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Spatio-temporal variation in the effect of herbaceous layer on woody seedling survival in a Chilean mediterranean ecosystem

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Abstract

Questions: What is the effect of herbaceous layer on seedling establishment of three woody pioneer species in open areas of central Chile under a semi-arid mediterranean climate? How do inter-annual and habitat conditions (slope aspect) modulate this effect? Under high stress conditions such as the drier year and habitat (north-facing slope) do herbs reach low abundance and have neutral effects on woody seedlings? Under medium stress conditions for these woody species, such as the wetter year and south-facing slope, does the herbaceous layer reach greater abundance and have positive effects on woody seedlings due to increasing soil water content?

Location: A watershed on the outskirts of Santiago, Chile, subjected to clearing of woody vegetation through firewood extraction and human-set fires.

Methods: In spring 2007, we set up 20 plots ($3\,m \times 2\,m$). Half of each plot had herbs removed manually and by application of herbicide. In both halves of each plot, one seedling (8 months old) of each of the three native woody species (*Colliguaya odorifera, Schinus polygamus* and *Quillaja saponaria*) was planted and survival monitored subsequently. The experiment was repeated in two consecutive growing seasons (2007–2008 and 2008–2009) that differed significantly in total precipitation (152 and 256.5 mm, respectively), and replicated in two sites that differed in aspect and abiotic conditions: a moister south- and a drier north-facing slope.

Results: In the first and drier year, the herbaceous layer had low cover and no significant effect on seedling survival of woody species. During the second year, herbs had greater cover and a significant positive effect on spring survival of *C. odorifera* in the north-facing slope, which was lost after summer. During this wetter year on the south-facing slope, herb cover had a positive effect on survival of *S. polygamus* (mainly during summer).

Conclusions: The role of mostly ruderal herbs on woody seedling establishment depended on the species, rainfall of the current year and slope aspect, and may be explained by soil moisture patterns. This suggests that the effect of ruderal herbs on woody seedlings shifts from neutral under high stress conditions produced by drought to positive under moderate stress conditions. Our results contribute to understand interactions between ruderal herbs and woody species under contrasting abiotic conditions. Therefore, control of the herbaceous layer may not be needed in restoration programmes for this region. Moreover, herbs may benefit restoration of woody cover in mesic habitats.

Introduction

Plant–plant interactions can strongly influence the composition and structure of plant communities and succession (Grime 1977; Callaway 2007; Maestre et al. 2009). Open areas, where woody vegetation has been eliminated by human activities, are often initially colonized by a diverse array of herb species, both native and exotic

(Grime 1977; Archer et al. 1988; Arroyo et al. 1995). Thereafter, recovery of woody vegetation in such areas may be affected by herbaceous cover, particularly in the early stages of woody recruitment and years when herbs are more abundant (Knoop & Walker 1985; Owens et al. 1995; Brown et al. 1998; Brown & Archer 1999; Davis et al. 1999; Maestre et al. 2001; Jurena & Archer 2003; Armas & Pugnaire 2005).

Herbs may negatively affect woody seedling survival by monopolizing soil resources, light or space (e.g. Harrington 1991; Davis et al. 1999; Rey Benayas et al. 2002, 2003, 2005, 2007; Armas & Pugnaire 2005; Pitt et al. 2009). Positive effects may be related to reduction of soil water evaporation rates due to shading and enhancement of nutrient availability due to nitrogen fixation and production of more labile litter (Mitchley & Willems 1995; Maestre et al. 2003). Herbs can also indirectly affect woody seedling survival by modulating herbivore or parasite populations (Rudgers & Orr 2009). Hence, the net effect of herbs on woody seedling survival is the result of a balance among negative and positive effects, which may depend on the abiotic conditions (Bertness & Callaway 1994; Holmgren et al. 1997; Callaway 2007; Maestre et al. 2009). According to the stress gradient hypothesis (Bertness & Callaway 1994), plant–plant interactions (and thus the effect of herbs on woody seedlings) should shift from positive, under more stressing conditions, to competitive when stress decreases. However, general predictions of the stress gradient hypothesis were recently refined by Maestre et al. (2009), specifying the outcome of interactions depending on the life-history attributes of plant species (sensu Grime 1977) and the nature of the limiting factor (resource versus non-resource). However, this new model focused only on stress-tolerant and competitor strategies, excluding ruderal species (sensu Grime 1977). This is relevant to predict the effect of herbs on woody seedlings as many herb species in open areas of different ecosystems can be considered as ruderals (Grime 1977; Arroyo et al. 1995).

