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Do heat and smoke increase emergence of exotic and native plants in the matorral of central Chile?

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ABSTRACT

We studied the effect of heat shock and wood-fueled smoke on the emergence of native and exotic plant species in soil samples obtained in an evergreen shrubland of central Chile, located on the eastern foothills of the Coastal Range of Lampa. Immediately after collection samples were dried and stored under laboratory condition. For each two transect, 10 samples were randomly chosen, and one of the following treatments was applied: 1) Heat-shock treatment. 2) Plant-produced smoke treatment. 3) Combined heat-and-smoke treatment. 4) Control, corresponding to samples not subjected to treatment. Twenty-three species, representing 12 families, emerged from the soil samples. The best-represented families were Poaceae and Asteraceae. All of the emerged species were herbs, 21 were annuals, and 14 were exotic to Chile. Fire-related triggers used in this study did not increase the emergence and/or abundance of exotic species with respect to natives in soil samples. Interestingly, this study provides evidence that heat-shock can increase the emergence of native herbs.

1. Introduction

Central Chile harbors a diverse exotic flora, principally of Eurasian origin, which represents at least 20% of the flora in this region (Montenegro et al., 1991; Arroyo et al., 2000; Figueroa et al., 2004b). The sclerophyllous evergreen shrubland (= matorral) is the dominant vegetation type in central Chile, and is the most invaded plant association in the country (Montenegro et al., 1991; Figueroa et al., 2004b). Originally, the matorral probably covered the majority of central Chile, with the most dense and continuous forest covering the mesic sites (Aronson et al., 1998). Currently, it is characterized by clumps of

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trees and shrubs, surrounded by the herbaceous stratum dominated by exotic annual species (Gulmon, 1977; Keeley and Johnson, 1977; Fuentes et al., 1983; Groves, 1986).

The factors that facilitate the expansion of exotic species in the matorral remain unknown (Figueroa et al., 2004b). Exotic plant invasions are frequently associated with disturbance in plant communities (Hobbs, 2000). Fire is among the most important disturbances in central Chile (Montenegro et al., 2002), and during the last centuries, central Chilean shrublands have withstood large changes due to the intensive use of fire (Fuentes, 1990; Aronson et al., 1998; Holmgren, 2002; Montenegro et al., 2002). However, it has not been clarified how fire affects the richness, distribution and dominance of exotic and native plants in the matorral (Arroyo et al., 2000; Holmgren et al., 2000; Figueroa et al., 2004b). In this region, fires are almost exclusively originated by humans, and occur during the dry summer months (Montenegro et al., 2002). In some regions with Mediterranean-type climate, fire facilitates the expansion of exotic plant species in detriment of native ones (Trabaud, 1991), but in California fire facilitates the regeneration and dominance of native plant species over the exotics (Keeley et al., 2003). For central Chile the effects of fire on invasibility of the matorral are not clear because the evidence is contradictory (Figueroa et al., 2004b). For instance, Avila et al. (1981) reported that fire increased the abundance of naturalized herbs, same as Sax (2002) who showed that fire favored exotic species richness and cover over native species in a xeric matorral. In contrast, Keeley and Johnson (1977) and Holmgren et al. (2000) reported that fire did not have differential effects on the relative abundance and composition of exotic and native herbs in the Chilean matorral.

Recurring man-made fires are historically recent in central Chile (Montenegro et al., 2002), and therefore native plants are not expected to display adaptations to fire (Muñoz and Fuentes, 1989; Montenegro et al., 2002; Gómez-González et al., 2008). In contrast, exotic species, many of which come from regions where fire is natural or is a millenary practice, may have adaptations to respond to triggers related with it, showing an advantage to recruit rapidly after fires (Naveh, 1975; di Castri, 1989). Many species in Mediterranean-type climate regions recruit from soil-stored seeds that require fire as a trigger for germination (Gill, 1981; Keeley, 1991; Enright et al., 1997; Enright and Kintrup, 2001; Hill and French, 2003). Heat, smoke and their combination are important germination cues in responses to fire (Clarke and French, 2005; Thomas et al., 2007). For example, heat acts as important trigger for breaking seed dormancy in a large number of plants from several Mediterranean-type regions (Keeley, 1995; Vázquez-Yanes and Orozco-Segovia, 1998). Additionally, wood-fueled smoke promotes seed germination in a number of Mediterranean-type environments (Lloyd et al., 2000; Read et al., 2000; Enright and Kintrup, 2001). In other studies, heat shock and smoke have interacted to affect germination (Thomas et al., 2007). However, with the exception of native woody plants of central Chile (Muñoz and Fuentes, 1989; Gómez-González et al., 2008), germination cues related to fire (i.e., heat and smoke) have not been experimentally evaluated as putative causes for the expansion of exotic and native plant species in the matorral. The objective of this study is to compare the effect of heat shock, plant-originated smoke and their combination on the emergence of native and exotic plant species from soil samples obtained in the matorral of central Chile.

