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Species-specific effects of the herbaceous layer on recruitment of woody species under different shading and precipitation conditions

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ABSTRACT

Herbs may affect the recruitment of woody species. However, most studies have evaluated the impact of one particular herb species or the herbaceous layer as a whole. It is less known if different herb species have different effects on recruitment of woody species, and whether these effects depend on environmental conditions. In this paper, we evaluated the effects of different native and exotic herb species on recruitment of nine woody species in central Chile, under different conditions of shading and precipitation. The experiment was carried out in an open ruderal area in Santiago, Chile. We conducted a factorial experiment with 360 1 × 1 m pots with monospecific crops of eight herb species and a control without herbs, two levels of irrigation (245 and 534 mm) simulating two precipitation regimes, and the presence or absence of artificial shade simulating a woody canopy. Nine woody species common to the region were sown in each pot. Luminosity (PAR), soil moisture, herb volume, richness of woody species and seedling density of woody species recruited were measured. The effects of herb species on woody species richness varied from neutral in the open condition to mainly negative in the shaded condition. Differences in irrigation did not modify the effects of herbs on species richness. The effects of herb species were more variable when woody species were considered individually. Negative and neutral effects predominated, although some positive effects were observed under shaded and wetter conditions. Our results suggest that different herb species have distinct effects on recruitment of specific woody species and species richness, which mainly depend on shade conditions and secondarily on the precipitation regime, and that herb-woody species interactions are highly specific. Thus, management focused in herb controlling should be species-specific, in terms of herb and woody species, and dependent on climate and woody cover.

1. Introduction

Plant-plant interactions strongly influence the composition, structure and dynamic of vegetation (Maestre et al., 2009) and hence should be considered when planning management and restoration strategies (Gómez-Aparicio, 2009). Most of forest ecosystems have herbaceous layers that vary spatially in species and abundance (Gilliam, 2014). Herb species influence light, soil moisture, chemistry, and other biotic and abiotic factors (Morris et al., 1993; Davis et al., 1999; Olson and Wallander, 2002; Coll et al., 2003; Callaway et al., 2003; Curt et al., 2005), and may therefore affect the natural regeneration or reforestation processes (Gilliam, 2007, 2014). Most studies of the role of the herbaceous layer on woody regeneration have observed negative impacts (Facelli and Pickett, 1991; Castro et al., 2002a; Rey Benayas et al., 2003, 2005, 2007; Lawes and Chapman, 2006; Kunstler et al., 2006; Gilliam, 2007, 2014; Cuesta et al., 2010), although some neutral and positive effects have also been documented (Maestre et al., 2001; Tonioli et al., 2001; Becerra et al., 2011). This variability of outcomes seems to depend on the woody species, probably related to the ecological niche of each species, and the environmental conditions where interactions occur (Johnson et al., 2015; Loranger et al., 2017). A less known issue is the distinct effect of different herb species on regeneration of the same species or the same assembly of woody plants. Herb species can reach varying biomass levels and modify microenvironments differently (Montenegro et al., 1978; Figueroa et al., 2004a; Gilliam, 2014). Therefore, the effects of herbs may vary according to the species in the herbaceous layer.

Plant-plant interactions can depend on environmental conditions, for example, climate (Bertness and Callaway, 1994; Maestre et al., 2009; Holmgren and Scheffer, 2010). Therefore, the effect of herb

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species on the regeneration of woody plants may vary among different abiotic conditions. Although some studies have evaluated how the effect of trees or shrubs on tree regeneration varies with abiotic conditions (Castro et al., 2002b; Maestre et al., 2009), there have been few studies assessing how environmental conditions modify the effect of herb species on the regeneration of woody species. For example, vegetation canopy can facilitate regeneration of other species by enhancing soil moisture and reducing water stress in dry climates, while inhibit it under wetter conditions (Holmgren and Scheffer, 2010). However, the role of precipitation on the effect of herbs on regeneration of woody species remain unclear. For instance, Cuesta et al. (2010) observed that the effects of herb competition on seedlings is more significant in rainy years than in dry ones. Instead, an intermediate year in terms of precipitation trigged positive effects of herbs on the survival of woody seedlings in a semiarid climate, in contrast to a dry year in which herbs had neutral or negative effects on seedling survival (Becerra et al., 2011). Similarly, Maestre and Cortina (2004) found that herbs had a negative effect on shrub seedlings under xeric and extreme moisture conditions, while the effects were positive at intermediate moisture levels.

Another factor that produces different abiotic conditions is the shade from vegetation and other natural elements of ecosystems (stones, tree trunks). Shade can influence the effect of herbs because it can affect the level of stress experienced by the seedlings and seeds of woody species (Davis et al., 1999; Rey Benayas et al., 2002, 2005; Curt et al., 2005). Shade often results in higher soil moisture compared to open areas (Holmgren and Scheffer, 2010). If open sites are more stressful for woody seeds and seedlings due to lower soil moisture, which is typical in semiarid climates (Bertness and Callaway, 1994; Castro et al., 2002b, Becerra and Montenegro, 2013), and if a canopy of herbs increases soil moisture (e.g. Becerra et al., 2011), herbs may facilitate recruitment of woody species in open areas. In contrast, under shrub or tree shade, the increase in soil moisture produced by a canopy of herbs would not be significant compared to other site without herbs under tree shade, and hence herbs would not facilitate recruitment of woody species in this condition. As well, shade may influence the effect of herbs on woody seedlings and seeds by modifying herb species composition and/or biomass (Caldeira et al., 2014). For instance, microclimatic conditions under woody patches can induce dominance of different herb species than in open sites (Gómez-González and Cavieres, 2009; Griffith, 2010).