Mediterranean ecosystems have a climate with a pronounced dry season of nearly 4–6 months that strongly limits plant productivity (di Castri & Hajek 1976; di Castri et al. 1981; Arroyo et al. 1995). Moreover, inter-annual variation in precipitation and differences among habitats produce great temporal and spatial heterogeneity within such regions (di Castri & Hajek 1976; Armesto & Martínez 1978; di Castri et al. 1981). Vegetation of these ecosystems is frequently described as a mosaic of woody patches separated from one another by herbaceous patches as consequence of human disturbance and livestock grazing (di Castri et al. 1981; Fuentes et al. 1984, 1986). In central Chile, characterized by a mediterranean climate, herbaceous cover is mainly comprised of exotic annual ruderal species, which reach their peak growth during late winter and spring, but dry out completely during summer (Fuentes et al. 1989). The role of herbs in recruitment of woody species in central Chile is largely unknown, despite the widespread presence of herbs in these open areas. Previous research (Fuentes et al. 1989; Holmgren et al. 2000) suggests that herbs have mainly negative effects on woody seedling survival. However, given the temporal and spatial variability of conditions for herbaceous growth and woody species establishment in mediterranean ecosystems such as central Chile, the effect of herb species on woody seedlings may depend on the specific environmental conditions (Bertness & Callaway 1994; Goldberg & Novoplansky 1997; Maestre et al. 2009).

Here, we experimentally test the effect of the herbaceous layer on seedling survival of three pioneer woody species from the mediterranean climate vegetation of central Chile (Fuentes et al. 1984; Armesto & Pickett 1985): *Colliguaya odorifera* Mol. (Euphorbiaceae), *Quillaja saponaria* Mol. (Rosaceae) and *Schinus polygamus* (Cav.) Cabr. (Anacardiaceae). We also assessed the role of inter-annual abiotic variability and habitat differences in modulating the effect of herbs on woody seedling survival. To assess the role of inter-annual variability, we replicated the study during a year with rainfall near the average for the region and another year with a significant shortage of precipitation for the region (corresponding to La Niña event). To assess the role of habitat variability, we replicated the study in two habitats with contrasting aspect and abiotic conditions, a north-facing (drier) and a south-facing (moister) slope (Armesto & Martínez 1978). Given that the study was carried out in a semi-arid region, the moister year and habitat may be considered as medium stress conditions for these species, as they also distribute under more rainy and wetter climates (low stress levels) within Chile. In turn, the drier year and habitat may be considered as high stress conditions for these species. Based on the original stress gradient hypothesis, we would expect that the herb effect should shift from negative or neutral in the moister year and habitat (medium stress level) to positive in the drier year and habitat (high stress level). However, abundance of ruderal herbs is also modulated by the stress conditions (Grime 1977). Cover and density of ruderal herbs is frequently low under high stress conditions, especially when stress is produced by a resource (e.g. water) (Grime 1977). In turn, under medium stress levels, ruderal herbs may reach greater cover and reduce soil water evaporation rates. Therefore, we expect that under higher stress conditions, such as in the drier year and habitat (north-facing slope), herbs should reach low abundance and have neutral effects on woody seedlings. In turn, under medium stress conditions (the wetter year and south-facing

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slope), the herbaceous layer should reach greater abundance and have positive effects on woody seedlings due to increasing soil water content.

Results of this study are relevant to understand the role of herb–woody species interactions during succession and to assess the importance of controlling herb cover during restoration of woody cover in open areas under a mediterranean climate.

