No evidence of a trade-off between drought and shade tolerance in seedlings of six coastal desert shrub species in north-central Chile

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Abstract

Question: Is there evidence of a trade-off between drought and shade tolerance in coastal desert shrubs?

Location: Arid scrubland, Atacama desert, north-central Chile.

Methods: One-week-old seedlings of six coastal desert shrub species (*Centaurea chilensis*, *Encelia canescens*, *Flourensia thurifera*, *Pleocarphus revolutus*, *Senna cumingii* and *Haplopappus parvifolius*) were planted in the field under six treatment combinations: three light environments (low, intermediate and high radiation) and two water levels (natural rainfall (55.4 mm) and natural rainfall plus 100 mm irrigation). We quantified seedling survival for each species during 22 weeks, estimated relative growth rate, and examined how light and water affect whole-plant responses, particularly specific leaf area, leaf mass ratio and root–shoot ratio.

Results: We found species-specific differences in the temporal pattern of mortality. Water and/or light levels affected seedling survival of all species, excluding *C. chilensis*. Relative growth rate (RGR) increased in low-light conditions in *C. chilensis* and *P. revolutus*, but otherwise did not vary in response to differences in either light or water, independently or to their interaction. Across species, the effect of water on specific leaf area (SLA) was inconsistent, increasing both in drought conditions (*C. chilensis*) and in treatments with supplemental water (*S. cumingii*). Additionally, SLA tended to increase with decreasing light levels for most species (*F. thurifera*, *H. parvifolius*, *C. chilensis*). In our study, only *F. thrurifera* and *C. chilensis* showed changes in leaf mass ratio (LMR) and only with respect to light levels; specifically, LMR tended to increase with decreasing light level. Biomass allocation was independent of light and water for all species except *F. thurifera*, which showed an increase in root biomass in drought conditions.

Conclusions: Overall, we did not find evidence to support a trade-off between drought and shade tolerance during early plant establishment. Our results suggest that water is the most important resource that limits recruitment in the coastal desert. Therefore, increased aridity in this system is likely to severely hinder seedling recruitment of the native coastal desert shrubs.

Introduction

Species-specific differences in seedling and juvenile performance along environmental gradients have been considered key factors in determining plant community structure and dynamics (Grubb 1977; Silvertown 2004; Sánchez-Gómez et al. 2006). These differences result from performance trade-offs, which can ultimately determine the range within a resource gradient that can be occupied by a plant (Sack 2004; Baraloto et al. 2005; Seiwa 2007).

Consequently, differential tolerance to environmental stress among plants may be an important component that underlies geographic patterns of vegetation – a critical concept for understanding the structure and dynamics of terrestrial ecosystems (Chapin et al. 2002; Squeo et al. 2007).

In arid or semi-arid ecosystems, plant establishment, growth and survival are strongly limited by water availability, which is markedly unpredictable and highly variable both spatially and temporally (Noy-Meir 1973). When water is available, however, other resources, including light, may limit growth (Prider & Facelli 2004; Sánchez-Gómez et al. 2006). In arid or semi-arid environments the relative amounts of light and water available can be modified beneath plant canopies (Belsky et al. 1989; Callaway 1995; Tracol et al. 2011) where seedlings often establish. Typically, these microhabitats have more available water than the surrounding open areas, through (1) water redistribution from deeper to surface soil by the plants roots (i.e. hydraulic lift), (2) higher water infiltration rates, and (3) less evaporation (Flores & Jurado 2003; León et al. 2004; Muñoz et al. 2008; Prieto et al. 2010). In addition to higher water levels, the microenvironment beneath plant canopies is also characterized by having less available light through shading effects (Forseth et al. 2001; Hastwell & Facelli 2003). Generally, the shade provided by plant canopies reduces water stress, provided that competition for water does not nullify the benefits of decreasing the evaporative demand and radiative loads by shading (Callaway & Walker 1997; Callaway 1998; Maestre et al. 2003; Maestre & Cortina 2004; Valladares et al. 2008).

A key question for understanding plant community dynamics in arid environments is whether shade and drought have interactive effects on plant performance. Smith & Huston (1989) hypothesized that the response of plants to the joint effects of irradiance and water is characterized by a trade-off between drought and shade tolerance, so that species that can tolerate higher levels of shade are more vulnerable to drought than species that are more light-demanding. The trade-off hypothesis was based on physiological responses of plants to water and irradiance (photosynthetic active radiation, PAR hereafter). Specifically, Smith & Huston (1989) hypothesized that (1) dry conditions should drive plants to allocate relatively more biomass to roots than to above-ground structure, and (2) growth rate should decrease as tolerance to either low light or low water increases. An implicit assumption of this model, however, is that irradiance and water conditions can vary independently, while in natural conditions high irradiance is usually correlated with reduced water availability. Alternative hypotheses to explain potential interactions of shade and drought on plant performance consider the facilitative effects that plants can have in reducing drought though shading (Facilitation hypothesis; Holmgren 2000), and a hypothesis that, contrary to Smith & Huston (1989), predicts that drought should have a proportional impact across irradiance levels; in other words, shade and drought have independent impacts on growth and biomass allocation (Sack & Grubb 2002).