Like other areas with Mediterranean-type climates, central Chile is characterized by a seasonal climate with hot dry summers and cold humid winters, with significant inter-annual and spatial variability in precipitation and moisture (Armesto et al., 2007). It is also known that moist habitats and rainy years increase recruitment of woody species from the sclerophyllous forest (Holmgren et al., 2006; Fuentes-Castillo et al., 2012; Becerra et al., 2016). Vegetation in central Chile has been strongly disturbed by anthropogenic drivers like clearing, fires and raising livestock (Médail and Quézel, 1999; Myers et al., 2000; Holmgren, 2002; Armesto et al., 2007). These disturbances have changed continuous forests into mosaics of woody patches and open areas (Van de Wouw et al., 2011; Fuentes-Castillo et al., 2012), resulting in highly variable micro-environmental conditions. Both open areas and woody patches have been invaded by exotic herbs, producing a diverse mixture of native and exotic species (Montenegro et al., et al., 1978; Holmgren et al., 2000; Figueroa et al., 2004a; Gómez-González et al., 2011). Several studies have documented that the regeneration of woody species in this semiarid region is facilitated by previously established woody species (Armesto and Pickett, 1985; Fuentes et al., 1984; Becerra and Montenegro, 2013), although under moist conditions facilitation appears to be less important for some species (Holmgren et al., 2000). Furthermore, the herbaceous layer can have different effects on the survival of woody species seedlings depending on habitat conditions of this region (Becerra et al., 2011). Thus, this region is an ideal system to evaluate species-specific effects of herbs on recruitment of woody species under different abiotic conditions. This knowledge would allow to establish management recommendations about necessities of herb control, if this control should be species-specific, and if this depends on shade and precipitation conditions.

In this paper, we evaluated the effect of different native and exotic herb species on recruitment of several woody species native to central Chile. We also examined whether the variability in the effects of herbs depends on shading and precipitation conditions.

2. Methods

2.1. Species used in the experiment

The woody species selected were *Acacia caven* (Molina) Molina, *Kageneckia oblonga* Ruiz & Pav., *Lithrea caustica* (Molina) Hook. & Ar., *Maytenus boaria* Molina, *Podanthus mitiqui* Lindl., *Porlieria chilensis* I. M. Johnst., *Quillaja saponaria* Mol., *Schinus polygamus* (Cav.) Cabr., and *Senna candolleana* (Vogel) H.S. Irwin & Barneby. These species were selected because of their abundance among native vegetation in central Chile. All of them are tree species except *P. mitiqui* which is a shrub. All these species have been observed growing in open areas, at least in moist habitats in central Chile, or under canopies in other environmental conditions (Fuentes et al., 1984; Armesto and Pickett, 1985; Becerra and Montenegro, 2013; Becerra et al., 2013). Highly shade-tolerant and drought-intolerant species that are less likely to recruit in open and drier conditions were excluded.

The herb species selected for the experiment are common in different sites of the Chilean Sclerophyllous forest (Becerra et al., 2011), they have the same successional status (pioneer), although are able to grow in open or shaded patches (Gutiérrez et al., 1993, Gómez-González et al., 2011). We used four native species: (Ac) *Amsinckia calycina* (Moris) Chater., (He) *Helenium aromaticum* (Hook.) L.H. Bailey, (Mp) *Moscharia pinnatifida* Ruiz & Pav., (Pb) *Phacelia brachyantha* Benth., and four exotic species: (Cm) *Centaurea melitensis* L., (Em) *Erodium moschatum* (L.) ĹHér. ex Aiton, (Ec) *Eschscholzia californica* Cham. and (Mm) *Matricaria matricarioides* (Less.) Porter. All these species are annual, except *E. californica*, which may behave as biennial. We did not use grasses to avoid species with too different plant architecture. All species had segmented leaves (compound, lobed, or pinnatisect). Also, all these herb species reach heights up to 50–60 cm, although height may depend on environmental conditions. Nevertheless, many biological traits probably differ among them as they are different species. Although we do not know differences between them in respect to a number of biological traits (e.g. allelopathy, resource uptake rate, etc), this study rather represents a first approach to explore to what extent apparently similar herb species produce different effects on recruitment of woody species.

2.2. Experimental design

The field experiment was carried out in an open grassland at the Faculty of Agronomy and Forestry, Campus San Joaquin, Pontificia Universidad Católica de Chile, from September 2015 to March 2016. However, seeds and fruits of the selected species were collected in the spring and summer before the experiment (October 2014–March 2015). To avoid bias by local adaptability, seeds of woody species were collected from a pool of different trees and localities in central Chile and then mixed. Fleshy pulp from fruit of *L. caustica, P. chilensis and S. polygamus* were removed manually and washed. For *M. boaria,* pulp was removed by friction with sand. Both procedures resemble how seeds are found in Mediterranean seed banks after dispersal by birds or foxes (Figueroa et al., 2004b; Reid and Armesto, 2011). *A. caven* and *S. candolleana* seeds were inspected and discarded in case of any damage or the presence of weevils. Seeds with hard coat were selected by a floatability test, and then quickly dried with paper towels. Finally, seeds of *Q. saponaria, P. mitiqui* and *K. oblonga* seeds were selected by visual inspection and empty seed shells were discarded. After collecting seeds of woody species, seeds were stored in boxes with a dry and dark environment. Before starting the experiment, seeds were stored at approximately 3 °C in darkness for two months (July-August) to simulate the climatic conditions of winter that woody species seeds experience after dispersal and before germination.