Methods

Study site and species descriptions

The study was carried out in the San Ramón watershed, in the Andean foothills, at an elevation of 900 m a.s.l., on the outskirts of the city of Santiago (33°30′S, 70°30′W), central Chile. The climate is mediterranean semi-arid, with five to seven extremely dry months per year and 90% of the annual precipitation concentrated during the winter months (May–August). Mean annual precipitation (1960–1990) is 330 mm and annual mean temperature is 15 °C (di Castri & Hajek 1976). During the period of monitoring the field experiments (8 months, June–March, 2007 and 2008), monthly mean temperatures and total precipitation were: 14.6 °C and 152 mm in the first year (2007) and 15.5 °C and 256.5 mm in the second year (2008), whereas total annual precipitation was 170 mm in 2007 and 350 mm in 2008. In addition, during the first year, rainfall was almost absent during spring months (September–December), in contrast to the second year when some rain events occurred between September and November (Fig. 1). However, both years had strong summer droughts (Fig. 1), characteristic of the region.

We replicated the experiment in two habitats present in the study site: a north- and a south-facing slope. North-(equatorial) facing slope and a south-(polar) facing slopes differ greatly in soil moisture, with a more humid south-facing slope having greater plant biomass and woody species cover (Armesto & Martínez 1978). On both habitats, woody cover was patchy, with open spaces between shrubs dominated by herbaceous cover, including native geophytes and annual mostly ruderals such as *Pasithea coerulea, Bromus berteroanus, Clarkia tenella, Amsinckia calycina, Moscharia pinnatifida, Helenium aromaticum*, and exotics such as *Conium maculatum, Centaurea melitensis, Fumaria capreolata, Carduus pycnocephalus, Erodium cicutarium* and *Brassica rapa*. The study watershed has been protected from logging, cattle grazing and fire for the past 10 years.

The three woody species selected for seedling survival trials are evergreen sclerophyllous of common occurrence in central Chile. *Colliguaya odorifera* is a shade-intolerant shrub species occurring mainly in open sites of dry and mesic habitats (Armesto & Martínez 1978). *Quillaja saponaria* is a shade-intolerant tree species that can reach 20-m tall, and inhabits dry and mesic habitats (Holmgren et al. 2000). It is a frequent colonizer in open sites, but requires nurse shrubs to regenerate in drier habitats (Fuentes et al. 1986). *Schinus polygamus* is a tall shrub (up to 10 m) that occurs mainly in open, dry habitats, or in disturbed sites in more humid habitats (Fuentes et al. 1986). All three are used in shrubland restoration assays in disturbed matorral sites.

Experimental design

During the austral autumn, we installed a total of 40 3 m × 2 m plots (20 per habitat), and then removed the herbaceous cover entirely from one half of each plot. Removal was achieved by adding a non-selective systemic herbicide (Roundup®, Glyphosate: N-phosphonomethyl-glycine). The herbicide acts on leaf contact but does not damage roots. During the period of the experiment, all herbs that reappeared in the plots were removed manually every month. Herbaceous cover in the treated plots was kept at < 2%. Three weeks after herbicide application, one 8-month-old seedling of each of the three native woody species (*Colliguaya odorifera, Schinus polygamus* and *Quillaja saponaria*) was planted in each half of the plots.