Although the interactive effects of shade and drought on seedling and juvenile growth and physiology have been reasonably well documented, these effects have rarely been explored for multiple species simultaneously (e.g. Zavala et al. 2000; Valladares & Pearcy 2002; Zavala & Zea 2004). Additionally, most studies have been conducted in semi-arid ecosystems (e.g. mediterranean ecosystems; Sánchez-Gómez et al. 2006; Rey Benayas et al. 2005; Valladares et al. 2005), while little information is available on how plants respond to the combination of light and water limitation in extremely dry environments, such as coastal desert ecosystems like the Atacama Desert.

In this study, we experimentally investigated the seedling responses of six common coastal desert plant species from north-central Chile across three irradiance levels and two water availability regimes. Our aim was to determine whether seedling responses conform to light and water trade-offs as predicted by Smith & Huston (1989). Specifically, we examined if: (1) there are interactive effects of water and light availability on seedling survival so that plants that have high seedling survival in drought conditions (i.e. drought tolerant) have low survival in low-light conditions, and vice versa; (2) growth rate decreases as tolerance to either low light or low water availability increases; (3) in low-light conditions plants show an increase in both specific leaf area and leaf mass ratio; and (4) there is higher allocation of biomass to roots vs above-ground structures when water is limiting.

To our knowledge, no other study has experimentally manipulated light and water levels in the field to evaluate the mechanisms underlying trade-offs in the use of light and water for multiple species of native Atacama Desert shrubs during early establishment. In this ecosystem, where rainfall is well below 100 mm per year, understanding the effects of shade and drought interactions is of pivotal importance for several reasons. First, it is key to predict potential responses of the native plant communities to the increased aridity that is predicted for the region (Christensen et al. 2007; Foden et al. 2007). Second, this knowledge will allow us to evaluate the potential role of nurse plant interactions in these ecosystems (Holmgren & Scheffer 2010). Finally, identifying seedling responses along resource gradients and their implied trade-offs is essential for the design of effective ecosystem restoration strategies in the face of the increasing desertification of the Atacama Desert.

Methods

Study area and species

We conducted this study at Quebrada El Romeral, located 21 km north of La Serena, Chile (29°43′ S, 71°14′ W; 300 m a.s.l.). The climate in the study area is characterized by a mean annual temperature of 14.5 °C, with a mean maximum temperature of 27.2 °C in the warmest month, and a mean minimum temperature of 3.5 °C in the coldest month. During the last 30 yr, annual rainfall at the study site has averaged 76.5 mm; rainy years are associated with ENSO events (Squeo et al. 2006). The wettest months are July and August, and the dry season typically lasts 10 mo. The average annual evaporation is 994 mm, reaching a monthly maximum in January (122 mm) and a monthly minimum in June (48 mm). Mean maximum PAR ranges between 1300 µmol m^{-2}·s^{-1} (June) and 2500 µmol m^{-2}·s^{-1} (December). During the study period specifically, the area received a total of 55.4 mm of rainfall. The maximum monthly temperature was 20.4 °C in October, and the minimum monthly temperature was 7.7 °C in July. The longest rainless period was 78 d, spanning from 27 July to 13 October.

For this study, we selected six endemic shrub species that are common in the study area, and for which we have information about the root systems (Squeo et al. 1999; Olivares 2003), water requirements for germination (Pacheco 2000), leaf habits (Olivares 2003; León et al. 2011) and species distributions (Table 1). All species can recruit either in open areas (i.e. high light environments) or under the canopy of other shrubs (i.e. medium or low light environments).

Control of water supply

Water supply in each treatment combination was controlled using soil water potentials. To measure water potentials, we installed Peltier-cooled soil phsychrometers (model PST-55; Wescor, Inc., South Logan, UT, USA) at 40-cm depth – the zone that potentially influences seedling roots. Measurements were made using a microvolt meter (Wescor, model HR-33T) every week for the first 10 wk, and then every 2 wk until the end of the experiment.

Seedling survival

Seedling survival was measured in a complete randomized block design in field conditions. Each of five blocks contained six experimental units (plot). Within each plot we randomly placed one of each treatment combination: three light environments (low, intermediate and high light) and two water levels (natural rainfall and natural rainfall plus 100 mm of supplemental water). Supplemental water was applied in four events of 25 mm each after 4, 9, 14 and 20 wk following the initial planting (see below). This watering schedule was established according to the expected natural rainfall in the area in order to assure shrub establishment. Light levels were achieved by placing neutral shade-cloth (black rashell net) 1 m above the ground surface in each plot. Ambient light levels obtained for each treatment were: 5.9 ± 0.5% (low light; ca. 100 µmol·m^{-2}·s^{-1}), 12.7 ± 0.5% (intermediate light; ca. 180 µmol·m^{-2}·s^{-1}) and 82 ± 0.1% (high light; ca. 1100 µmol·m^{-2}·s^{-1}). We chose these light treatments because they are representative of the light environments seedlings encounter in open desert areas (high light) and under plant canopies (intermediate and low light). All experimental plots were surrounded with a wire fence to protect seedlings from trampling or herbivory by goats or rabbits.

