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Growth and early seedling survival of four Atacama Desert shrub species under experimental light and water availability regimes

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Abstract

Background: In arid environments, where light and water supply are patchy in space and time, differences in how seedlings tolerate drought and shade conditions will determine the ability of a species to establish. Understanding seedling responses to the interactive effects of water and shade is critical to predict the future impact of increasing drought frequencies on plant communities across many arid ecosystems of the world. In this study, we used an experimental field approach to assess how different light (15%, 75%, and 95%) and water (natural rainfall (NR), NR +50 mm, NR +100 mm) levels affect seedling survival and growth of four Atacama Desert shrub species (*Calliandra chilensis*, *Encelia canescens*, *Proustia cuneifolia*, and *Senna cumingii*). We predicted that under drought conditions, maximum seedling survival and growth would occur at intermediate levels of shade.

Results: Shade and water had independent effects on seedling survival of all species. In contrast, the interaction between shade and water only affected seedling survival of *E. canescens*. Seedling survival of the four species tended to be higher in environments with intermediate shade and 100 mm of added water than in high or low shade environments with either 50 mm or no additional water. Relative growth rates (RGR) of all species, except *E. canescens*, were only positive at intermediate or high shade levels with 50 or 100 mm of added water.

Conclusions: Our results not only highlight the importance of water for plant recruitment in arid ecosystems but also stress the positive role of shade as a factor influencing seedling establishment.

Keywords: Seedling establishment; Facilitation; Drought; Atacama Desert

Background

Seedling establishment is recognized as one of the most vulnerable phases in the life cycle of plants (Harper 1977). This is particularly true in arid environments, where early establishment is highly dependent on water, which is not only scarce but also extremely variable at both temporal and spatial scales (Noy-Meir 1973; Schwinning and Sala 2004). Moreover, low water availability typically occurs in conjunction with high temperatures and irradiance (Ehleringer and Cooper 1992), which ultimately lead to soil desiccation, thus increasing the effects of aridity (Valladares and Pearcy 1997). As a

result, seedling establishment in arid environments is often facilitated near adults of some plant species that can act as nurse plants by ameliorating the stressful environmental conditions (Holmgren et al. 1997; Maestre et al. 2003a).

A nurse plant's canopy can change environmental conditions in various ways (Holmgren et al. 2012). For example, the canopy reduces the amount of soil surface area exposed to direct sunlight and hot air, which results in a reduction of 1) the total amount of photosynthetically active radiation available and 2) air and soil temperatures beneath the canopy (e.g., Belsky et al. 1989; Franco and Nobel 1989; Callaway 1995). Lower temperatures lead to less evapotranspiration (Holmgren et al. 2012), which ultimately results in greater availability of soil water underneath nurse plant canopies than in surrounding open areas. Thus, in arid environments, spaces beneath shrubs

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usually constitute safe sites (*sensu* Harper 1977) for germination and/or establishment.

The provision of a more mesic environment mediated by shade is one of the most important effects of the presence of a nurse species (Callaway 1995). However, different shrub species differ in the shade intensities they provide (e.g., Pugnaire et al. 2004); hence, the quality of safe sites is contingent on shrub species, ontogeny, and size, among other factors. Nonetheless, it is expected that in arid environments shrubs that provide intermediate shade intensities should provide the best conditions for seedling growth and survival (Holmgren et al. 1997) because they ameliorate environmental conditions, while still allowing sufficient light arrival to allow carbon assimilation by the beneficiary.

The Atacama Desert is considered one of the most arid places on Earth. This region experiences recurrent long periods of strong drought from September to June, which overlaps with summer (December to March), when temperature and radiation are at their maxima. Plant recruitment in this desert is rare, strongly limited by microhabitat availability (Martinez-Tillería et al. 2012), and often requires a series of favorable climatic events (Holmgren et al. 2006). In this context, it becomes particularly important to gain an understanding of species' environmental tolerances at the time of establishment, as this phase can drive community dynamics (Grubb 1977). Early recruitment phases constitute a bottleneck for plant populations; consequently, understanding how the environmental conditions associated to the microhabitats created by nurse plants promote plant recruitment is of fundamental importance in terms of species persistence in the communities. Given the extreme aridity of Atacama, we could expect that safe sites provided by shrubs should be especially important for seedling germination and early survival. However, the degree to which the environmental conditions in these habitats benefit the recruits is likely species specific and depends on the drought and shade tolerances of the beneficiaries.