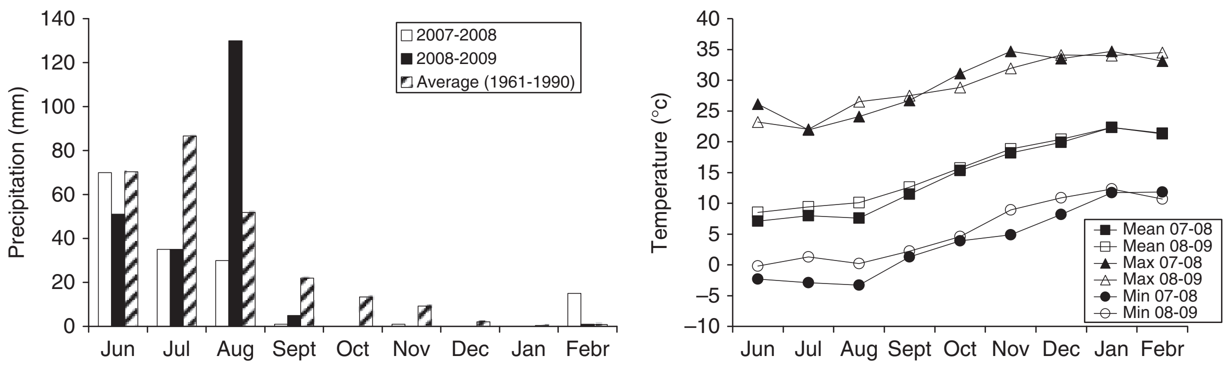

Fig. 1. Monthly precipitation (bars) and mean temperature (minimal, average and maximal, lines on the right) during the period of the experiments in the growing seasons of 2007–2008 and 2008–2009. Long-term averages (1961–1990) are also shown for comparison (http://met.dgf.uchile.cl/clima).

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Seedlings were separated by 50 cm from one another. Plots were fenced to exclude vertebrate herbivores and were separated by at least 10 m from one another. All plots were set up in open sites without woody cover. During this first year we irrigated half of a plot in each habitat in order to simulate a moister year by adding 50 mm of water four times between August and October 2007 (200 mm total). However, we found that this treatment did not influence seedling survival or the effect of the herbaceous layer on seedlings. Therefore, we have excluded these analyses and results from this paper.

The experiment was repeated in two consecutive years (2007–2008 and 2008–2009) between June and March, but in the second year we could analyse only 12 plots per habitat with and without herb cover due to destruction of fences in the remaining plots. In this second experiment, one new woody seedling of each of the same three species and from the same provenance was planted in half of a plot with cover removed and in half with intact cover. Living and dead seedlings from the first experiment (2007–2008) were removed from both plots.

Seedlings of each of the three woody species used in both years were grown from seed in a greenhouse in polyethylene bags with 1000 cm^3 of organic soil and were planted in holes in the field with the same soil volume (10 cm depth). We used 8-month-old seedlings because germination of these species in a greenhouse (and also in nature) occurs during late winter and early spring (between July and October), and because experimental planting must be performed during autumn (May–June) to ensure water availability after planting. Thus, we had to wait until June for planting out, which is approximately 8 months after germination. Nevertheless, 8-month-old seedlings of these species (as most of woody species of central Chile) still were shorter than the herbaceous layer even at the end of the experiment. Seedling heights at time of planting for the first experiment were 27.7 ± 8.7 cm, 25.7 ± 5.7 cm and 35.8 ± 7.0 cm (mean ± SD) for *C. odorifera, Q. saponaria* and *S. polygamus*, respectively. For the second year, woody seedling heights at time of planting were 29.7 ± 6.2 cm, 19.8 ± 2.8 cm and 29.1 ± 6.4 cm (mean ± SD) for *C. odorifera, Q. saponaria* and *S. polygamus*, respectively. There were no significant differences in height of planted seedlings between different herb treatments at the beginning of each year.

Survival assessments and measurements

Woody seedling survival after planting was assessed every 3 months between June (mid-winter) and March (end of summer drought) in each of the 2 years of study. A planted seedling was considered dead when its shoots were dry and had no green leaves.

We evaluated soil water content for both herb treatments in each habitat and year of study. Soil moisture was determined gravimetrically, taking a soil volume of 785 cm^3 from the first 10 cm of soil (excluding litter) from each plot ($N = 20$ for each herb treatment during the first year, $N = 12$ for each herb treatment during the second year). Measurements were made once in November (austral spring), which is the peak of the growing season for herbs, and repeated in March (end of summer), when the herbaceous layer is almost entirely dry or dead.

Ground cover of all herbs was estimated at the peak of the growing season (November) in 2007 and 2008, by identifying the herbaceous plants intercepting each of 100 points within a 1 m × 1 m grid placed at the centre of the areas with and without herbicide application in each plot, directly above the planted woody seedlings. Herbaceous cover was expressed as a percentage from the 100 points intercepted. Height of herbs was strongly correlated with ground cover, so only the latter is reported.