We conducted a factorial experiment with three factors: herb species (nine treatments with eight herb species and a control without herbs), shade (shaded versus open), precipitation regime (wetter versus drier). We used a total of ten replicates per treatment combination. Thus, the experiment included a total of 360 experimental units (2 × 9 × 2 × 10), spaced 0.7 m apart. The experimental units were carried out in pots, 1 × 1 m × 30 cm deep in black polyethylene bags to which a mixture of 50% river sand and 50% clay was added. The treatments were randomly distributed among pots. The shade was provided by black nylon shade-cloth with 80% sunblock, which covered pots at a height of 50 cm, supported with wooden sticks buried at the corners of 1 × 1 m areas where the pots were located. A comparable level of light reduction is common among woody patches in central Chile (Becerra and Bustamante, 2011; Becerra and Montenegro, 2013). The shade treatment was established in August, before sowing the woody seeds and after producing herb treatments.

The herb treatments were produced between June and August 2015 (winter). To do this, naturally and recently germinated herbs were collected from three sites around Santiago, Chile, and transplanted to experimental bags (before sowing woody species). Most of the herb species were present in two or three of the sites and plants of all herb species were collected from all the sites where they were present. Thus, different herb species were collected from the same sites. The plants of the different herb species were randomly distributed among pots. Each pot was composited either by one herb species or the control without herbs. The soil in which the herbs had originally been growing was removed almost completely before transplanting, so no herb species conserved nutrients from the sites from where they were collected. Initial cover of transplanted plants reached at least 50%, however, some plants died after being transplanted. In these cases, dry stored seeds of these herb species, collected from the same sites in March 2015, were added to homogenize the initial cover of each herb species treatment. Before sowing woody species, herb species were irrigated daily with the same amount of water per pot.

The experiment started when the cover of each herb species per pot was at least 50% (after transplanting and sowing herbs) (September 2015), date when woody species were sown. Other herb species around or in the pots were periodically removed manually. Seeds of the nine woody species were sown in each pot, burying one cm underground and adding a 0.5-cm layer of sterilized leaf litter to simulate natural conditions. The number of seeds sown per woody species varied according to seed availability. Thirty seeds of the species *A. caven, K. oblonga, L. caustica*, *M. boaria*, *P. mitiqui*, *Q. saponaria, S. candolleana*, 65 of *S. polygamus* and 12 of *P. chilensis* were sown per pot. Thus, a total of 287 seeds were sowed in each pot. Seeds of each woody species were uniformly distributed through the pot, avoiding that two seeds of the same species touch each other. In general, seeds of the same species were located approximately 15 cm apart in the case of species using 30 seeds, approximately 12 cm in the case of the species using 65 seeds, and approximately 20 cm in the case of the species using 12 seeds. Also, the sowing avoided that two seeds of different species touch each other. In this way, we reduced the probability of interaction between seeds. The period when woody species were sown (September, late winter), is when most of these species start to germinate in central Chile (Figueroa et al., 2004b).

After woody species were sown, we started to apply precipitation treatments. Precipitation regimes were simulated by irrigation, providing two different quantities of water (245 vs 534 mm), each to half of the pots (Table S1). Two typical climatic areas of this Mediterranean-type region were simulated: a dry interior area and a wet coastal one. Historical monthly precipitation averages from the DGA (Dirección General de Aguas de Chile) were used to establish the precipitation regimes (Table S1) for two areas in central Chile: Lago Peñuelas (33°09′S-71°32′W) in a coastal area (wetter regime) and the city of Santiago (33°27′S-70°40′W) in the central valley (drier regime). The records used, which covered the last 20 years, were for the months when herb species achieve the greatest biomass and woody species germinate and recruit in central Chile. Because of the unpredictability of rainfall in a determined month, and the possibility that a high level of monthly rainfall exceeds the water requirements for the drier regime, we simulated precipitation with a two-month lag, given that precipitation levels decrease toward the summer. For example, historical precipitation in September was simulated in November. In this way, we obtained a determined rainfall level (especially for the drier condition), by adding water in addition to natural precipitation. Natural precipitation was checked after each rainfall event in the nearest weather station. Irrigation was applied mainly in the afternoon or at night to simulate temperature conditions during typical rainfall episodes. Irrigation was applied one or two days per week, providing between 5 and 20 mm of water with each application until reaching the simulated precipitation planned for that month.

2.3. Measurement of variables

To evaluate the performance of woody species we used the final recruitment per species observed in March 2016 (counting the number of living seedlings). We also calculated species richness in the final recruitment. All these woody species can be present in a same locality through the central region of Chile, and hence evaluation of species richness in this experiment may be useful to explore the potential effect of herb species on woody species richness. Final recruitment (March) represented the performance of woody species after considering the effects of living and dead herbs, as all the herb species died during the summer.

We also evaluated the performance of herbs per pot in terms of height and cover. Cover per pot was measured by visual estimation and height by a ruler. For this estimation, the pots were divided conceptually into quarters, so that four values were obtained per pot. These values were averaged to provide an average per pot. Data from November, when herbs reached maximum growth, were used to describe the performance of the herbs. We calculated an index of herb volume per pot, multiplying cover as area (m^2) by height (m), in order to get a proxy of herb biomass as indicator of herb performance.

