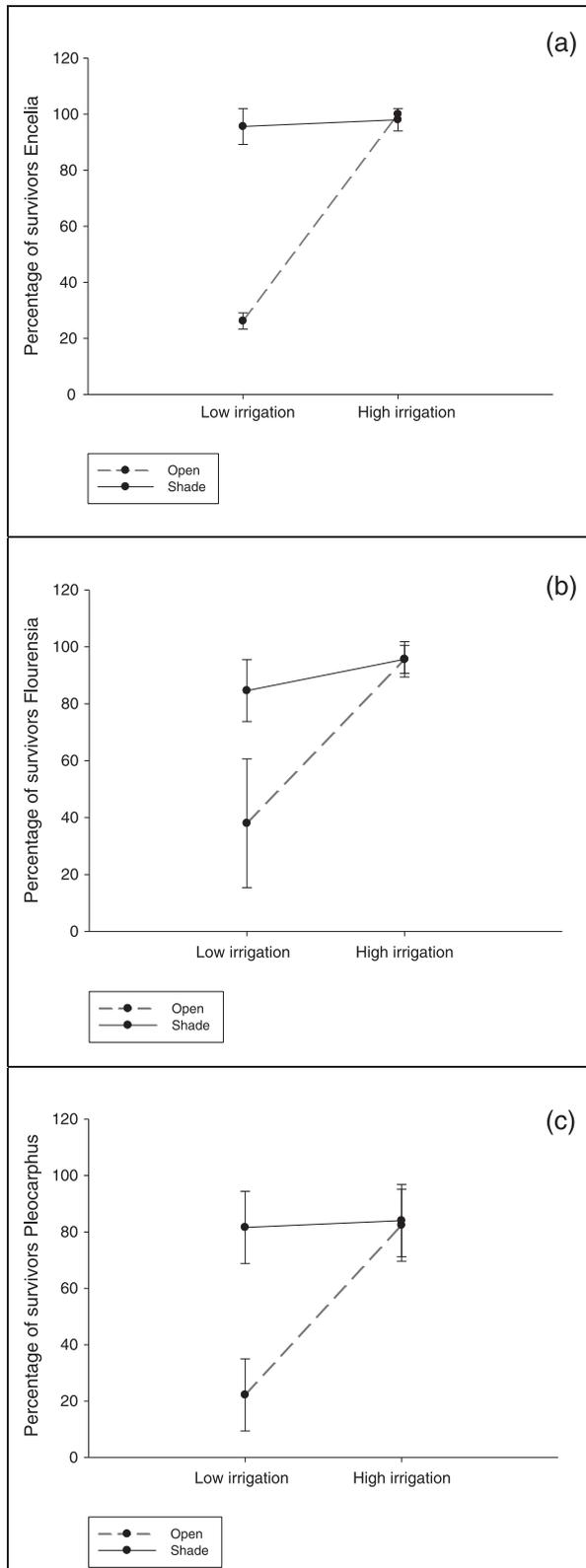
Fig. 3. Survival of individuals of (a) *Encelia canescens*, (b) *Flourensia thurifera* and (c) *Pleocarphus revolutus* observed in open and shaded conditions as a function of irrigation level. Bars indicate standard deviations.

Microhabitat seems not to play an important role in species emergence, except for *E. canescens* very early, in the first weeks (as recorded in the first experiment before the rains), and for *P. revolutus* (as shown in the second experiment). *E. canescens* appears as a more heliophilous species, given that it shows a tendency to germinate better in open spaces. This was clearly reflected in the emergence before the natural rainfall. It must be highlighted that the natural rain fallen during the experiment brought about a new wave of emergences in *E. canescens*, pointing to the importance, for the successful germination of at least some species, of an adequate distribution of rainfall over time (e.g. Reynolds *et al.* 2004). The differential response to water of *P. revolutus* in the two experiments may be related not only to differences in the quality of shade (deep shade in the first experiment *vs.* moderate in the second) but also to the conditions of both experiments (such as differences in pot depth or water addition). Also, seeds in the second experiment showed a much lower emergence fraction. This shows that *P. revolutus* seeds lose viability rapidly, as seeds came from the same stock. Seeds that retain viability may be a non-random subset from the original seed stock in terms of responses to water, and this may also explain their different responses to water.