Data analyses

Herbaceous cover differences between habitats and years, considering the intact half of the plots only, were assessed using a two-way factorial ANOVA. Soil water content for spring and summer were compared between herb treatments and habitats (as fixed factors) using repeated measures ANOVA (season as within-subject variable) for each year separately. Data of herb cover and soil moisture satisfied assumptions of ANOVAs.

Differences in seedling survival (mortality rates) between treatments (with and without herbs) per each year and habitat were evaluated separately for each species using a Kaplan-Meier procedure with a log-rank (Mantel-Cox) survival curve test. All statistical analyses were conducted using SPSS 15.0 (SPSS, Chicago, IL, US).

Results

Herbaceous cover

On the north-facing slope, total herbaceous cover averaged $42.2 \pm 3.9\%$ (mean ± 1SE) during the first year, and $80.4 \pm 3.2\%$ during the second year, whereas on the south-facing slope, herb cover averaged $34.2 \pm 4.2\%$ during the first year and $78.3 \pm 4.2\%$ during the second and wetter year. Therefore, total herbaceous cover was significantly greater in the second and wetter year than in the first year (ANOVA, $F_{1,60} = 92.66$, $P < 0.001$) on both habitats, but there were no differences between habitats in either year (ANOVA, $F_{1,60} = 1.39$, $P = 0.24$). The interaction between year and habitat was not significant (ANOVA, $F_{1,60} = 0.48$, $P = 0.49$).

Doi: 10.1111/j.1654-1103.2011.01291.x

Soil water content

During the first year, soil water content differed significantly between habitats ($F_{2,75} = 46.89$, $P < 0.0001$) and between herb treatments ($F_{2,75} = 11.36$, $P < 0.0001$), but the interaction between these two factors was not significant ($F_{2,75} = 0.08$, $P = 0.92$). In the same way, during the second year soil water content differed significantly between habitats ($F_{2,41} = 46.16$, $P < 0.0001$) and between herb treatments ($F_{2,41} = 13.22$, $P < 0.0001$), but the interaction between these two factors was not significant ($F_{2,41} = 1.23$, $P = 0.30$). When soil water content results were analysed separately between seasons, in the first and drier year, spring soil water content did not differ between habitats and herb treatments (Table 1). In turn, soil water content in summer was significantly greater on the south-facing than on north-facing slope, although as in spring, we observed no significant difference between herb treatments (Table 1). During the second and wetter year, spring soil moisture did not differ between herb treatments on the south-facing slope, but the treatment with herbs had significantly greater soil moisture than the treatment without herbs on the north-facing slope (Table 1). In addition, when herbs were removed, soil water content in spring was significantly greater on the south- than on the north-facing slope (Table 1). Finally, soil water content recorded in summer of the second year was significantly higher on the south- than on the north-facing slope in both herb treatments, and significantly higher with herbs than without herbs only on the south-facing slope (Table 1).

Differences between years in soil water content were not analysed because soil moisture may strongly be dependent on the date and number of days since the last rainfall event.

Woody seedling survival

On the north-facing slope, woody seedling survival was lower with herbs than without herbs (Fig. 2), although we found no significant difference between herb treatments for any species in the first and drier year (Table 2). In contrast, in the same habitat, woody seedling survival was generally higher with herbs than without herbs in the second and wetter year (Fig. 2), although differences were significant only for *C. odorifera* (Table 2). Nevertheless, this positive effect of herbs on seedling survival was short-lived (only during spring and early summer) because final seedling survival recorded after summer was zero, both with and without a herb layer (Fig. 2). On the other hand, on the south-facing slope, i.e. the wetter habitat, woody seedling survival did not differ between treatments with or without herbs, regardless of species and year (Fig. 2), except in *S. polygamus*. In this species seedling survival was higher when herbs were present (Table 2), and this difference was produced mainly during the summer of the second year (Fig. 2).