Photosynthetically active radiation (PAR) was determined per pot with an Apogee BQM-1 Quantum PAR meter at the soil surface level on a cloudless day in early December 2015. Finally, the soil water content (SWC) of all the pots was measured with a Campbell Hydrosense II Time Domain Reflectometer (TDR), and a 12-cm deep probe sensor in randomly selected positions. SWC was measured once 4 days after an irrigation in December 2015 and again March 2016.

2.4. Statistical analyses

Our main goal in this study was to determine if different herb species have similar or different effects on the recruitment of woody species and if these effects depend on environmental conditions of shade and precipitation. To do this, we performed multi-factorial analyses to evaluate and describe the effects of herb species, shade and irrigation, and the statistical interactions among factors, on species richness and woody species recruitment. These data correspond to non-normal variables, which were analyzed through generalized linear models (GLM) and LSD Fisher post-hoc tests ($P < 0.05$). We used a negative binomial distribution and a log link function for species richness and number of seedlings alive from the woody species. We also tested if experimental treatments produced different environmental conditions (PAR, SWC and herb volume) through factorial analyses.

Variables that satisfied normality (Shapiro-Wilk test) (herb volume and soil water content) were evaluated by a GLM using a Gaussian distribution and Identity link function ($P < 0.05$), while PAR (which was not normally distributed) was evaluated by a GLM using a Gamma distribution and an Inverse link function.

Models were fitted in R 3.3.1, with package stats (RStudio Team, 2016) and function “glm” for Gaussian and Gamma GLM, and package MASS (Venables and Ripley, 2002) and function “glm.nb” for negative binomial GLMs. Post-hoc tests were made with package agricolae (De Mendiburu, 2014).

3. Results

3.1. Species richness in recruitment

Recruitment was generally low. There was no recruitment in 159 of the 360 pots, although in 86 of these 159 pots there was initial germination and then mortality. The maximum value of recruitment per pot was 23.34% (67 seedlings) and 30% of pots had less than 4% of recruitment.

The species richness of woody seedlings at the end of the experiment was significantly higher in the wetter treatment than the drier one, and higher with shading than without shade (Table 1, Fig. 1). The effect of specific herb species on woody species richness depended on the shade treatment, but not on the irrigation treatment. No herb species had a significant effect on species richness in the open condition, with no significant difference in woody species richness between the control pots and the pots with herb species (Table 1, Fig. 1). In contrast, some herb species had significant effects under shade. The native species *H. aromaticum* and *P. brachyantha* had negative effects, while the other native species produced no significant effect (Fig. 1). In contrast, the four exotic herb species negatively affected species richness (Fig. 1).

3.2. Recruitment of specific woody species

We observed significant positive effects of shading on all species (Table 1, Fig. 2). On the other hand, irrigation had significant positive effects on the recruitment of five woody species (*L. caustica, M. boaria. P. chilensis, P. mitiqui* and *S. polygamus*) (Table 1, Fig. 2). Recruitment of all woody species varied significantly among herb species treatments (Table 1). Comparing the recruitment between the control and every herb species treatment, we observed that herb species had positive, negative and neutral effects on woody species depending on the woody species and environmental conditions (Table 2, Fig. 2). In open and drier conditions, we could evaluate interactions between five herb species and *A. caven* and one interaction between an herb species and *S. candolleana* (Table 2). In all these cases no significant effect of herb species was observed (Table 2). In spite of the rest of woody species germinated in many pots, they were not able to recruit under these experimental conditions, and hence it was not possible to statistically evaluate the interaction with herb species. Under open and wetter conditions, we could evaluate the effect of eight herb species on *A. caven* and the effect of two herb species on *S. candolleana* (Table 2). Six herb species had neutral effects on *A. caven*, while two herb species had negative effects. In contrast, no herb species had a significant effect on *S. candolleana* (Table 2). Under shaded and drier conditions, herb species-specific effects varied between negative, neutral and positive on two woody species, on another five woody species the effects were negative or neutral, and the effects of all herb species were negative on only two woody species (Table 2). In this case, herb species-specific effects were predominantly negative, and there were more neutral than other effects on only one woody species (Table 2). The herb species that had negative effects were mostly exotics, and the only herb species that had positive effects were natives (Table 2). Under shaded and wetter conditions, the herb species had exclusively negative effects on only one woody species, four woody species received negative and neutral effects, one woody species received negative and positive effects, one woody species received neutral and positive effects, and the three types of effect were observed on only two woody species (Table 2). In this case, the effects of herb species were also predominantly negative. The herbs that had negative effects under shaded and wetter conditions were also mostly exotics, while neutral and positive effects were mainly associated to native species (Table 2).

3.3. Environment produced by experimental treatments

The herb volume varied significantly among herb species, as well as among shade and irrigation treatments (Table S2). All two-way interactions were significant, indicating that, although volume differed among herb species globally, these differences depended on the shade and irrigation condition (Table S2). In general, the exotic species *E. moschatum* and *M. matricarioides* and the native species *P. brachyantha* and *A. calycina* had the lowest volumes, while the native species *H. aromaticum* and *M. pinnatifida* and the exotic species *E. californica* and *C. melitensis* had the highest volumes under all environmental conditions (Fig. S1). In general, herb volume was higher under shade and the wetter treatments (Fig. S1).

PAR differed significantly among shade treatments and herb species, and the interaction between these two factors was significant, indicating that differences in PAR among herb species depended on the shade condition (Table S2, Fig. S2). Also, PAR was significantly higher under open than shaded conditions in all herb species treatments (Fig. S2). On the other hand, in most of the cases, PAR was significantly reduced by herb species, which occurred in both irrigation treatments (Fig. S2).