2. Materials and methods

2.1. Study site

Soil samples were collected in Lampa (33°10′S, 70°50′W), which is located on the eastern foothills of the Coastal Range. Lampa has a Mediterranean-type climate, with a cool rainy winter (May–September) and a summer drought period of 6–7 months. Mean annual precipitation is ca. 300 mm, falling as rain. Temperatures are moderate, rarely falling below 0 °C.

Vegetation at the study site was dominated by an evergreen matorral with a diverse herbaceous stratum dominated by annual species. Among the dominant woody species, the most frequent were native shrubs such as *Lithrea caustica*, *Baccharis* spp. and *Colliguaja odorifera*. Among dominant herbaceous species were exotic forbs such as *Anthriscus caucalis* and *Erodium* spp., and annual grasses such as *Vulpia* spp. The native annual herbs *Bromus berteroanus* and *Oxalis micrantha*, as well as native perennials of the genus *Gamochaeta*, were dominant in sheltered microsites less disturbed by grazing horses. In Lampa, small-size fires occur annually, although no quantitative records exist.

2.2. Soil collection and treatments applied

Soil samples were collected in an area of ca. 5 ha. During February 2003, after the peak of the seed-dispersal period and when fires are more frequent (CONAF, 2003), two linear transects 200-m long each were placed in random directions. At each transect, a soil sample was obtained every 5 m. Soil samples were taken with a 5-cm-diameter cylindrical metal bore, dug to 5 cm depth (volume of soil was ca. 100 cm^3). We focused on the superficial stratum of the soil seed bank (0–5 cm depth) because this horizon generally holds most of the viable seeds (Buhler, 1995; Figueroa et al., 2004a). The 40 samples taken at each transect were maintained separate to analyze whether variation was random within the site.

Immediately after collection, all samples were dried and stored under laboratory conditions for 2 weeks. For each transect, 10 samples were randomly chosen, and one of the following treatments was applied: 1) Heat-shock treatment, which was performed by placing soil samples in paper trays and heating them in a drying oven at 100 °C for 10 min. The temperature and the duration applied were chosen to simulate a short hot burn, which is the typical in the matorral of central Chile (Muñoz and Fuentes, 1989; Gómez-González and Cavieres, in press). 2) Wood-fueled smoke treatment, which was applied in a sealed 1.7 × 1.7 × 0.3 m polyethylene chamber connected to a smoke source generated in a 50-L metal drum through combustion of plant wood for 30 min. The combusted material consisted of a mixture of dry litter and green foliage of *L. caustica* and *Quillaja saponaria* (50:50), species chosen on account of their dominance in a typical matorral. For further detail on the smoke treatment see Gómez-González et al. (2008). 3) Combined heat-and-smoke treatment, where the samples were submitted to heat shock as described previously and then exposed to the smoke treatment

with an elapsed time of 4 hours between treatments. 4) Control treatment, which corresponded to samples not subjected to treatment. Thus, these treatments allowed us to separate the effects of heat, smoke and their combination as germination cues for native and exotic species in the central Chilean matorral, affecting their emergence from the soil seed bank.

2.3. Germination essays

Seedling emergence from the easily germinating soil seed bank was investigated in all the soil samples exposed to the three treatments and the control. The study was carried out in a greenhouse with 12:12 photoperiod, PAR of ca. 500 μmol m^{-2} s^{-1}, and mean temperature of ca. 25 °C in the summer and ca. 15 °C during the winter. Each soil sample was placed over a 2-cm deep coarse sand layer in ca. 500-cm^3 plastic trays. After that, soil samples were watered at field capacity, and checked daily for emergence of seedlings over a 90-day period. Tray positions in the glasshouse were randomized every 15 days. After 90 days, there was almost no new germination in all soil samples, and thus the number of germinating seeds per species per m^2 of soil was determined for each treatment and control. Dormant seeds (i.e., those seeds where dormancy was not broken by heat, smoke or their combination), were not recorded. In cases where identification of seedlings at the species level was dubious, they were grown until flowering and then identified. Nomenclature follows Marticorena and Quezada (1985).