Discussion

We found evidence that the effect of the herbaceous layer on survival of woody seedlings of colonizing species in semi-arid Chile varied between neutral and positive, depending on the abiotic conditions of the year, habitat and target species. Similar to our initial hypothesis, positive effects of the herbaceous layer were observed under less stressful conditions of the study area (medium stress conditions for these species), although only in *S. polygamus* and temporally (only in spring) in *C. odorifera*. Neutral or slightly negative effects were observed mainly in more stressful conditions (high stress conditions for these species).

Our results may be partly explained by the differences in soil water availability between herb treatments, years and habitats. During the first and drier year, woody seedling mortality began earlier than during the second year, presumably because of lower spring rainfall (Fig. 1). Likewise, final survival of woody seedlings was higher in the second wetter year than in the first year. Furthermore, woody plant survival during spring and at the end of summer was generally higher on the more humid south-facing slope than on the north-facing slope. These results suggest that survival of woody species is strongly water-limited and that effectively, the second year and

Table 1. Differences in soil water content (SWC) between herb treatments and habitats (slope aspect). Values are means ± 1SE. $N = 20$ for the growing season 2007–2008 and $N = 12$ for 2008–2009. Different superscripts indicate significant differences between habitats for a given herb treatment, season and year ($P < 0.05$ Tukey tests). Lowercase letters indicate significant differences between herb treatments for a given season, habitat and year ($P < 0.05$ Tukey tests).

	South-facing slope		North-facing slope	
	With herbs	Without herbs	With herbs	Without herbs
SWC spring 07–08 (%)	3.7 ± 0.3^{Aa}	5.9 ± 1.0^{Aa}	3.1 ± 0.2^{Aa}	4.5 ± 0.5^{Aa}
SWC summer 07–08 (%)	3.7 ± 0.2^{Aa}	3.3 ± 0.2^{Aa}	2.2 ± 0.1^{Ba}	1.9 ± 0.1^{Ba}
SWC spring 08–09 (%)	10.1 ± 0.9^{Aa}	8.2 ± 0.7^{Aa}	7.3 ± 0.4^{Aa}	4.3 ± 0.3^{Bb}
SWC summer 08–09 (%)	4.1 ± 0.3^{Aa}	3.2 ± 0.2^{Ab}	2.2 ± 0.1^{Ba}	1.9 ± 0.1^{Ba}