Soil water content (SWC) was higher at the end of spring (December) than at the end of summer (March) in all irrigation, shade and herb treatments (Fig. S3). Shade and irrigation significantly increased SWC in both seasons (Table S2, Fig. S3), while SWC varied significantly among herb treatments only in the spring (Table S2), since

Table 1

Statistical results (GLM analyses, negative binomial distribution, and log link function) for final recruitment in terms of woody species richness and seedling recruitment per woody species, in response to shade (S), irrigation (I), herb species (HS) and their interactions. Values correspond to $\chi 2$. Significance of the effects are denoted by *P < 0.05, **P < 0.01, ***P < 0.001.

Dependent Variable	Shade	Irrigation	Herb Species	S × I	S × HS	I × HS	S × I × HS
Species richness	915.02***	17.95***	87.3***	3.42	23.32**	8.98	7.28
A. caven (Ac)	70.90***	3.12	57.17***	3.23	21.65**	10.07	7.48
K. oblonga (Ko)	129.38***	0.01	62.54***	0	0	9.19	0
L. caustica (Lc)	295.48***	19.17***	38.30***	0	0	20.64**	0
M. boaria (Mb)	641.18***	21.01***	18.51*	0	0	6.48	0
P. chilensis (Pc)	410.72***	9.43**	71.73***	0	0	8.77	0
P. mitiqui (Pm)	94.64***	4.59*	58.32***	0	0	23.23**	0
Q. saponaria (Qs)	206.57***	1.11	49.44***	0	0	14	0
S. candolleana (Sc)	161.10***	2.44	73.79***	0.2	12.7	11.75	0.99
S. polygamus (Sp)	269.95***	4.05*	31.73***	0	0	16.90*	0

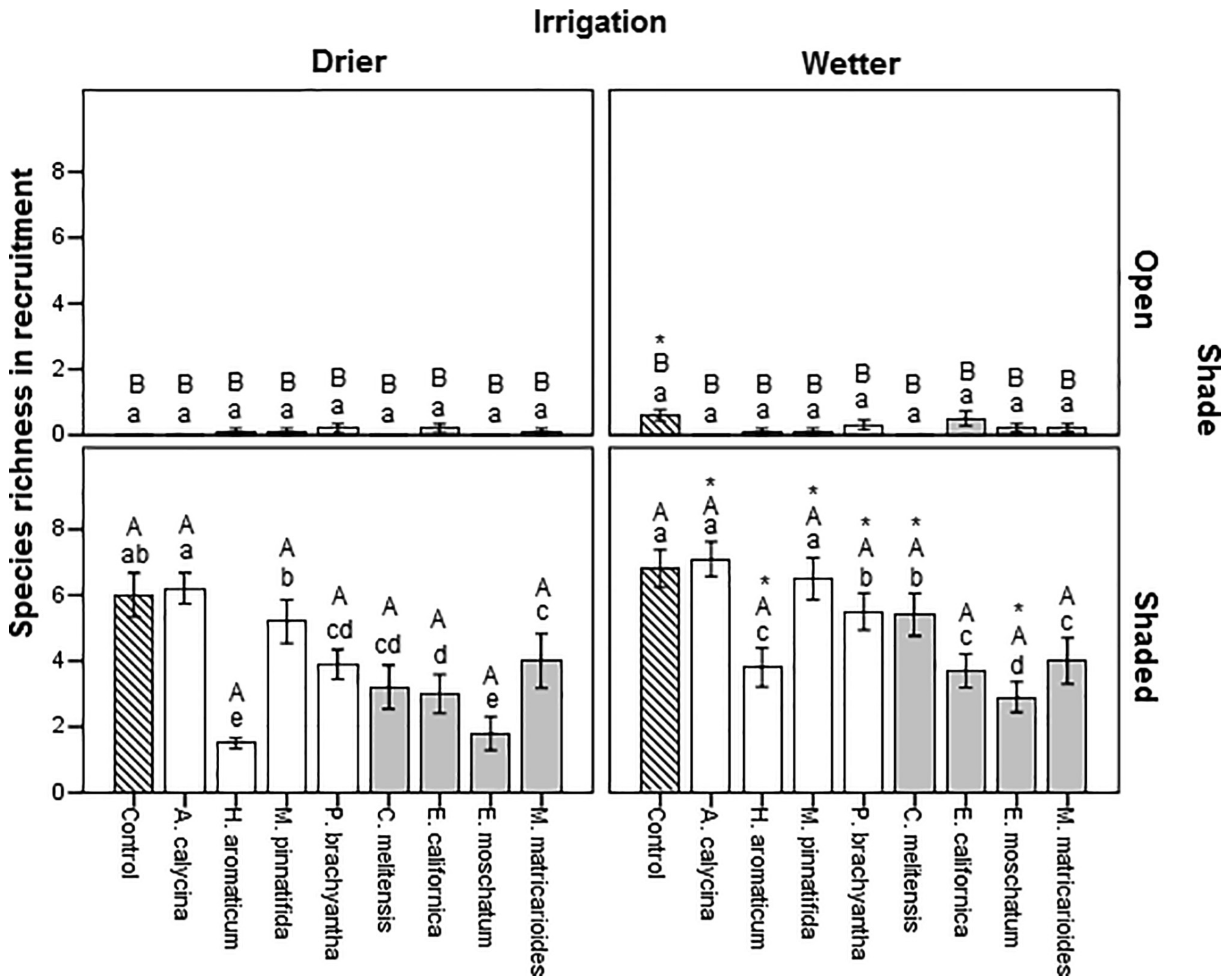

Fig. 1. Recruitment of woody species richness (mean ± 1 S.E.) with all herb species, and irrigation, and shade treatments. White and gray bars are native and exotic species, respectively. Controls (without herbs) are in hatched bars. Different lower-case letters indicate statistical differences (GLM, LSD post-hoc test, $P < 0.05$) between herb species for a single irrigation and shade treatment. Different upper-case letters indicate statistical differences (GLM, LSD post-hoc test, $P < 0.05$) between shade treatments for single herb species and irrigation treatment. Asterisks denote significant differences between irrigation treatments in a single herb species and shade treatment.