In late May 2006, we transplanted 20 seedlings of each of the six species (raised for 1 wk after germination in a growth chamber) into each of the plots. Within a plot, seedlings were separated by 30 cm, which minimized root overlap among individual seedlings. One day prior to transplanting, the field soils were pretreated with 15 mm of water to emulate conditions that would typically follow emergence in these species (Pacheco 2000). To estimate survivorship, we counted the number of seedlings alive every week for the first 10 wk, and every 2 wk thereafter until the end of the experiment (week 22).

Table 1. Information on the root system, leaf habits and distribution of the study species (data from Olivares & Squeo 1999 and Olivares 2003).

Species	Root system	Leaf habits	Distribution	Habitats according to water availability
Centaurea chilensis	Superficial	Deciduous	Endemic, central Chile	Arid areas (<100 mm) with 6–10 mo droughts
Encelia canescens	Superficial	Evergreen or deciduous	Endemic, north-central Chile	Arid areas (<100 mm) with 6–10 mo droughts
Flourensia thurifera	Dimorphic	Deciduous	Endemic, central Chile	Dry areas (400–800 mm) with 3–5 mo droughts
				Arid areas (<100 mm) with 6–10 mo droughts
Haplopappus parvifolius	Deep root	Evergreen	Endemic, north-central Chile	Arid areas (<100 mm) with 6–10 mo droughts
Pleocarphus revolutus	Dimorphic	Evergreen	Endemic, north-central Chile	Arid areas (<100 mm) with 6–10 mo droughts
Senna cumingii	Dimorphic	Evergreen or deciduous	Endemic, north-central Chile	Dry areas (400–800 mm) with 3–5 mo droughts
				Arid areas (<100 mm) with 6–10 mo droughts

Relative growth rate

The number of leaves per seedling was recorded on the same dates as the seedling survival censuses (see above). We calculated relative growth rate (RGR) as (ln (final leaf number) – ln (initial leaf number))/time (Salgado-Luarte & Gianoli 2011), where time was expressed as number of weeks since the initial measurement. Initial leaf number was recorded on the week when true leaves appeared on a seedling (i.e. in contrast to cotyledons), which occurred between the second and third week after seedlings were transplanted. Final leaf number was recorded as the number of leaves on the last week a plant was observed alive, or at the end of the experiment (i.e. week 22).

Morphological measurements

After *ca.* 5 mo of growth in their respective light and water treatments, a sample of seven to 12 seedlings for each light and water level combination was harvested. For each individual seedling, we determined total leaf and root area (cm^2) with a leaf area meter (CI-203, CID, Inc., Departamento de Biología, Universidad de La Serena, La Serena, Chile). Additionally, leaf, stem and roots were dried in an oven at 70 °C until reaching a stable weight (ca. 48 h), and dry mass was recorded for each fraction using an analytical balance. These measurements were used to calculate specific leaf area (SLA; leaf area/leaf weight) ($cm^2 \cdot g^{-1}$), leaf mass ratio (LMR; leaf weight/whole plant weight) ($g \cdot g^{-1}$) and root/shoot ratio (R/S; $g \cdot g^{-1}$).

Statistical analyses

We analysed the individual and interactive effects of water and light availability on seedling survival with a Cox's proportional hazards model for each species separately (clustered by block). Specifically, this analysis examines the relationship between the seedling survival distribution and water and light levels, and allows for censoring and non-normality that cause difficulty when analysing survival data with other statistical models (Lagakos 1992; Fox & S.M. Scheiner 2001). Here, the dependent variable is the hazard function, which describes how the hazard (e.g. risk of seedling mortality) changes over time, and the effect parameter describes how the hazard relates to different water and light levels and to the interaction between water and light. Specifically, we used the following model:

$$h(t) = [h_0(t)]e^{(\beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 * X_2)}$$

where, h (t) denotes the hazard function at time t, h_0 (t) corresponds to the baseline hazard, and β is the expected change in the log-relative hazard for a unit change in

water (X_1), light (X_2) and the interactive effects of water and light ($X_1 * X_2$). For these analyses, we choose the treatment with no supplemental water (i.e. natural rainfall conditions) and high light as the standard for comparisons (i.e. baseline hazard) because this combination resembles most the natural conditions to which seedlings at the study site are exposed during average years.