2.4. Data analyses

The effect of heat, smoke, and their combination on the total number of species emerged, the number of native and the number exotic species emerged per sample, were modeled by fitting Generalized Linear Mixed Models (GLMMs). According to the sample design, the experimental treatments were blocked on transects. The experimental treatments (heat, smoke, their combination and the control) were considered a fixed factor whereas the blocking factor created by the transects was considered a random factor. The most appropriate error distribution and link function were chosen a priori based on the expected properties of the response variables (Quinn and Keough, 2002). For example, species richness data were analyzed using a Poisson error distribution and a log link function as suggested by Quinn and Keough (2002). To assess differences on the total density of native and exotics emerged, the raw seed densities were transformed to $\ln(x+1)$ and the GLMM was fitted with a normal distribution for the response variable and identity as the link function. Further, this last model was also used to assess specific responses to treatments for the most abundant native and exotic species emerged. We considered that treatments significantly affected the response variable when $P < 0.05$. All statistical analyses were done with R (R-Development Core Team, 2008).

3. Results

Twenty-three species, representing 12 families, emerged from the soil samples (Table 1). The most abundant families were

Poaceae and Asteraceae. All of the emerged species were herbs, and approximately 60% (14 species) were exotic to Chile. Only for one taxon of the genus *Euphorbia* the species and its origin could not be determined.

Considering all the treatments applied, the species that emerged with the highest abundance were of exotic origin, such as the annual grass *Vulpia bromoides* and the forbs *Erodium cicutarium* and *Erodium bothrys* (Table 1). The native species that emerged with the highest abundance in all treatments were the annual grass *B. berteroanus* and the forbs *Bowlesia incana* and *Soliva sessile* (Table 1).

Two native species and four exotics showed differences in their emergence after the application of fire-related germination cues. The native grass *B. berteroanus* significantly increased its emergence compared to the control after the heat-shock treatment and after exposure of both, heat and smoke (Table 1). In contrast, the native *O. micrantha* was negatively affected by the smoke and heat + smoke treatments (Table 1). Among the exotic species, while the forb *E. cicutarium* significantly decreased its emergence after the heat treatment, its congener *Erodium moschatum* significantly increased its emergence after the heat treatment (Table 1). The exotic grass *V. bromoides* also significantly increased its emergence after the heat treatment and decreased its emergence after the smoke treatments when compared to the control. The exotic annual grass *Poa anua* significantly increased its emergence after the smoke and heat + smoke treatment (Table 1). In the remaining 17 species recorded, of which ca. 75% were exotic, seedling emergence was not significantly affected by any of the treatments (Table 1).

Heat significantly increased the mean number of species emerged per sample compared to the control (Wald $X^2_{(3)} = 11.86$, $P = 0.008$). However, smoke alone and smoke combined with heat did not change the mean number of species emerged with respect to the control. Among the exotics, the mean number of species that emerged from soil samples did not change significantly with respect to the control for any of the treatments applied (Wald $X^2_{(3)} = 4.09$, $P = 0.25$; Fig. 1). In contrast, heat, and smoke combined with heat significantly increased native species richness per sample compared to the control (Wald $X^2_{(3)} = 14.89$, $P = 0.002$), although this increase was, on average, on one species (Fig. 1).

Heat and heat + smoke significantly decreased the density of exotic seedlings emerged in comparison with the control (Wald $X^2_{(3)} = 10.52$, $P = 0.015$; Fig. 2). In contrast, heat and heat + smoke increased the mean density of native plants emerged by about double that in the control (Wald $X^2_{(3)} = 14.96$, $P = 0.002$; Fig. 2).

4. Discussion

The fire-associated triggers analyzed in this study (heat, smoke, and combination of both), did not increase the emergence of exotic species over that of native ones in soil samples from a Chilean matorral. Quite the opposite, this work provides evidence that heat-shock can increase the emergence of native herbs. Indeed, heat-shock promoted the emergence of one of the most abundant native herbs in the study site, which is also very common in the Chilean

Table 1 – Mean plant density (Number emerged seedlings/m^2) with regard to different treatments applied to soil samples from central Chile matorral. In parentheses is indicated ±1 standard error. Nd=Not determined. P values are from GLMM (see Methods). Responses compared to the control treatment: 1: promoted by heat; 2: promoted by smoke; 3: promoted by heat and smoke combined; 4: inhibited by heat; 5: inhibited by smoke; 6: inhibited by heat and smoke combined; -: indifferent. All the species are herbs. All the species are annual except *Hypochaeris glabra* (mainly annual) and *Leontodon saxtilis* (perennial).