in summer SWC did not differ significantly among any herb species and the control (Fig. S3). The interaction between shade and herb species was significant in spring, indicating that the effect of herb species on SWC depended on shade conditions (Table S2). Differences in SWC among herb species were stronger under shaded conditions in both irrigation treatments (Fig. S3).

4. Discussion

Our results indicate that different herb species have distinct effects on woody species recruitment, either when species richness or abundance of particular woody species was considered. However, the level of variability of the effects among herb species depended on environmental conditions. In terms of woody species richness, variability in the effects of herbs depended mainly on shade conditions as the effects of herbs were the same between the two irrigation conditions. When particular woody species were analyzed, variability in the effects of herbs also depended on shade rather than irrigation. The variability of effects among herb species also depended on the woody species. All the effects of herbs observed in this study could have occurred during the period when the herbs were alive, as well as one or two months after they had died, through remaining dry organic matter.

The effects of herb species on the richness of woody species in our experiment were the same in the two irrigation treatments. However, some differences emerged between irrigation treatments when we considered woody species separately. The effects of herb species on *A. caven* and *S. candolleana* under the open condition were not the same in the two irrigation treatments. Similarly, under the shaded condition, the effects of herb species on all woody species, with the exception of *S. candolleana,* differed between the two irrigation treatments. This suggests that differences in precipitation among localities in central Chile may modulate the effect of herb species on recruitment of specific woody species. Interestingly, the effects of herbs on woody recruitment were more positive in the wetter treatment than in the drier one. In our case, the wetter experimental condition should be considered as an intermediate level of stress for the studied woody species (a mild environment sensu Holmgren and Scheffer, 2010), regarding the summer drought that affects all woody species in central Chile, which was also simulated in our experiment. These results agree with other studies that document how positive plant-plant interactions are more common at intermediate levels on the stress gradient (Maestre et al., 2009, Holmgren and Scheffer, 2010). However, our results suggest that this shift is not always related to the improvement in soil moisture produced by the canopy, in our case the herb canopy.