To compare treatment effects on the R/S ratio, we used a general linear model, with log-transformed values of the R/S ratio to meet normality requirements. To determine if SLA, LMR and RGR change with light and water we used generalized linear models. To examine if soil water potential changed with time we used a repeated measures analysis of variance (R-ANOVA). Statistical analyses were performed using the R statistical environment (R Development Core Team 2008; R Foundation for Statistical Computing, Vienna, AT), and Jump 8.0.2 (SAS Institute Inc., Cary, NC, US).

Results

Soil water treatments

The watering treatment resulted in significantly higher soil water potentials within each of the light treatments. Soil water potential (Ψ_{soil}) at 40-cm depth varied significantly among light ($F_{2,8} = 300.83$, $P < 0.001$) and water ($F_{1,8} = 149.18$, $P < 0.001$) treatment levels. In addition, Ψ_{soil} levels varied across time treatment (R-ANOVA $F_{15,120} = 34.66$, $P < 0.001$). Temporal Ψ_{soil} patterns, however, where not consistent across light (time x light interaction: $F_{30,120} = 14.56$, $P < 0.001$) or water (time x water: $F_{15,120} = 4.35$, $P < 0.001$) treatments and Ψ_{soil} levels were dependent on the treatment combination (light × water interaction: $F_{2,8} = 55.66$, $P < 0.001$). Moreover, Ψ_{soil} levels across treatment combinations differed temporally (time x light x water: $F_{30,120} = 4.47$, $P < 0.001$).

Mean Ψ_{soil} over the course of the experiment was -0.41 ± 0.10 MPa, but changed with each natural rain event and each irrigation application (Fig. 1). Mean Ψ_{soil} in treatments with irrigation was 0.3 MPa higher than that for treatments without supplemental water, whereas mean Ψ_{soil} under high radiation was 0.5 MPa lower than that of the low and intermediate light treatments.

Seedling survival

Overall, the temporal pattern of seedling survival showed a complex species-specific response in relation to either different water or light levels, or to the interaction of water and light. For example, the temporal risk of seedling mortality of *C. chilensis* did not differ with respect to the water or light treatments separately, or in relation to the interaction between water and light (Table 2). Conversely, the seedling
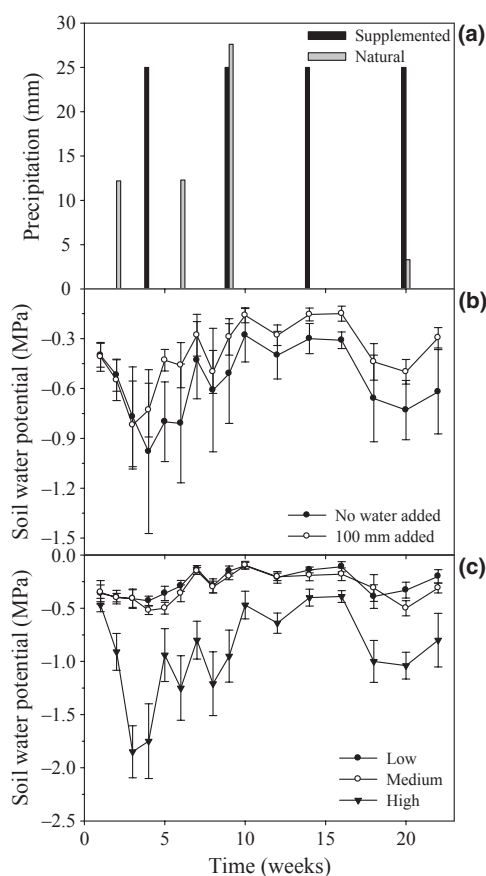
Fig. 1. Events after natural and supplemented precipitation (**a**) over the 22 wk of this study. Soil hydraulic potential (MPa) based on water treatment (**b**), and on radiation levels (**c**) over this same period (means ± SE).

survivorship curves of the other five species were significantly different, either among different water or light treatments or in response to different combinations of water and light. In the case of *E. canescens*, the hazard of seedling mortality was 63% higher (1-βexp; Table 2) in plots with low light compared to plots with high light (Fig. 2). Additionally, the hazard of seedling death was decreased by 73% (1-βexp) in plots with supplemental water (Table 2, Fig. 3). Similarly, for *P. revolutus* and *F. thurifera* the risk of seedling mortality was reduced by 56% and 32%, respectively, in plots with supplemental water (Table 2, Fig. 3). Compared to plots with high light, the hazard of seedling mortality of *S. cumingii* decreased by 60% in plots with medium light (Fig. 2). Moreover, for this species and for *F. thurifera*, the hazard of seedling death is increased by 147% and 83%, respectively, in plots with medium light and supplemental water (Table 2). Finally, compared to plots with high light, the chance of seedling death for *H. parvifolius* decreased by 51% in plots with medium light.