Species	Origin	Control	Heat	Smoke	Heat-Smoke	P	Responses
Affected by fire cues							
Bromus berteroanus	Native	88 (26)[a]	210 (40)[b]	25 (12)[a]	195 (54)[b]	0.01	1, 3
Erodium cicutarium	Exotic	765 (164)[a]	255 (78)[b]	583 (58)[ab]	600 (130)[ab]	0.002	4
Vulpia bromoides	Exotic	605 (69)[a]	853 (108)[b]	390 (61)[c]	585 (58)[a]	0.001	1, 5
Oxalis micrantha	Native	23 (13)[a]	58 (25)[a]	3 (3)[b]	0[b]	0.005	5, 6
Poa anua	Exotic	8 (5)[a]	35 (10)[a]	120 (48)[b]	100 (20)[b]	0.001	2, 3
Erodium moschatum	Exotic	33 (18)[a]	255 (78)[b]	55 (25)[a]	85 (60)[a]	0.001	1
Indifferent							
Bowlesia incana	Native	55 (30)	63 (23)	90 (29)	130 (36)	0.05	–
Soliva sessile	Native	55 (30)	63 (24)	90 (29)	130 (36)	0.05	–
Amsinkia hispida	Native	0	3 (3)	0	10 (10)	0.6	–
Gamochaeta coarctata	Native	0	0	5 (5)	3 (3)	0.6	–
Juncus bufonius	Native	0	3 (3)	0	0	0.4	–
Pectocarya linearis	Native	0	0	0	3 (3)	0.4	–
Antriscus caucalis	Exotic	8 (5)	5 (3)	0	3 (3)	0.5	–
Aphanes arvensis	Exotic	0	0	8 (8)	18 (18)	0.6	–
Avena barbata	Exotic	5 (3)	13 (13)	25 (17)	13 (9)	0.5	–
Erodium bothrys	Exotic	378 (125)	478 (173)	568 (157)	238 (88)	0.4	–
Galium aparine	Exotic	3 (3)	0	8 (8)	0	0.6	–
Hypochaeris glabra	Exotic	0	3 (3)	0	0	0.4	–
Leontodon saxtilis	Exotic	0	13 (13)	32 (18)	0	0.1	–
Lophochloa cristata	Exotic	5 (5)	45 (16)	13 (9)	23 (12)	0.2	–
Medicago polymorpha	Exotic	3 (3)	0	0	0	0.4	–
Trifolium glomeratum	Exotic	45 (13)	13 (7)	38 (15)	35 (9)	0.2	–
Euphorbia sp.	Nd	0	0	3 (3)	0	0.4	–

matorral: *B. berteroanus*. The fact that the heat treatment and heat and smoke combined increased the density of native seedlings emerged was mainly due to the enhanced germination of this native grass species. There is only one previous study dealing with the effect of heat-shock on seed germination of Chilean matorral species (Muñoz and Fuentes, 1989). However, this work was done only with native shrub species,

and reported that a heat-shock increased the germination of seeds in three out of seven species tested after 5 min at 100 °C (Muñoz and Fuentes, 1989). The fact that native herbaceous species were positively stimulated by heat, challenges current ideas about the role of fire in the germination and establishment of plant species in the matorral of central Chile (Keeley, 1995; Holmgren et al., 2000; Montenegro et al., 2002).