The few studies examining seedling establishment in the Atacama Desert (Holmgren et al. 2006; Squeo et al. 2007; Gutierrez et al. 2007; León et al. 2011) reveal that recruitment is predominantly limited to years with high rainfall (i.e., ENSO years). This suggests that water may be more critical for recruitment than shade. However, unraveling the interactive effects of shade and drought is a key to understanding regeneration dynamics in arid environments and to assess the potential responses of plant communities in the Atacama Desert to expected global change scenarios. Therefore, a better understanding of the interactive effects of water availability and irradiance on survival and growth of seedlings is critical to predict future impact of climate change of plant communities in this region.

In this study, we used an experimental field approach to assess how light and water affect seedling survival and growth of four native coastal desert shrub species from the southern edge of the Atacama Desert. These shrubs not only are common species in this system but also differ in important aspects of their life histories; therefore, they provide an opportunity to examine how safe site requirements vary among species during their early developmental stages. We predicted that under drought conditions, maximum seedling survival and growth would occur at intermediate levels of shade, which would provide a more mesic microenvironment for plants but allow sufficient light penetration for carbon assimilation.

Methods
Study site
The study was conducted from December 2007 to December 2008 at El Romeral basin, located 21 km north of La Serena, in Coquimbo, Chile (29°43′ S to 71°14′ W, 300 m a.s.l.). Mean annual precipitation in the study area for the last 30 years is 78 mm, whereas mean annual temperature is 14.5°C (Squeo et al. 1999; Squeo et al. 2006). During 2008, mean annual temperature was 14.8°C and the cumulative rainfall was 86.1 mm (CEAZA-Met, Romeral Meteorological station).

The soil at El Romeral is of alluvial origin and has a sandy texture mixed with stones and gravel (Squeo et al. 2006). The dominant plant community corresponds to a coastal shrub steppe, consisting of hard-leaved low shrubs (Gajardo 1994) with a plant cover of around 25%. The dominant plant species are *Pleocarphus revolutus* and *Flourencia thurifera* with average photosynthetically active radiation (PAR) levels beneath their canopies of 208 and 196 µmol m^{-2} s^{-1}, respectively. In open sites, PAR levels reach on average 1,947 µmol m^{-2} s^{-1}, which is an order of magnitude higher than beneath shrubs.

Study species
We selected four native shrubs common in the study area for which we have information on their root systems (Squeo et al. 1999; Olivares 2003) and leaf characteristics (Olivares 2003; León et al. 2011). Briefly, *Calliandra chilensis* is a small deciduous shrub (approximately 50 cm tall) with a superficial root system; *Encelia canescens* is a small evergreen or deciduous shrub (80 cm tall) with a superficial root system; *Senna cumingii* is a deciduous shrub (approximately 1.5 m tall) with a dimorphic root system; and *Proustia cuneifolia* is a deciduous shrub (approximately 1.5 to 2 m tall) with a deep root system. All of these species have an open canopy, except for *C. chilensis* which has a compact canopy. All four species are propagated by seed (Pacheco 2000).

Experimental design

We assessed seedling survival in a field experiment set up in a complete randomized block design. Before starting the experiments, all experimental blocks were surrounded with a wire fence to protect seedlings from trampling and vertebrate herbivores. Additionally, a neutral shade cloth (which provided approximately 15% of shade) was placed above the whole experimental site to protect seedlings from birds.

The experiment consisted of five blocks, which is the experimental unit. Each block contains nine experimental plots randomly placed within the block. Individual plots were approximately 2 by 2 m, and each had a unique combination of one of three shades (low, intermediate, and high shades) and three water (natural rainfall (NR) [86.1 mm], natural rainfall plus 50 mm [total water 136.1 mm], and natural rainfall plus 100 mm irrigation [total water 186.1 mm]) treatment levels. The shade levels were obtained by covering individual plots with a shade cloth 1 m above the ground surface. The shade levels for each treatment were 15% in plots without shade (low shade treatment; here, shade was provided only by the shade cloth covering the experimental site), 75% in plots at intermediate shade, and 95% in plots at deep shade. Ambient light levels obtained at midday for each treatment level were approximately 1,100, 180, and 100 μmol m^{-2} s^{-1} for the low, intermediate, and high shade treatment levels, respectively, which quite closely mimic PAR levels in natural conditions. Irrigation was applied using sprinklers of 1-m diameter in four events of 12.5 and 25 mm for the treatments with 50 and 100 mm, respectively. Plants were watered once a week from the first to the fourth week after initial planting. During the experiment, no soil fertilization was applied.