Relative growth rate

The RGRs of *E. canescens*, *H. parvifolius*, *F. thurifera* and *S. cumingii* were not affected by changes in light or water, either independently or by their interaction. In contrast, RGR of both *C. chilensis* and *P. revolutus* was higher in low light conditions (Table 3, Fig. 4).

Morphological measurements

We excluded *E. canescens* and *P. revolutus* from the morphological analyses because at the end of the experiment there
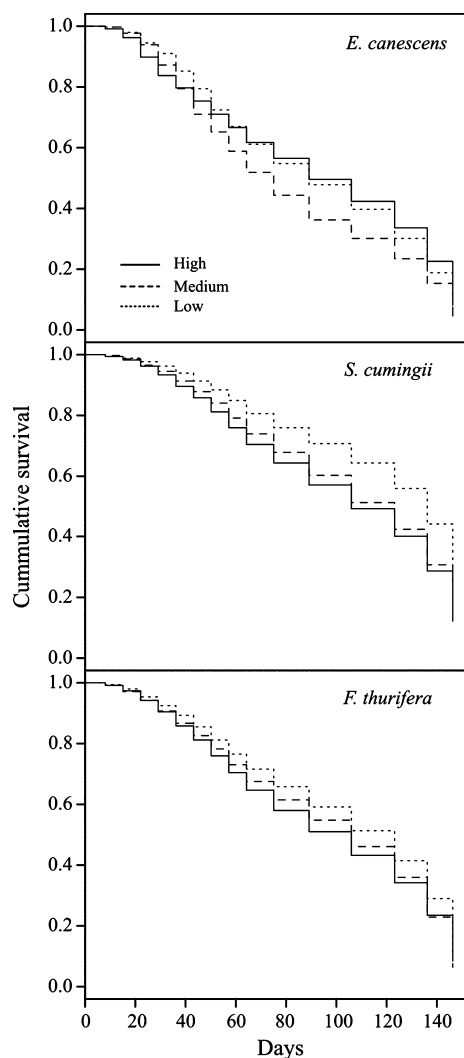
Table 2. Cox proportional hazards regressions of seedling survival clustered by block. Because the dependent variable in the model is a hazard rate, negative β coefficients indicate that a factor has a positive effect (1-βexp) upon seedling survival. In contrast, positive β coefficients mean a negative effect (βexp-1) on survival. Note that all treatments were compared against the risk of a seedling dying in plots that have natural rainfall and high light levels (baseline hazard condition, i.e. β = 0 and βexp = 1).

Factors		Species					
		Centaurea chilensis	*Encelia canescens*	*Pleocarphus revolutus*	*Senna cumingii*	*Haplopappus parvifolius*	*Flourensia thurifera*
Low light	β	0.20	0.49*	0.25	−0.12	0.20	−0.16
	βexp	1.22	1.63	1.28	0.88	1.22	0.85
Medium light	β	−0.71*	0.43	−0.43	−0.90*	−0.71*	−0.49
	βexp	0.49	0.65	0.65	0.40	0.49	0.61
100 mm water added	β	−0.15	−1.30*	−0.82*	−0.52	−0.15	−0.39*
	βexp	0.86	0.27	0.44	0.59	0.86	0.68
Low light*100 mm water added	β	−0.45	0.02	0.10	0.12	−0.45	0.31
	βexp	0.63	1.02	1.10	1.13	0.63	1.36
Medium light*100 mm water added	β	0.33	0.80	0.54	0.90*	0.33	0.60*
	βexp	1.39	2.22	1.72	2.47	1.39	1.83

*Significant at the 0.05 level.

Fig. 3. Estimated seedling survival functions of *E. canescens*, *P. revolutus*, *H. parvifolius* and *F. thurifera* for the Cox regression of time to seedling death for the two water treatments.

Table 3. Generalized linear model fits (*t*-values) of light and water effects on specific leaf area (SLA), leaf mass ratio (LMR), relative growth rate (RGR) and root:shoot (R/S) ratio of native coastal desert shrubs. Note that no morphological values were taken from *E. canescens* and *P. revolutus* because seedlings did not survive to the end of the experiment in some or all of the treatment combinations (see text).

	SLA	LMR	RGR	R/S
Encelia canescens				
Light	–	–	1.43	–
Water	–	–	1.66	–
Light*water	–	–	−1.38	–
Haplopappus parvifolius				
Light	28.00*	3.84	0.86	4.82
Water	3.21	0.92	0.62	2.67
Light*water	8.55*	0.68	−0.46	0.5
Flourensia thurifera				
Light	16.6	2.08	0.17	2.08
Water	0.04	9.33*	0.33	6.98*
Light*water	0.58	2.00	0.95	1.74
Senna cumingii				
Light	5.12	1.29	0.53	0.35
Water	10.23*	0.05	0.29	1.15
Light*water	3.25	0.35	−0.07	1.58
Centaurea chilensis				
Light	11.36*	2.94	2.82*	2.33
Water	6.80*	1.41	1.58	1.31
Light*water	0.22	6.45*	−1.17	4.09
Pleocarphus revolutus				
Light	–	–	2.32*	–
Water	–	–	1.57	–
Light*water	–	–	−1.55	–

*Significant at the 0.05 level.