Heat did not significantly affect the emergence of exotic plants. However, there were contrasting responses of individual species to this fire-related cue. For example, while
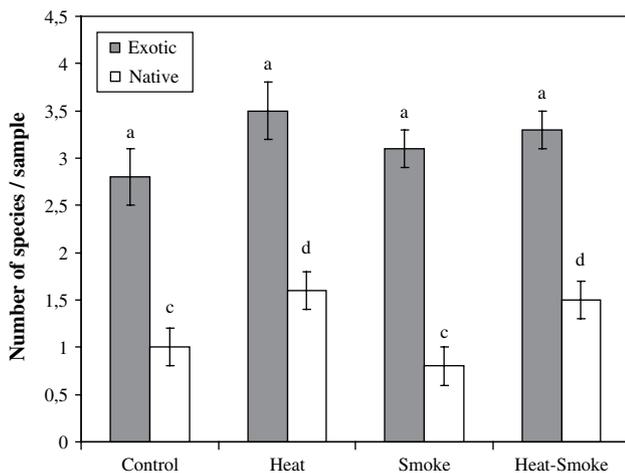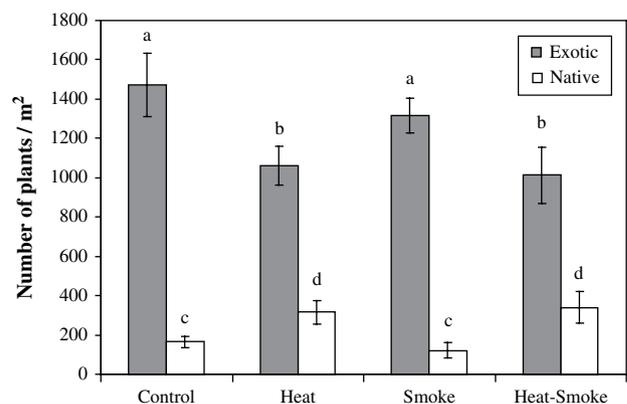

Fig. 1 – Mean exotic and native emerged species per soil sample treated with fire-related stimuli. Different letters indicate significant differences (GLMM, $P < 0.05$). Bars indicate ±1 standard error.

Fig. 2 – Native and exotic plant density (number of emerged plants/m^2) for each fire-related treatment. Different letters indicate significant differences (GLMM, $P < 0.05$). Bars indicate ±1 standard error.

E. moschatum and *V. bromoides* increased their emergence with heat, *E. cicutarium* decreased it, suggesting that these contrasting responses are producing an overall neutral effect of heat on the emergence of exotic species.

Although our study did not provide evidence that wood-fueled smoke affected species composition and total plant density, 2 species were affected in their emergence from the soil samples. On one hand, smoke stimulated the emergence of the exotic annual grass *Poa annua*. On the other hand, the emergence of the native annual *O. micrantha* was inhibited by smoke, indicating probably the toxic character of smoke in the concentrations used in this study for this species. The effect of wood-fueled smoke on seed germination in central Chile has been only studied in native woody species from the matorral, and it has been shown that smoke decreased the germination in 44% of the 18 dominant native woody species studied (Gómez-González et al., 2008). Thus, the smoke-depressed germination in some herbs and some woody native species could facilitate the post-fire colonization of aggressive exotic and native grasses such as *P. annua*, as it has been observed in the field (Segura et al., 1998). Complementarily, our results show that seeds of the majority of the annual grass species, both native and exotic, are resistant to heat-shocks of 100 °C and to wood-fueled smoke, which could be involved in the high replacement of woody species by native and exotic annuals observed in early successional post-fire sites of the Chilean matorral (Altieri and Rodríguez, 1974; Avila et al., 1981).

The role played by fire in determining the prevalence of exotic species over native ones in other Mediterranean-type ecosystems changes from region to region. In the southern France maquis fire promotes the rapid colonization of exotic terophytes, although they quickly disappear due to competition with native species (Trabaud, 1991). The California chaparral is resilient to plant invasions, even in close proximity to sources of exotic propagules (Keeley et al., 2003). Nevertheless, exotic annual species are abundant during the first year after fire, post-fire sites are free of exotic, because the closed canopy of shrubs is not a favorable site for invasive species and because chaparral fires are of high intensity, thus destroying most of the exotic seeds buried in the soil (Keeley et al., 2003). In the Cape fynbos of South Africa, however, fires favor the invasion of exotic woody plants, which dominate native vegetation and perpetuate themselves (Jones, 1963; Kruger and Bigalke, 1984; Richardson et al., 1994). In the central Chilean matorral, fire facilitates the emergence of a few common native herbs (e.g. *B. berteroanus* in this study) and the germination of colonizer woody natives (Gómez-Gonzalez et al., 2008). Therefore, post-fire colonization is a complex process that depends on many factors, especially fire intensity and frequency and alien seed source (Keeley et al., 1999; Pignatti et al., 2002; Gómez-González and Cavieres, in press).

Acknowledgments

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