Survival of the three species was in agreement with our hypothesis: the less tolerant (*P. revolutus*) had a lower survival (22%) in the more stressing conditions (low irrigation – open), the more tolerant (*F. thurifera*) had the best survival (38%) and *E. canescens* had an intermediate response. The prediction that the less tolerant species would have a greater positive response to water increase when passing from the low-precipitation to the high-precipitation treatments was not completely supported, however, as the emergence fractions increased by 62% in *P. revolutus* and *E. canescens* and 58% in *F. thurifera*. This could be related to the fact that differences between irrigation treatments were not very great. It is interesting to see the differential response to microhabitat in *F. thurifera* and *E. canescens*. In both species, shade increased survival in the first experiment but failed to do so in the second. This is undoubtedly related to the fact that in the second experiment, the evaluation took more weeks and so we had more opportunity to record mortalities, but it could also be a consequence of differences in shade quality. The positive effects may have arisen from deep shade conditions of the first experiment, and somewhat less desiccating conditions, because the first experiment was conducted in winter (*vs.* early spring for the second one). This suggests that dominant shrubs of the coastal desert benefit in early survival from the dark, humid conditions near a nurse.

Only *P. revolutus* exhibited differences in seed emergence in terms of soil type. It is not clear how soils from open spaces may trigger increased emergence fractions in this species, as soils with more organic matter should
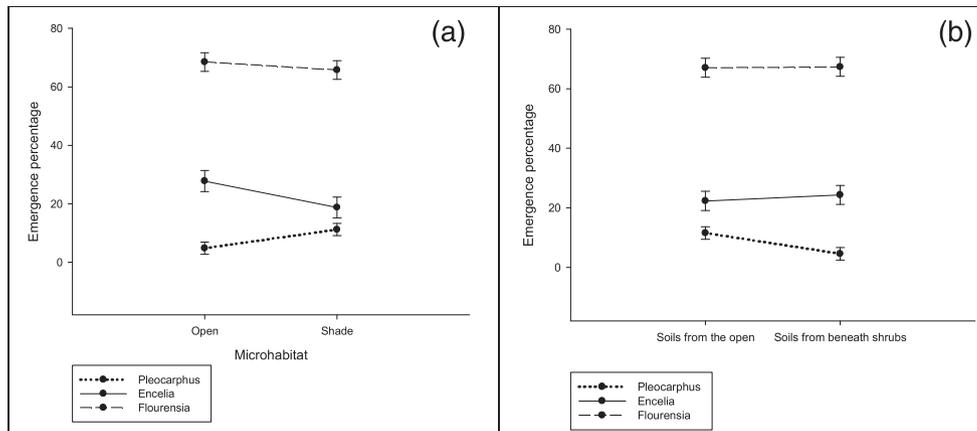
Fig. 4.   Emergence fractions of the three shrub species employed in this experiment as a function of (a) microhabitat and (b) soil type. Bars indicate standard deviations.
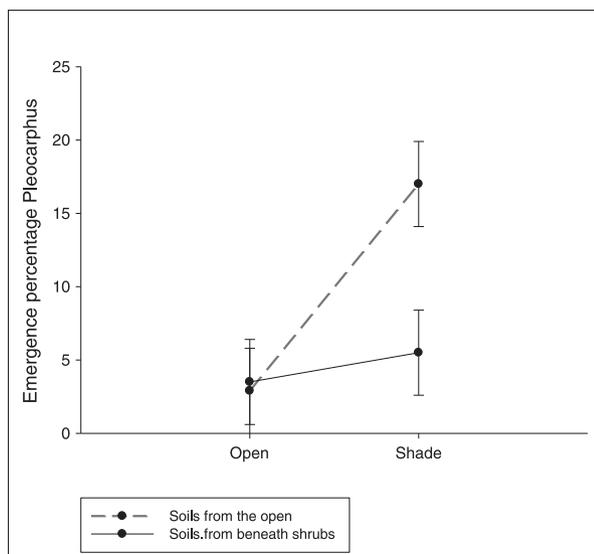

Fig. 5.   Emergence of individuals of *Pleocarphus revolutus* observed in soils of open spaces and soils from under shrubs as a function of microhabitat. Bars indicate standard deviations.

retain more water useful for germination, albeit this did not translate into increased emergence in *F. thurifera* or in *E. canescens*.