Fig. 2. Estimated seedling survival functions of *E. canescens*, *S. cumingii* and *F. thurifera* for the Cox regression of time to seedling death for treatments with low, medium and high light.

were no surviving seedlings in some or all of the treatment combinations.

Specific leaf area

Light and water treatments affected the leaf area/leaf weight ratio (SLA) in all four species (Table 3). In *S. cumingii*, SLA increased in treatments with supplemental water, whereas in *F. thurifera* it increased in medium and low light conditions (Table 3). SLA of *H. parvifolius* responded negatively to light (i.e. it tended to decrease with increasing light levels) and to the interaction of light with water (Table 3). Finally, in *C. chilensis*, SLA was higher in treatments with no added water and in those with medium and low light (Table 3, Fig. 5).
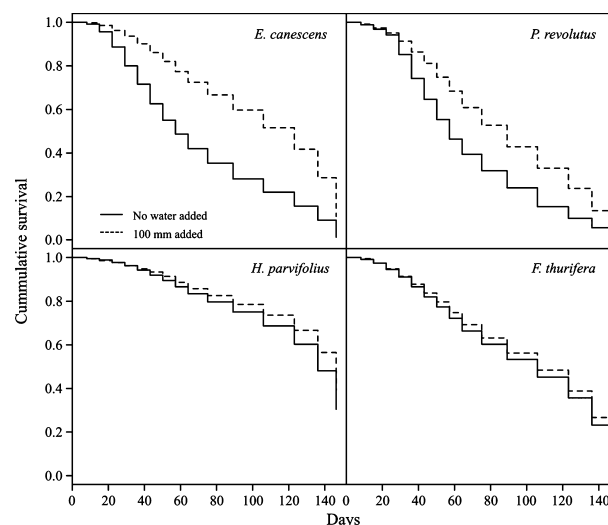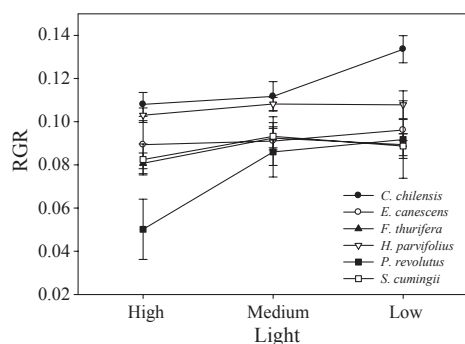
Fig. 4. Mean relative growth rates (RGR) of seedlings under high, medium and low light treatments. Error bars indicate 1 SE around the mean.

Fig. 6. Leaf mass ratio (LMR) of *F. thurifera* and *C. chilensis* plants grown under three light conditions (high, medium and low light) and two water treatments (natural rainfall only and natural rainfall plus 100 mm of supplemental water). Bars represent SE of the means.
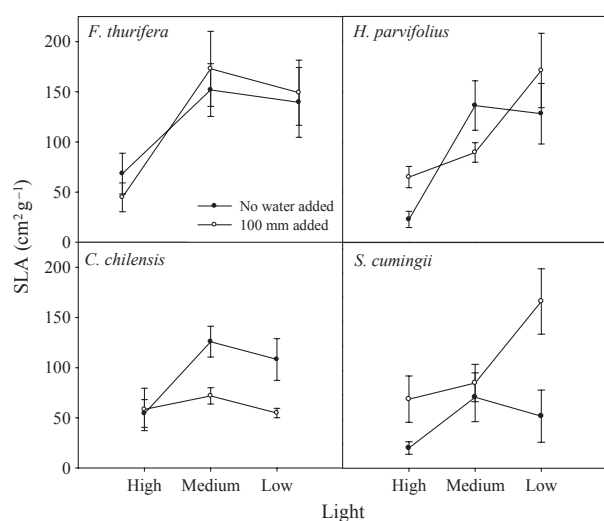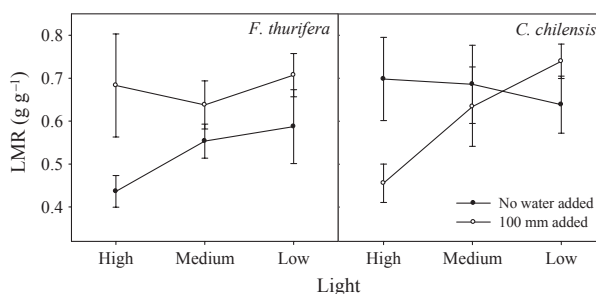

Fig. 5. Specific leaf area (SLA) of *F. thurifera*, *H. parvifolius*, *C. chilensis* and *S. cumingii* plants grown under three light conditions (high, medium and low light) and two water treatments (natural rainfall only and natural rainfall plus 100 mm of supplemental water). Bars represent SE of the means.