In the beginning of December 2007, we transplanted 20 seedlings from each of the four selected species into each plot. Before transplanting, these seedlings were kept in petri dishes for 2 weeks after emergence in a growth chamber (Binder, model KBWF 240; BINDER, Tuttlingen, Germany) with a 12-h photoperiod, with a stable temperature of 20°C, and with 60% of relative humidity. One week before plants were transplanted to the field, we manually removed all weeds present in the experimental setting. Because experiments were initiated during the drought period, 1 day prior to transplanting, we applied 15 mm of water to emulate conditions that would typically follow emergence in these species (Pacheco 2000, Martínez-Tillería 2012). Moreover, 2 weeks after seedlings were transplanted, we applied 35 mm of irrigation to all plots to ensure seedling establishment prior to the start of the experimental treatments. No seedling mortality was registered during the 2 weeks before seedling survival was estimated.

Estimation of seedling survival and growth

To estimate seedling survival, we counted the number of living seedlings every week for the first 8 weeks and every 2 weeks thereafter until the end of the experiment (week 53). To examine seedling growth, we randomly selected five plants of each species for each treatment combination and counted the number of leaves on each plant. The leaf number was recorded on the same days that seedlings were censused. We chose the number of leaves instead of the plant height as a measure of growth, because stem elongation of plants in shade can confound results (Salgado-Luarte and Gianoli 2011). Relative growth rate (RGR) was calculated as: RGR = (ln H_2-ln H_1)/(t_2-t_1), where H_2 is the final number of leaves at time (t_2) and H_1 is initial number of leaves at time (t_1). The initial number of leaves was recorded the first week after transplanting, whereas final leaf number was recorded on week 53.

Statistical analyses

We examined the effects of shade and drought on seedling survival in two different ways. First, we used generalized linear models (GLMs; Crawley 2007) to examine if shade and drought interacted to determine seedling survival at the end of the experiment. For this analysis, we used a Poisson error distribution and considered

Table 1 Results of the two-way GLM testing on total seedling survival for each species

Species	Parameter	d.f.	χ^2	P
C. chilensis				
	Block	4	0.0	1.000
	Shade	2	1.42^{-7}	1.000
	Water	2	235.33	<0.0001*
	Shade × water	4	5.59	0.23
E. canescens				
	Block	4	5.95	0.2065
	Shade	2	34.5	<0.009*
	Water	2	26.5	<0.009*
	Shade × water	4	11.6	0.021*
P. cuneifolia				
	Block	4	0.15	0.70
	Shade	2	1.01^{-7}	1.00
	Water	2	103.8	<0.0001*
	Shade x water	4	7.4	0.12
S. cumingii				
	Block	4	2.32	0.13
	Shade	2	6.99	0.03*
	Water	2	13.05	0.0001*
	Shade × water	4	5.54	0.24

*indicates significant differences among treatments.

water, shade, and block as the main factors and the number of seedlings alive by week 53 as the response variable. Second, to examine if the temporal pattern of seedling mortality differed among treatments, we performed a Cox's proportional hazards model for each species separately (clustered by block). This analysis describes how the hazard or risk of seedling mortality changes over time in response to explanatory covariates (i.e., shade or water levels) (Fox 2001; Lagakos 2009). For this purpose, we used the following model:

$$h(t) = [h_0(t)] \, e^{(\beta_1 X_1 + \beta_2 X_2)}$$

Here, $h(t)$ represents the hazard function at time t, $h_0(t)$ is the baseline hazard (i.e., the risk of seedling mortality under user-specified control conditions), and β is the estimated change in the log-relative hazard for a unit change in water (X_1) and shade (X_2). For this analysis, we specified the treatments of natural rainfall and low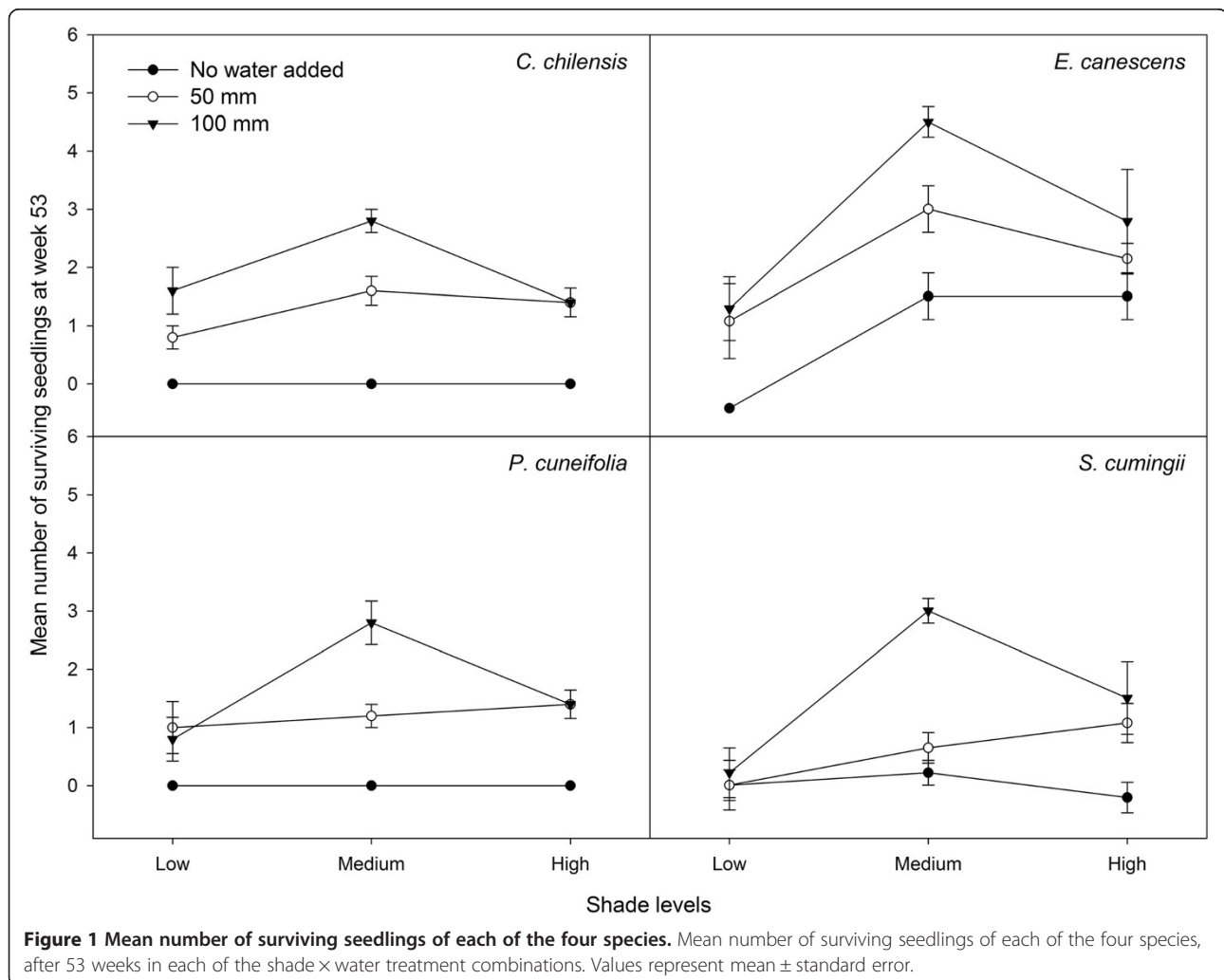 shade as the baseline conditions for comparison because these represent more closely environmental conditions of the study site.

To examine how water and shade affect the RGR of each species, we conducted a GLM, with water and shade as the main factors and RGR as the response variable. Statistical analyses were performed using the R statistical environment (R Development Core Team 2009) and JMP 8.0.2 (SAS Institute Inc.).

Results

Seedling survival

Shade affected seedling survival of *E. canescens* and *S. cumingii* (Table 1, Figure 1); specifically, survival was higher at intermediate shade than at either low or high shade levels. Increasing water irrigation had a significant positive effect on the number of surviving seedlings of all species (Table 1, Figure 1). The interaction between shade and water only affected seedling survival of *E. canescens* (Table 1). Overall, however, the number of surviving seedlings of all species tended to be higher in