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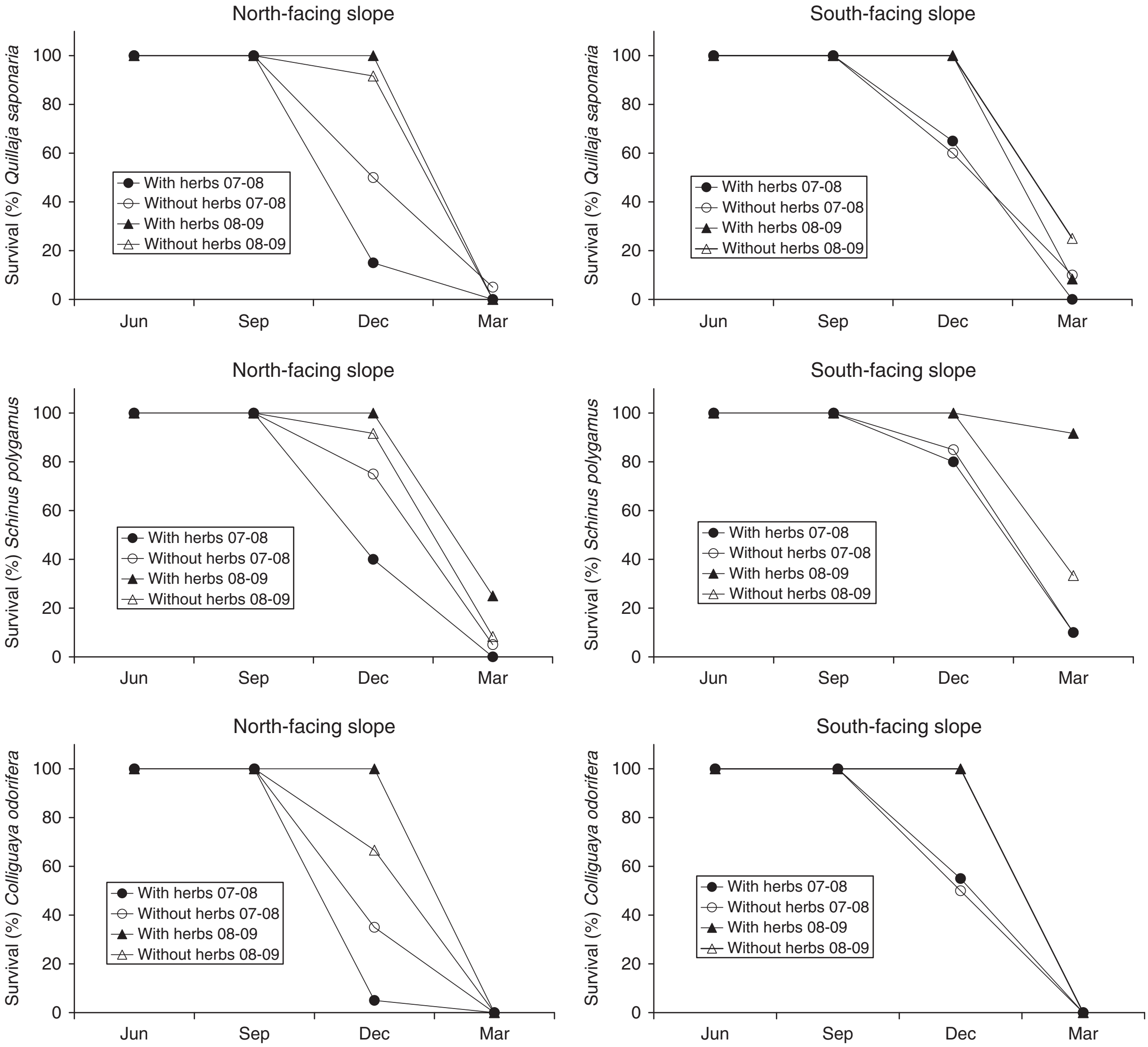

Fig. 2. Seedling survival curves of three woody species from central Chile planted into each half of the two plots (with and without herbs) in 2 years (2007–2008 and 2008–2009) and two habitats (north- and south-facing slopes). Each point is the percentage of seedlings remaining alive. $N = 20$ plots in year 1, and $N = 12$ plots in year 2.

the south-facing slope were less stressing conditions than the first year and north-facing slope for these species. Accordingly, it is probable that because no difference in soil water content was observed between herb treatments in either habitat during the first and drier year, the presence of herbs had no effect on seedling survival in this year. The absence of some effect of the herbaceous layer on soil moisture may be due to their lower cover (< 50% in both habitats) compared to the wetter year, when herbs had significantly greater ground cover (about 80%) and enhanced soil moisture with respect to the herb removal treatment. Such effects of herbs may be attributed to reduction of soil evaporation due to shading (e.g. Mitchley & Willems 1995; Holmgren et al. 1997; Maestre et al. 2003; Maestre & Cortina 2004). During the second year positive effects of the herbaceous layer on soil moisture were observed during spring in the north-facing slope, which may explain the positive although temporal herb effect on *C. odorifera* only in this site, and also during summer in the south-facing slope, which may explain the positive herb effect on *S. polygamus* only in this habitat. Thus, in *S. polygamus* we detected a shift from facilitation to neutral effects of herbs with higher abiotic stress conditions (from the south-facing to the north-facing slope during the second year and from the second to the first year in the south-facing slope). This shift likely occurred because the levels of the most limiting resource (e.g. water) became so low that the benefits provided by

Journal of Vegetation Science
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Table 2. Effects of the herbaceous layer removal on seedling survival of three woody species from central Chile. Statistical values are from Kaplan-Meier survival analyses (log-rank tests), comparing areas with and without herb cover, years of contrasting rainfall (see text) and habitats (slope aspect). (*: no statistical analysis due to identical curves; + indicates a significant positive effect of the herbaceous layer).