Leaf mass ratio

Water and/or light treatments did not affect LMR in *H. parvifolius* or *S. cumingii* (Table 3). For *F. thurifera* LMR increased in treatments with supplemental water (Table 3). LMR of *C. chilensis* showed a complex response to varying light and water treatments, where LMR was higher in treatments with no water added compared to treatments with supplemental water when the light levels were high, and vice versa when light levels were low (Table 3, Fig. 6).

Root/shoot ratio

Biomass allocation was independent of water, light or their interaction in seedlings of *C. chilensis*, *S. cumingii* and

H. parvifolius (Table 3). However, for *F. thurifera* water had a significant effect on the R/S ratio. Specifically, *F. thurifera* seedlings allocated more biomass to roots than shoots in treatments with no supplemental water than in those with 100 mm of supplemental water (Table 3).

Discussion

In this study we found complex, species-specific responses of survival, growth and morphology to the interactive effects of light and water, and there were few consistent responses across species. Furthermore, we did not find direct evidence of a trade-off between drought and shade tolerance in the six species examined.

Seedling survival

In our study, there were interspecific differences of survival responses to water stress in the contrasting light conditions, but species that tolerated higher levels of shade were not more vulnerable to drought, or vice versa. The trade-off hypothesis states that drought conditions should be detrimental to seedling survival under higher shade levels because of conflicts in the simultaneous demand for resource allocation to deal with above- and below-ground limitations (Smith & Huston 1989; Kubiske et al. 1996). In contrast, the facilitation hypothesis states that in drought conditions, the negative effects of reduced light levels can be compensated by its benefits for plant water status (Callaway 1995; Holmgren 2000). Our results provide evidence for both hypotheses. We found that a combination of low water and low or intermediate irradiance negatively affected seedling survival in one species (*E. canescens*), but positively influenced survival in three other species (*C. chilensis*, *S. cumingii* and *H. parvifolius*). The latter, which supports the facilitation hypothesis, might be expected because higher irradiance tends to increase evaporation rates and, consequently amplify drought levels, as

indicated by soils in the high irradiance environment being consistently drier that those in the other light treatments. In addition, the effect of low water combined with high irradiance has been shown to increase tissue desiccation, which together with high temperatures and photo-oxidative stress can have a direct impact on seedling growth and survival (Valladares & Pearcy 1997; Valladares 2001; Sack 2004; Sánchez-Gómez et al. 2006; Gómez-Aparicio et al. 2008).

In contrast, low seedling survival in low light and drought conditions, as expected by the trade-off hypothesis, may be a consequence of the low PAR levels in this environment (average 5.9%). The three light environments in our experiment were above the light compensation points of all six species in the supplemental water treatment (Martinez-Tillería 2007), but for only a small fraction of the day (14, 9 and 6 h for the high, medium and low light environments, respectively). Although we have no data for the compensation points in drought conditions, a prediction of the trade-off model is that the whole plant light compensation point should increase under dry conditions; consequently, PAR levels of the low light environment in drought conditions may not have been sufficient for seedlings to maintain a positive carbon balance, and thus ultimately lead to high mortality. Moreover, photosynthetic rates of seedlings measured at the different radiation levels in treatments with supplemental water (Martinez-Tillería 2007) revealed that the light saturation point was higher in intermediate and high light conditions compared to low light conditions, which further implicates light as a limiting factor for survival – and one that may be compounded by low water conditions. For example, Valladares & Pearcy (2002) showed that carbon gain was much more strongly limited by the development of drought stress in the shade than in the sun. Similarly, shade in drought conditions can affect water relations in *Pinus ponderosa* seedlings, and lead to cell walls so structurally weak that they collapse with dehydration (Vance & Zaerr 1991). Finally, our observations could also be interpreted as evidence for the 'interplay' hypothesis (Holmgren et al. 1997), where the detrimental effect of drought is comparatively strong at high irradiance, weaker in medium shade (because of facilitation), and also strong in low irradiance.

In the case of treatments with supplemental water, high light environments increased survival for all species (three significantly), which would be expected given that neither light nor water was limiting. Moreover, this result highlights the potential relevance of El Niño years for plant regeneration in this region (Squeo et al. 2007; León et al. 2011). Supplemental water, however, had no effect in low light conditions, which may suggest that the limitation of light is not altered even with additional water.