Figure 1 Mean number of surviving seedlings of each of the four species. Mean number of surviving seedlings of each of the four species, after 53 weeks in each of the shade × water treatment combinations. Values represent mean ± standard error.
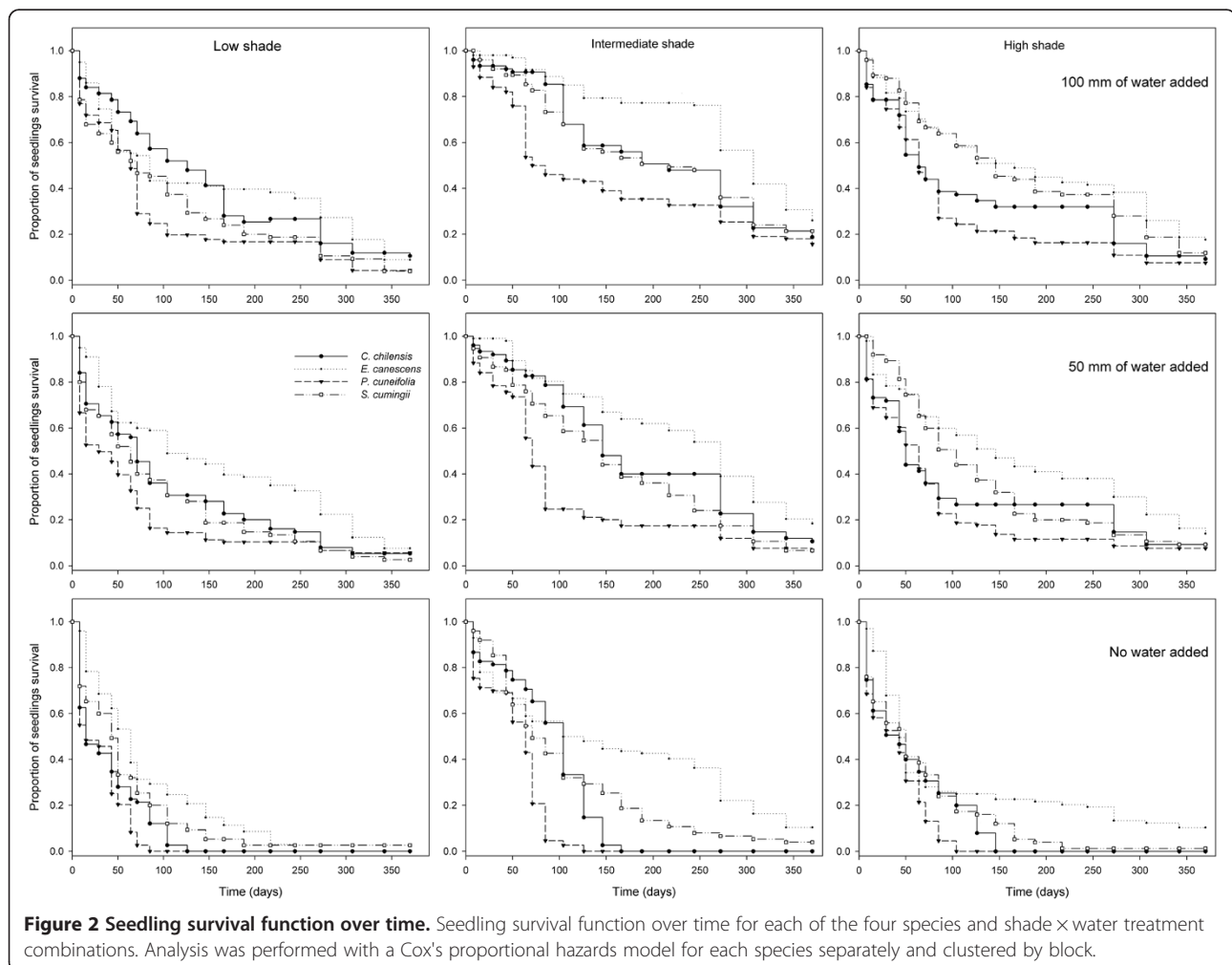
environments with intermediate shade and 100 mm of added water, than in high or low shade environments with either 50 mm or no water added (Figure 1).

The temporal pattern of seedling survival of all species differed significantly in response to shade treatments. Specifically, the risk of seedling mortality was decreased by 30%, 42%, 19%, and 32% for *C. chilensis* (Wald test = 28,537,544, d.f. = 4, *P* < 0.009), *E. canescens* (Wald test = 957.2, d.f. = 4, *P* < 0.009), *P. cuneifolia* (Wald test = 2,961, d.f. = 4, *P* < 0.009), and *S. cumingii* (Wald test = 147.6, d.f. = 4, *P* < 0.009), respectively, in plots with intermediate shade compared to plots with low shade (1-βexp, Additional file 1: Table S1). In high shade plots, only *P. cuneifolia* and *S. cumingii* showed a significant reduction in the risk of seedling mortality (7% and 17%, respectively) (Additional file 1: Table S1). Similarly, for all four species, both water addition treatments led to higher seedling survival than the treatment with only natural rainfall (i.e., no added water). Specifically, survival rate of *C. chilensis*, *E. canescens*, *P. cuneifolia*, and *S. cumingii*

was 39%, 38%, 29%, and 34% higher in plots with 100 mm of added water and 28%, 33%, 18%, and 22% higher in plots with 50 mm of added water than in plots with only natural rainfall (Additional file 1: Table S1).