Species	Slope	Experimental year	χ^2	*P*
Q. saponaria	North-facing slope	2007–2008	2.52	0.112
		2008–2009	1.01	0.317
	South-facing slope	2007–2008	0.57	0.451
		2008–2009	1.15	0.283
S. polygamus	North-facing slope	2007–2008	2.26	0.132
		2008–2009	1.79	0.180
	South-facing slope	2007–2008	0.07	0.783
		2008–2009	8.35	0.003 (+)
C. odorifera	North-facing slope	2007–2008	3.353	0.067
		2008–2009	4.60	0.031 (+)
	South-facing slope	2007–2008	0.21	0.648
		2008–2009	*	*

the facilitator (e.g. reduction of soil evaporation by shading from herbs) could not overcome its own resource uptake (e.g. Maestre & Cortina 2004), producing no positive effect on soil moisture and no facilitation, although no competition either. Therefore, soil moisture enhancement mediated by herbs seems to be a relevant mechanism through which herbs have a positive effect on the survival of seedlings of woody species (e.g. Thomas & Davis 1989; Moreno & Oechel 1992; Maestre et al. 2003; Maestre & Cortina 2004). However, we cannot rule out other mechanisms mediated by herbs that may enhance woody seedling survival in this semi-arid region, such as light filtering effects (Rey Benayas et al. 2002), changes of soil microbial communities (Rudgers & Orr 2009) or nutrient addition, e.g. from nitrogen-fixing forbs (Davis et al. 1999).

Other studies have also documented shifts in plant–plant interactions among years or habitats (e.g. Goldberg & Novoplansky 1997; Tielbörger & Kadmon 2000; Maestre & Cortina 2004; Kikvidze et al. 2006; revision in Callaway 2007). To predict these changes, Bertness & Callaway (1994) proposed the stress gradient hypothesis; however, our results did not support this hypothesis as positive herb effects (although only on two woody species) occurred mainly under medium stress levels, and neutral or slightly negative under high stress conditions, for these woody species. More recently, Maestre et al. (2009) refined this hypothesis, although only the outcome of interactions between competitors and stress-tolerant species were proposed. The three woody species contrasted here have broad habitat tolerances, occurring frequently in open, disturbed sites (Armesto & Martínez 1978; Fuentes et al. 1984, 1986; Holmgren et al. 2000), which suggest that they are not highly competitive (sensu Grime 1977). In turn, these species may be considered stress-tolerant, as they are able to inhabit xeric habitats within central Chile (Armesto & Martínez 1978; Fuentes et al. 1984, 1986). Therefore, our results suggest that the effect of ruderal herb species on stress-tolerant species may be neutral under high stress conditions and positive under medium stress levels. Finally, under low stress (not evaluated in this study) herbs could compete with woody seedlings, e.g. through light or nutrients, as water no longer limits plant growth (Rey Benayas et al. 2002, 2003, 2005, 2007; Maestre et al. 2003). In fact, under moister, and presumably less stressful, coastal habitats of central Chile, Holmgren et al. (2000) found a negative effect of herbs on one of our woody species (*Q. saponaria*).

Although these shade-intolerant woody species may be classified as stress-tolerant species, they showed relatively different responses to the herb treatments. This may be related to undocumented differences in water requirement, root system depth and shade tolerance, which need to be explored in future studies. Then, our results support the hypothesis that plant–plant interactions are species-specific (Callaway 1998; Lortie & Turkington 2008), and hence subtle differences in ecological requirements and tolerances even among apparently similar species may modify the outcome of their interactions with other species, in this case with an assembly of ruderal species.

Overall, we suggest that under high or moderate stress, typical of mediterranean climate areas, ruderal herbs should have neutral or positive effects on the survival of woody seedlings of pioneer species. Thus, although some particular herb species might have a negative effect (which is unknown and should be assessed in future studies), the entire herb species assemblage had no negative impact on seedling survival, and hence would not delay or slow down succession towards increasing woody cover. Therefore, in central Chile, as in other ecosystems where restoration of woody vegetation is strongly limited by drought stress, herbs may facilitate woody seedling survival through drought amelioration (e.g. Maestre et al. 2001), and hence restoration programmes should not include control or eradication of herbs.

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