Relative growth rate

The RGR changed only with low light conditions (i.e. higher) in *C. chilensis* and *P. revolutus*, and did not show differences between water treatments for any species. We found no evidence of trade-offs between RGR in high light and survival in shade, as would be predicted by the trade-off hypothesis. These results are comparable to other studies examining the interactive effects of light and water. For example, Sack & Grubb (2002) examined RGR and biomass allocation in seedlings of four shade-tolerant species in a greenhouse experiment, and found that drought reduced RGR equally across light treatments, but did not significantly alter any species' biomass allocation across irradiance treatments. Similarly, Holmgren (2000) showed that improvements of water conditions did not increase growth of tulip poplar seedlings under low irradiance levels, and high irradiance levels marginally increased plant growth in drought conditions compared to the effects under high water conditions. Finally, in Mediterranean ecosystems, Sánchez-Gómez et al. (2006) reported no evidence of trade-offs for shade and drought tolerances in seedlings of eight species growing in an outdoor nursery.

Morphological traits

Overall, our results showed that in response to lower radiation levels, SLA increased for each study species, a result that is consistent with those of other studies (e.g. Sack & Grubb 2002; Sack 2004; Aranda et al. 2007). In response to drought, however, SLA varied in our experiment. For example, while SLA increased in treatments with added water for *S. cumingii*, while the opposite pattern was observed for *C. chilensis*. According to the hypothesis proposed by Smith & Huston (1989), a trade-off can arise if plants in low radiation environments have a high SLA for efficient light capture at the expense of their root allocation, ultimately resulting in a greater sensitivity to drought. However, no such pattern was observed.

In our study, evidence to support the hypothesis that dry conditions should result in plants allocating relatively more biomass to roots than to above-ground structures (Smith & Huston 1989) was only provided by *F. thurifera*, which has a dimorphic root system. Dimorphism within the root system is important to co-optimize the acquisition of multiple soil resources, and plants that allocate root mass to deep horizons, and particularly the tap root, have been shown to be better adapted to drought conditions (Ho et al. 2004, 2005). In particular, the root morphology of *F. thurifera* appears to facilitate hydraulic lift (León et al. 2004), which is a mechanism in desert ecosystems that allows plants to enhance transpiration rates, decrease water stress and maintain a higher water potential, which

can ultimately prevent root shrinkage and embolism (Tyree & Sperry 1989; Dawson 1993). Here, we observed more biomass allocation to roots of *F. thurifera* in dry conditions, but we did not examine specifically how root architecture changes under different water treatments. In a recent study conducted in the same area, León et al. (2011) observed that seedlings in irrigated treatments had roots significantly longer than seedlings in control plots with natural rainfall only, but there were no observed changes in the R/S ratio. These results suggest that root architecture and plasticity should be explicitly considered in addition to changes in biomass allocation in future studies. Moreover, root architecture and biomass allocation to roots can also change with ontogeny (Lusck 2004); therefore, it is possible that trade-offs in biomass allocation may occur at later stages in plant development.

According to the trade-off hypothesis, responses of LMR in low-light conditions should be higher for plants that are less tolerant to shade, and should limit the plants' ability to survive in drought conditions (Smith & Huston 1989). In our study, *F. thrurifera* and *C. chilensis* were the only species that showed changes in LMR, and as predicted, where LMR tended to increase with increasing shade levels. In contrast to what is predicted by the trade-off hypothesis, however, survival of *C. chilensis* seedlings was not affected by water treatments, and although in *F. thurifera* overall mortality was increased in drought conditions, this was a response solely to water levels; i.e. there were no interactive effects of light and water on seedling survival.

One of our study's limitations to detect trade-offs between drought and shade tolerance was that although we had a treatment with low light (approx. 5% PAR) and no supplemental water (i.e. only 55.4 mm of natural rainfall water available), we did not achieve a true 'dry shade' treatment, as reflected by soil water potentials in the shade environments (Fig. 1). Future studies may benefit from conducting differential irrigation regimes to achieve 'dry shade' environments. However, given that the negative effects of low water on seedling survival were so pronounced irrespective of the light treatment, we believe this limitation does not hinder the overall conclusions of our study.

As global climate change leads to an increasingly drier coastal desert, with an already recorded decrease in precipitation from 170 mm per year at the beginning of the 20th century to less than 80 mm per year by 2000 (Squeo et al. 1999), it is critical that we achieve a firm understanding of the interactive effects of water availability and irradiance on survival and growth of seedlings and juvenile plants. Here, we found that the interaction of light and water affected seedling survival of only two of the six species studied, and in both cases survival decreased with increasing shade. This suggests that facili-

tation may not be a prevalent mechanism for seedling recruitment in this ecosystem. In contrast, there was a positive relationship between water availability and seedling survival in all but one species, indicating that this is the most important resource that limits recruitment in the coastal desert. This conclusion is further supported with results from a recent study by León et al. (2011), who showed that seedling survival required at least 206 mm of water, which is twice the average current rainfall and approximately equivalent to the precipitation during an ENSO (El Niño Southern Oscillation) event in the region. Moreover, sufficient quantities of water are also key to trigger germination in this system (Squeo et al. 2007). Ultimately, our results suggest that increased aridity in this system may severely hinder seedling recruitment of the native coastal desert shrubs.

Acknowledgements

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