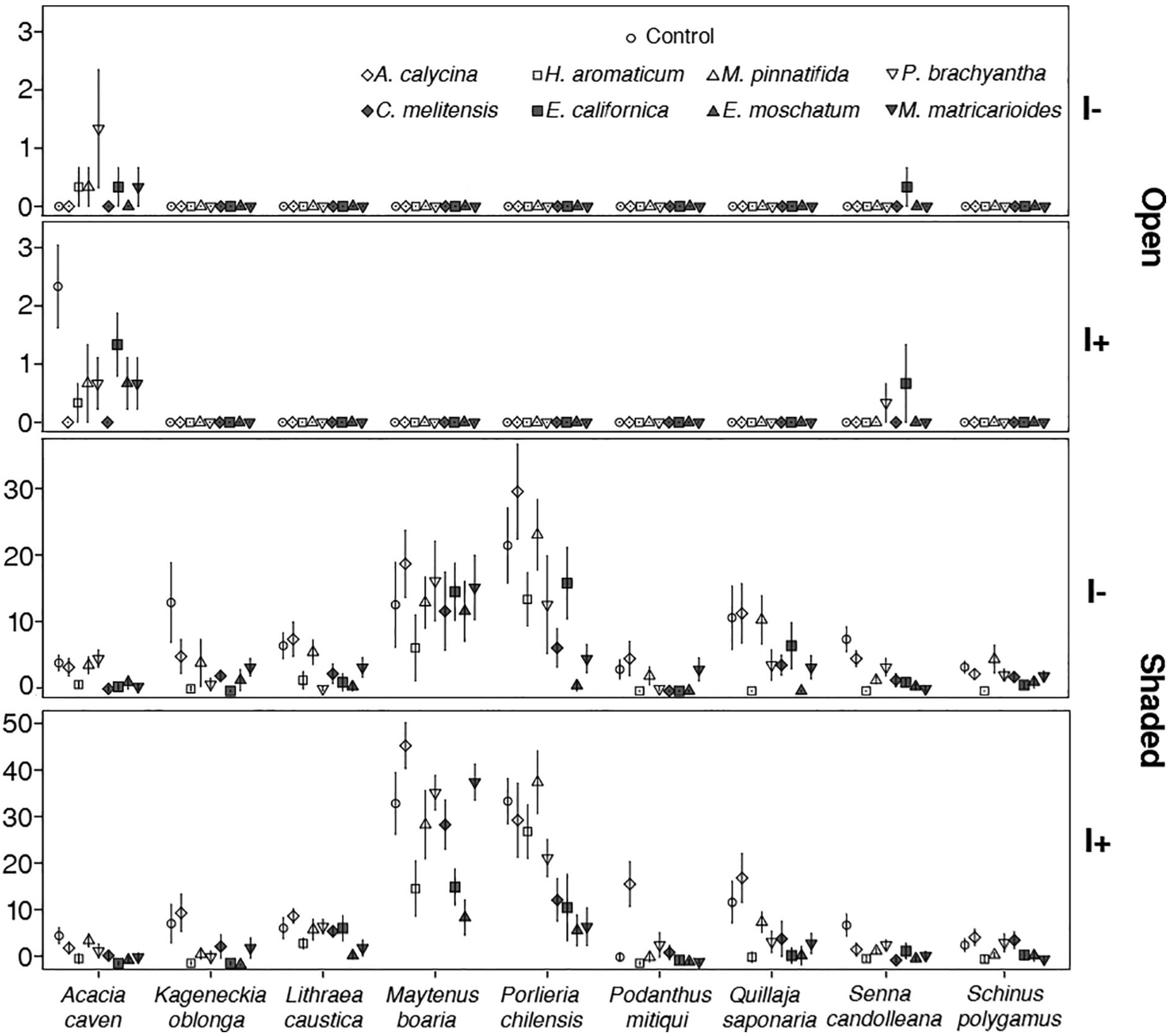

Fig. 2. Percentages (%) of recruitment (Y-axis) of each woody species (X-axis) on each treatment of herb species (open symbols: native herb species, black symbols: exotic herb species), Irrigation (I−: drier, I+: wetter), and shade (open and shaded). Note that Y-axis has different scales for different shade treatments.

The two shade conditions were associated with very different results in terms of the effects of herb species on species richness and recruitment of specific woody species. However, these distinct results were not due to different herb effects but rather were due to the inability of woody species to recruit without shade, with or without herbs, so that no effective interaction occurred. The absence or very low level of recruitment of woody species in open sites is common in central Chile, although we expected to observe better recruitment under wetter conditions (Fuentes et al., 1984; Armesto and Pickett, 1985; Holmgren et al., 2006; Fuentes-Castillo et al., 2012; Becerra and Montenegro, 2013). This suggests that even relatively rainy conditions were not high enough to achieve recruitment in many woody species in open sites, and that, probably, the shade is a more important factor than winter precipitation for recruitment of these species in Central Chile. Nevertheless, at least in terms of woody species richness, our results agree with other studies that document how the shade provided by woody cover influence interactions between herbs and woody seedlings (Bush and Auken; 1990; Pages and Michalet, 2003; Kunstler et al., 2006; Cuesta et al., 2010; Caldeira et al., 2014).

Our results might have been affected by some experimental limitations. For instance, some interaction between seeds or seedlings might have occurred in some pots. However, we believe that any such effect would have been negligible since seeds were sown maximizing the space between them. Similarly, the maximum number of surviving seedlings per plot was at the most only 67, and fewer than 1.6% of the pots had more than 50 seedlings. Hence, the surface of the pots (1 m^2) was sufficient to allow an area larger than 10 × 10 cm per seedling in the pots with higher abundance. Furthermore, the experimental period was short enough as to avoid that seedlings exceed 20 cm tall, avoiding above-ground interactions between them.

In this study we explored how the selected experimental factors produced different biotic and abiotic conditions (herb volume, PAR, SWC) that may have a role in the effect of these factors on recruitment of woody species, although other variables may also be influencing recruitment (allelopathy, soil chemistry, nutrients, etc). Different herb species reached distinct volumes, however, the species with the greatest volume were not associated with the lowest levels of recruitment of specific woody species or species richness. For example, *E. moschatum* was the herb species with lowest values of herb volume, but it was not associated to high values of recruitment in species richness nor specific woody species. Also, C. melitensis produced high values of herb volume, but it was not associated to the low est values in recruitment. While other studies have documented that denser herbaceous layers have more detrimental effects on seedlings (Esteso-Martínez et al., 2006; Loranger et al., 2017), in our study the distinct effects of herb species on woody species recruitment did not seem to be related to the

Table 2
Effects of exotic and native herb species on recruitment of woody species by each combination of irrigation and shade treatment. The numbers indicate the number of herb species with the corresponding effect: negative (−), if recruitment of the woody species was significantly lower than in the control; neutral (0), with no statistical difference with the control; and positive (+), if recruitment was significantly higher with the herb species than in the control. Cases in which recruitment was null in control as well as with the herb species are indicated as "no interaction" (ni) (GLM, LSD post-hoc test, $P < 0.05$). The names of herbs species are indicated in the methods.