We found interspecific differences in seedling survival among the treatment combinations. *E. canescens* had the highest survivorship and was the most tolerant species to both drought and shade; conversely, *P. cuneifolia* had the least tolerance to drought and shade as evidenced by having the lowest survival in treatments with either high shade or no added water (Figure 2). Seedling survival of *C. chilensis* and *S. cumingii* was similar across all treatment combinations, except for the combination of low shade and 100 mm of added water where *C. chilensis* had higher survival rates than *S. cumingii* (Figure 2). In all species, the combination of low shade and natural rainfall (i.e., no water added) had the greatest negative impact on survival. In contrast, survival rates were highest in plots with intermediate shade and 100 mm of added water (Figure 2). Finally, as evidenced by the

Figure 2 Seedling survival function over time. Seedling survival function over time for each of the four species and shade × water treatment combinations. Analysis was performed with a Cox's proportional hazards model for each species separately and clustered by block.

speed of mortality, the impact of drought on seedling survival was generally highest at low shade levels and lowest at intermediate shade (Figure 2).

Relative growth rate

Water and shade had independent effects on the RGR of seedlings of all species, whereas their interaction affected all, except for *P. cuneifolia* (Table 2). RGRs were consistently negative for seedlings in low shade treatments, irrespective of the amount of water added (Figure 3). Overall, positive RGRs were attained only at intermediate or high shade levels with either 50 or 100 mm of water added for all species but *E. canescens* (Figure 3). Moreover, drought (i.e., no water added) reduced RGR similarly across light treatments (Figure 3). Because our RGR estimator was the leaf number, these results reveal that plants tend to shed their leaves in low shade levels and in treatments with no water added (Figure 3).

Discussion

In this study, we have shown that seedling survival of common species in the Chilean coastal desert increased

Table 2 Results of the two-way GLM testing on total RGR for each species

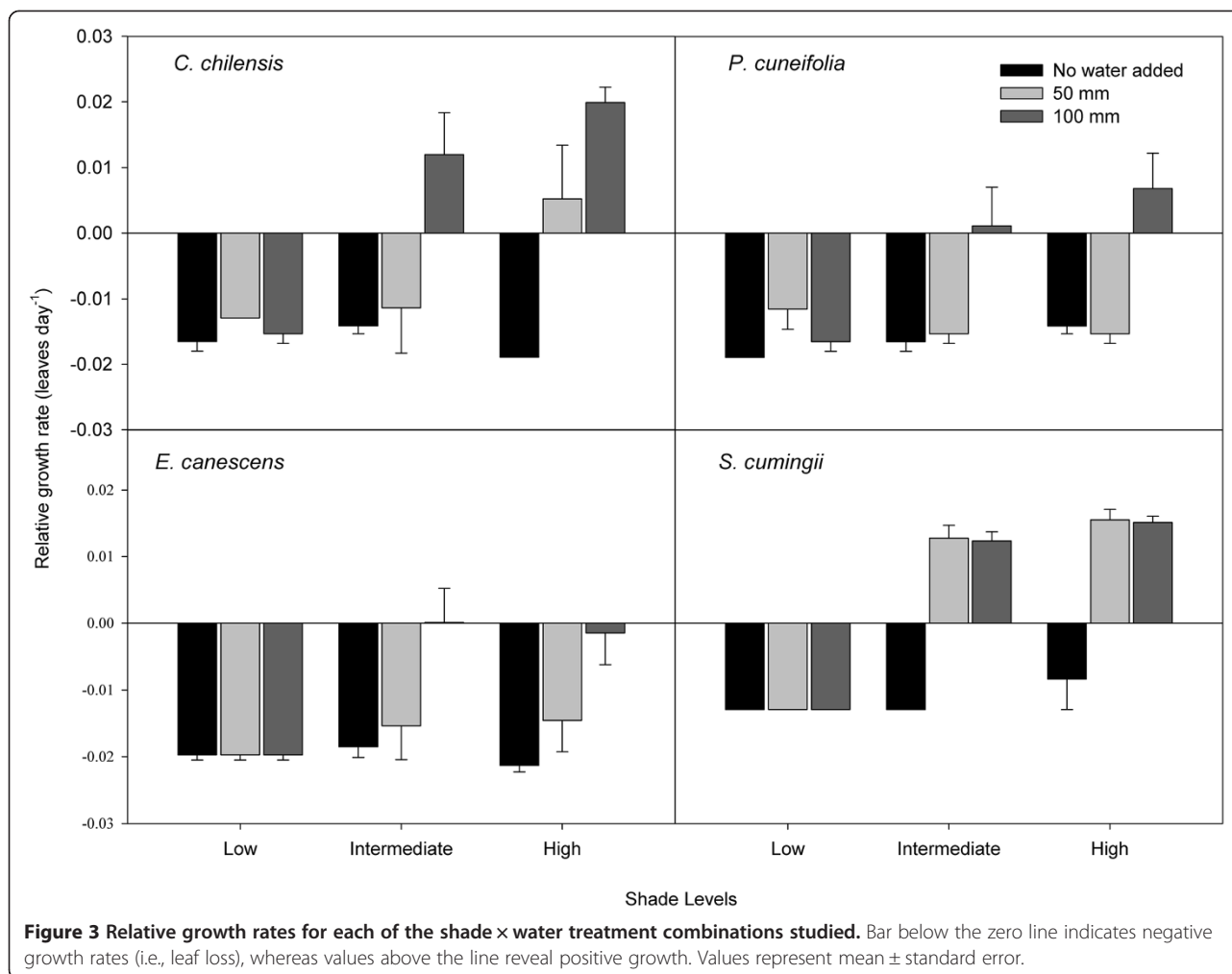| Species	Parameter	d.f.	Estimated	T value	P
C. chilensis					
	Intercept	40	0.07	5.86	<0.009*
	Shade	2	−0.03	−5.27	<0.009*
	Water	2	−0.03	−5.99	<0.009*
	Block	4	0.00	1.24	0.223
	Shade × water	4	0.01	4.06	<0.009*
E. canescens					
	Intercept	40	0.021	2.65	0.012*
	Shade	2	−0.02	−3.68	<0.009*
	Water	2	−0.02	−4.17	<0.009*
	Block	4	0.00	1.74	0.089
	Shade × water	4	0.01	2.78	<0.009*
P. cuneifolia					
	Intercept	40	0.02	2.49	0.017*
	Shade	2	−0.01	−2.59	0.014*
	Water	2	−0.01	−3.23	<0.009*
	Block	4	0.00	0.58	0.565
	Shade × water	4	0.00	1.72	0.094
S. cumingii					
	Intercept	40	0.05	6.35	<0.009*
	Shade	2	−0.02	−5.06	<0.009*
	Water	2	−0.00	−4.52	<0.009*
	Block	4	−0.00	−0.27	0.786
	Shade × water	4	0.01	2.87	<0.009*