Our study species are codominant species in several parts of the coastal desert that showed important differences in their emergence and early recruitment. This may ultimately favour their coexistence, supporting the regeneration niche hypothesis (Grubb 1977) in deserts, where competition was usually seen as a process or factor of lesser importance than abiotic severity. However, the species also responded similarly in other respects, for example, showing diminished survival in open, dry conditions. This may indicate a more general constraint for most species that cannot tolerate the extremely

desiccating atmosphere of open ground, which highlights once again the importance of the heterogeneity created by shrubs in arid regions.

However important the regeneration niche is for species coexistence, plants have another strategy for perpetuating themselves in the community: vegetative propagation. Its importance may be such that Bond and Midgley (2001) even coined the term 'persistence niche' for one form of vegetative reproduction: resprouting. Resprouters seem to be common in unproductive sites (Midgley 1996; Bellingham & Sparrow 2000). In some communities, it may even be the main way of existence (e.g. Ganatsas *et al.* 2004; Torres *et al.* 2014). Although no studies of this kind have been conducted in the coastal desert, vegetative propagation seems to be important (R. P. López, pers.obs.). Recruitment is known to be very important in arid environments only in sporadic, high-precipitation years. In the coastal desert, this usually happens in 'El Niño' years (Holmgren *et al.* 2006; Squeo *et al.* 2007). Despite the low frequency of these events, they create the conditions for the appearance of novel genetic combinations and for the spread of beneficial mutations; in brief, they bring about the variability necessary to cope with the ever-changing conditions of most earth regions.

Seed–seedling conflicts in the dominant species?

Encelia canescens has a tendency to have better emergence in the open, but its seedlings prefer undercanopy spaces. Thus, *E. canescens* would exhibit a totally discordant habitat suitability pattern and a seed–seedling conflict (Schupp 1995). *F. thurifera* shows a partially discordant pattern: albeit they are able to germinate in open ground, survival is favoured in shady habitats, unless there are abundant rains (significant effect of precipitation X microhabitat). *P. revolutus* shows a concordant pattern, with higher emergence and survival (second

experiment) under shade. This suggests that species less tolerant to drought do well only in one type of microhabitat. Schupp (1995) showed that this fully concordant pattern of patch suitability entails greater overall survival of seedlings. However, this depends on the maintenance in time of the best patches for germination and establishment. In deserts, this may happen rarely, as drought years are the norm, and this may imply great shrub mortality (Miriti *et al.* 2007). Species like *P. revolutus*, then, should prefer habitats with more constant characteristics. In fact, *P. revolutus* grows usually near wadis (seasonal water courses). Seedlings of species with discordant patterns have lower survival, but, unlike seedlings with concordant patterns, some of their seedlings may establish even in the driest microhabitats. This implies that these species may be able to respond positively even in the driest years. These species (in our case *E. canescens* and *F. thurifera*) are found in a more diverse array of habitats.

Our study has evaluated emergence of three important species in the coastal desert but has only monitored the first weeks of seedling survival. It might be argued that it is a very short time to make inferences about establishment, but we think that this early period is possibly the most critical for seedling establishment. It is true that if no more rains fall during the season, seedlings of a few weeks old may not survive, but if the region receives further rains, those plants that made it through the first weeks of existence have a good chance to be established. Thus, we think that our study reflects plant responses in a very important part of plant development. Moreover, despite this short time of observations, our results have shown important species differences in terms of emergence and early survival but have also shown some common responses, such as a response to small amounts of rain and to increasing precipitation. They also revealed the differences that exist between open and undercanopy microhabitats, but also that different levels in shading may have consequences for plant performance. Shade seems irrelevant for emergence (it even may be damaging for *E. canescens*) but may be crucial for survival in bad years. Our results show that survival may be favoured beneath shrub canopies in low precipitation years, and this has implications for community restoration or revegetation, as has been shown in other Mediterranean regions (e.g. Gómez-Aparicio *et al.* 2004). Although this study addressed still unknown aspects of the ecology of coastal desert species, we still need to evaluate the response of other dominant species belonging to other families. Consideration of species from the driest parts of the Atacama Desert would be especially interesting, as would be the long-term response (e.g. through what is considered the first bottleneck, which in these ecosystems is summer) and the response to other levels of shade, water or soil.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web site:

Appendix Table S1. ANOVA results for experiment 1.
Appendix Table S2. ANOVA results for experiment 2.
Appendix Table S3. Mean percentage emergence and survival of each species in each treatment in each experiment.