	Woody species	Drier								Natives				Exotics				Wetter								Natives				Exotics			
		Ac	*Ha*	*Mp*	*Pb*	*Cm*	*Ec*	*Em*	*Mm*	ni	−	0	+	ni	−	0	+	*Ac*	*Ha*	*Mp*	*Pb*	*Cm*	*Ec*	*Em*	*Mm*	ni	−	0	+	ni	−	0	+
Open	*A. caven*	ni	0	0	0	ni	0	ni	0	1		3		2		2		−	0	0	0	−	0	0	0		1	3			1	3	
	K. oblonga	ni	ni	ni	ni	ni	ni	ni	ni	4				4				ni	ni	ni	ni	ni	ni	ni	ni	4				4			
	L. caustica	ni	ni	ni	ni	ni	ni	ni	ni	4				4				ni	ni	ni	ni	ni	ni	ni	ni	4				4			
	M. boaria	ni	ni	ni	ni	ni	ni	ni	ni	4				4				ni	ni	ni	ni	ni	ni	ni	ni	4				4			
	P. chilensis	ni	ni	ni	ni	ni	ni	ni	ni	4				4				ni	ni	ni	ni	ni	ni	ni	ni	4				4			
	P. mitiqui	ni	ni	ni	ni	ni	ni	ni	ni	4				4				ni	ni	ni	ni	ni	ni	ni	ni	4				4			
	Q. saponaria	ni	ni	ni	ni	ni	ni	ni	ni	4				4				ni	ni	ni	ni	ni	ni	ni	ni	4				4			
	S. candolleana	ni	ni	ni	ni	ni	0	ni	ni	4				3		1		ni	ni	ni	0	ni	0	ni	ni	3		1		3		1	
	S. polygamus	ni	ni	ni	ni	ni	ni	ni	ni	4				4				ni	ni	ni	ni	ni	ni	ni	ni	4				4			
Shaded	*A. caven*	0	−	0	0	−	−	−	−		1	3			4			0	−	0	−	−	−	−	−		2	2			4		
	K. oblonga	−	−	−	−	−	−	−	−		4				4			0	−	−	−	−	−	−	−		3	1			4		
	L. caustica	0	−	0	−	−	−	−	−		2	2			4			0	−	0	0	0	0	−	−		1	3			2	2	
	M. boaria	+	−	0	+	0	0	0	0		1	1	2			4		+	−	−	0	−	−	−	+		2	1	1		3		1
	P. chilensis	+	−	0	−	−	0	−	−		2	1	1		3	1		0	0	0	−	−	−	−	−		1	3			4		
	P. mitiqui	0	−	0	−	−	−	−	0		2	2			3	1		+	0	0	+	0	0	0	0			2	2			4	
	Q. saponaria	0	−	0	−	−	−	−	−		2	2			4			+	−	−	−	−	−	−	−		3		1		4		
	S. candolleana	−	−	−	−	−	−	−	−		4				4			−	−	−	−	−	−	−	−		4				4		
	S. polygamus	0	−	0	0	−	−	−	0		1	3			3	1		+	−	−	0	0	−	−	−		2	1	1		3	1	

volume of herb species. On the other hand, SWC increased in the shaded condition with *E. moschatum* and *A. calycina* in the wetter treatment, and only with *E. moschatum* in the drier treatment. Coincidentally, under the shaded and wetter conditions, *A. calycina* had several positive and almost no negative effects on recruitment of woody species, suggesting that these effects may be related to the improvement in SWC caused by this herb. Other studies have suggested that facilitation provided by herbs may be related to their role increasing soil moisture (Seifan et al., 2010; Becerra et al., 2011). Instead, although *E. moschatum* significantly increased SWC under shaded conditions, it did not enhance recruitment of any woody species. In addition, our results suggest that the negative effects of many herb species on woody species richness and the recruitment of specific woody species were not triggered by a reduction in SWC, which contrasts to several studies documenting that herbaceous vegetation reduces recruitment and regeneration of woody species through competition for soil water (Gordon et al., 1989; Sala et al., 1989; Facelli and Pickett, 1991; Davis et al., 1998; Espigares et al., 2004; Esteso-Martínez et al., 2006; Van der Waal et al., 2009; Quinteros et al., 2017). Therefore, although some herb species may be producing positive effects on recruitment through increased soil moisture, water-mediated competition or facilitation mechanisms are not important enough as to modulate different effects of herb species on recruitment of woody species. On the other hand, herbs generally reduced PAR, although the degree of reduction varied among herb species. Although herb species reducing more strongly PAR (*C. melitensis, E. californica, M. matricarioides*) did not reduce more pronouncedly species richness recruiting nor the recruitment of some woody species, in shaded conditions recruitment of four woody species (*A. caven, S. candolleana, K. oblonga, Q. saponaria*) was significantly reduced by these herb species. This suggests that reduction in PAR may be a mechanism by which herb species affect the recruitment of particular woody species, which agree with other studies that document competition between herbs and woody seedlings for light (Davis et al., 1998, 1999, Rey Benayas et al., 2002; Setterfield et al., 2018). However, in our study this would not be generalized among woody species.

Although only four native and four exotic herb species were evaluated, our results show that exotic herb species tend to have negative effects more often than native species. Native species had a similar number of neutral and negative effects while exotic herb species mainly had significant negative effects on the recruitment of woody species. These differences in the effects of native and exotic herbs were observed in both irrigation treatments. Exotic species like *C. melitensis* and *E. californica* have been widely documented as strongly invasive (Leger and Rice, 2003; Callaway et al., 2006; Moroney and Rundel, 2013), but their detrimental effects on woody regeneration have not been heavily studied (Gómez-González et al., 2009). The effects of the other two exotic species and the native ones had not been explored yet. According to our results, exotic herbs may produce negative effects on native woody species more frequently than do native herbs. However, there is the need to research about the impact of a greater number of native and exotic herbs to elucidate if this is an ecological pattern.

5. Conclusions

Different herb species had distinct effects on the recruitment of specific woody species, and woody species richness. The variation in effects depended on the environmental conditions and specific woody species. Notwithstanding, herb species mostly had negative or neutral effects on woody species recruitment, and only under intermediate level of abiotic stress some positive effects were observed. Our results suggest that herb biomass and soil water content were not probably involved in the distinct effects of herbs, while PAR might have a role in this variability of effects in some woody species. The fact that herb-woody species interactions are very specific suggests that management in terms of herb control should be species-specific for both woody and herb species, and dependent on environmental conditions.

CRediT authorship contribution statement

Nicolás Velasco: Investigation, Formal analysis, Writing - original draft. **Pablo I. Becerra:** Conceptualization, Methodology, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.117864.

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