*incates significant differences among treatments.

both with higher water supply and with intermediate shade. These results not only highlight the importance of water for plant recruitment in desert ecosystems but also point to shade as a factor that enhances seedling recruitment. Additionally, except for *E. canescens*, we found no evidence of an interactive effect between shade and water. Responses of RGRs to water and shade showed that lower RGRs were generally associated to low shade environments and that drought has a similar impact across shade treatments. It is interesting to note that the different shrub species showed similar patterns, suggesting similar constraints on establishment (Figures 1 and 2).

Seedling survival

Seedling survival of all the species examined was highest at intermediate shade levels compared to low or high shade. Similar results were found by Martínez-Tillería et al. (2012) for six Coastal Atacama Desert shrubs. These positive effects of intermediate shade on seedling survival suggest first that, compared with low shade, artificial shelters could promote stress amelioration of the environmental conditions by reducing PAR levels (83% reduction compared with low shade). As a consequence of this reduction, water availability in the topsoil layers is increased and water stress is reduced (Maestre et al. 2003a), which reduces transpirational demands (Holmgren 2000) and ultimately results in an increase in seedling establishment (Schöb et al. 2013; McIntire and Fajardo 2014). In addition, shade can reduce tissue desiccation and photo-oxidative stress, both of which negatively impact seedling survival (Valladares and Pearcy 1997; Sack 2004). Second, higher survival in intermediate shade levels suggests that in deep shade conditions seedlings may not be able to maintain a positive carbon balance (i.e., the balance between carbon uptake in photosynthesis minus carbon lost by respiration) (Aranda et al. 2007). For example, Walters and Reich (2000) found that *Populus tremuloides* had a high CO_2 loss and low CO_2 gain at low PAR levels. Similarly, Baltzer and Thomas (2007) showed that carbon gain is constrained in low light environments and that plants have high CO_2 loss, which ultimately affects plant survival.

As expected, the addition of supplemental water enhanced seedling survival of all species. These results are consistent with other studies examining shrub seedling establishment in arid and semiarid ecosystems (Maestre et al. 2003a; León et al. 2011; Martínez-Tillería et al. 2012). For example, León et al. (2011) showed that seedling establishment in the Atacama Desert was possible only when rainfall levels were above 206 mm, which is similar to an El Niño event (Montecinos and Aceituno 2003). Similarly, Martínez-Tillería et al. (2012) found that the addition of water enhanced seedling survival of native Atacama shrubs. In summary, because seedlings

Figure 3 Relative growth rates for each of the shade × water treatment combinations studied. Bar below the zero line indicates negative growth rates (i.e., leaf loss), whereas values above the line reveal positive growth. Values represent mean ± standard error.

are very sensitive to dehydration (Evans and Etherington 1991), an additional water input can have a large impact on the regeneration dynamics of Atacama Desert shrubs, which corroborates the relevance of El Niño years for plant regeneration in this region.

Interactive effects between shade and water on seedling survival were only observed for *E. canescens*; specifically, the number of surviving seedlings was higher in environments with intermediate shade and high water than in high or low shade environments with either intermediate or low water addition. This result is in agreement with Holmgren et al.'s (2012) findings, who, in a meta-analysis of 65 published studies, found that along an irradiance gradient the positive effects of shade on plant performance are more likely at intermediate light levels than in high or low shade because the effect of drought is countered at intermediate irradiance. However, the absence of interactive effects of water and shade for *C. chilensis, P. cuneifolia*, and *S. cumingii* would imply that shade may not compensate for the stress produced by drought for these species, something that was found for other

species of the Coastal Atacama Desert (R.P. López, *personal observation*), thus suggesting that these species are more dependent on rain for seedling establishment. Finally, the positive effects of shade under dry conditions as well as with increased irrigation were even more evident when considering the trajectory of the survival curve with the Cox's proportional hazards model, which showed a positive effect in all four species. Our results are in agreement with those of other studies that show that a facilitative effect of shade under dry conditions is a key driver for seedling establishment not only in Mediterranean (Maestre et al. 2003b, Sánchez-Gómez et al. 2006) and desert ecosystems (Martínez-Tillería et al. 2012) but also in a wet tropical environment (Holmgren et al. 2012).

Seedling growth

Our results showed that RGRs were negative (i.e., plants shed their leaves and/or produced fewer leaves) in low shade treatments (irrespective of the water treatments) and that higher RGRs were reached at intermediate and

high shade levels with either 50 or 100 mm of added water for all species but *E. canescens*. It is interesting to note that shade did not compensate the negative effects of drought (no water added) on leaf number, especially in *E. canescens*, but it did so at moderate drought levels (50 mm of added water) for *C. chilensis* and *S. cumingii*, again showing the importance of shaded microhabitats beneath shrubs. As described above, the effect of shade on RGR is probably due to an increase in water availability at the top soil layers (Maestre et al. 2003a). Thus, plants grow faster than in low shade because there is no need to allocate a large amount of biomass to roots. Conversely, plants subjected to drier conditions need to allocate relatively more biomass to roots than to aboveground structures (Smith and Huston 1989), which increases a plant's ability to acquire water (Heschel et al. 2004) and ultimately its survival (Lloret et al. 1999). On the other hand, because we used the number of leaves to estimate RGR, low RGR in plants in high light may be a mechanism to avoid damage to the photosynthetic apparatus (Powles 1984). For example, Valladares and Pearcy (1997) found that plants exposed to full sunlight showed chronic photoinhibition, even in well-watered conditions. Chronic photoinhibition leading to leaf abscission was also observed in semi-deciduous shrubs of the genus *Cistus* in drought conditions (Werner et al. 1999).

Conclusions

In conclusion, our results illustrate how abiotic conditions, especially those related to water economy, can constrain seedling establishment. Moreover, we show that environmental conditions provided by nurse plants can promote seedling survival and growth and are consistent with the idea that under-canopy microhabitats may be safe sites for woody species of the coastal desert. In fact, the early phases in the life cycle of desert shrubs constitute a true bottleneck, and any improvement in the microenvironment conditions can be considered as important in terms of survival of the seedling. In our study, shade did not compensate the stress produced by drought for *C. chilensis*, *P. cuneifolia*, and *S. cumingii*, suggesting that these species would be more vulnerable to changes in the amount of rainfall predicted by climate change scenarios. Finally, our results highlight the importance of a better understanding of the interactive effects of water availability and irradiance on survival and growth of seedlings to predict future impact of climate change in plant communities of the Atacama Desert.

Additional file

Additional file 1: Table S1. Cox proportional hazards regressions of seedling survival clustered by block. Because the dependent variable in the model is the risk of seedling mortality, negative coefficients (β)

indicate that a factor has a positive effect on seedling survival (and vice-versa) when compared against the hazard in plots that have no water added and high light levels.

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