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RESEARCH ARTICLE

# The effect of heat and smoke on the emergence of exotic and native seedlings in a Mediterranean fire-free matorral of central Chile

## Efecto del calor y el humo sobre la emergencia de plántulas exóticas y nativas en un matorral mediterráneo libre de fuego en Chile central

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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 matorral of central Chile that has been free of fire for decades. It is located on the eastern foothills of the Andes Range in San Carlos de Apoquindo. Immediately after collection samples were dried and stored under laboratory conditions. For each two transect, ten 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, and (4) control, corresponding to samples not subjected to treatment. Twenty-seven species, representing 13 families, emerged from the soil samples. The most abundant families were Asteraceae and Poaceae. All of the emerged species were herbaceous, and 18 species were exotic. Respect to general hypothesis, there is no evidence for the proposition that fire-free matorral has lower proportion of exotic and native species with fire-related cues than matorral with fires. Among the exotic and native, 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. Nevertheless, important species-specific responses were observed. Smoke and heat-smoke combination significantly increased the emergence of the exotic species *Anthriscus caucalis*. While smoke-related cues significantly increased the emergence of the exotic species *Avena barbata*, the emergence of the exotic *Aphanes arvensis* and the native *Bromus berteroanus* decreases. For several species our results showed inconsistent responses to fire-related cues compared to those reported in the literature. We suggest that these differences might be related with the fire-history in the populations, an important issue poorly acknowledge in the literature.

**Key words:** central Chile, exotic herb, fire, heat-shock, smoke.

## RESUMEN

Nosotros estudiamos el efecto del golpe de calor y del humo de la combustión de material leñoso sobre la emergencia de especies de plantas nativas y exóticas en muestras de suelo obtenidas en un matorral siempreverde de Chile central que ha estado libre de fuego por décadas, ubicado en el piedemonte occidental de la Cordillera de los Andes en San Carlos de Apoquindo. Las muestras fueron secadas y almacenadas en condiciones de laboratorio, inmediatamente después de las colectas. En cada uno de los dos transectos, diez muestras fueron aleatoriamente elegidas para la aplicación de los siguientes tratamientos: (1) golpe de calor, (2) humo producido por material vegetal, (3) calor y humo combinado, y (4) control, que corresponde a muestras que no fueron tratadas. Veinte y siete especies, que representan a 13 familias, emergieron de las muestras de suelo. Las familias más abundantes fueron Asteraceae y Poaceae. Todas las especies que emergieron fueron especies herbáceas y 18 fueron exóticas. Respecto a la hipótesis general, no hay evidencias para postular que el matorral libre de incendios tienen una menor proporción de especies exóticas y nativas con señales relacionadas al fuego que el matorral sometido a fuegos. El número promedio de especies que emergieron desde las muestras de suelo no cambiaron significativamente con respecto al control para ninguno de los tratamientos aplicados, ya sea entre las nativas y las exóticas. No obstante, importante respuestas especie específica fueron observadas. El humo y el humo-calor combinado incremetó significativamente la emergencia de la especie exótica *Anthriscus caucalis*. Mientras las señales relativas al humo incrementaron significativamente la emergencia de la especie exótica *Avena barbata*, la emergencia disminuyó en la exótica *Aphanes arvensis* y en la nativa *Bromus* *berteroanus*. En varias especies nuestros resultados mostraron respuestas inconsistentes a las señales relacionadas al fuego, comparadas a esas registradas en la literatura. Nosotros sugerimos que estas diferencias pueden estar relacionadas con la historia del fuego in las poblaciones, un tema importante pobremente reconocido en la literatura.

**Palabras clave:** Chile central, fuego, golpe de calor, hierbas exóticas, humo.

## INTRODUCTION

Fire is an important factor on the evolutionary history and regeneration dynamics of plant communities in many Mediterranean-type ecosystems, such as California, the southwestern Cape of Africa, southwestern Australia and the Mediterranean basin (Moreno & Oechel 1994). Plant species in these fire-prone ecosystems show a wide variety of reproductive adaptations to fire, such as fire-stimulated flowering and the presence of serotinous cones and fruits that release and disperse seeds only after fires (Rundel 1995, Lamont et al. 2000). Many species in these 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 & Kintrup 2001, Pignatti et al. 2002, Hill & French 2003), where cues related to fire such as heat, smoke or some combination of both are important (Clarke & French 2005, Thomas et al. 2007). For example, heat acts as an important trigger for breaking seed dormancy in a large number of plants from several Mediterranean-type regions (Keeley 1995, Vázquez-Yanes & Orozco-Segovia 1998, Pignatti et al. 2002). Additionally, wood-fueled smoke promotes seed germination in a number of Mediterranean-type environments (Lloyd et al. 2000, Read et al. 2000, Enright & Kintrup 2001). In other studies, heat shock and smoke have interacted to affect germination (Thomas et al. 2007).

It is well known that fire plays an important role on the invasion success of exotic species, especially in ecosystem where fire is a novel disturbance (D'Antonio 2000, Brooks et al. 2004). The role played by fire in determining the prevalence of exotic species over native in some Mediterranean-type ecosystems is highly variable. For instance, in the Mediterranean basin there is evidence that fire promotes the colonization of exotic therophytes, although they quickly disappear due to competition with native plants (Trabaud 1991). The Californian chaparral is resilient to exotic plant invasions, even in close proximity to sources of exotic propagules (Keeley et al. 2003). Although, exotic annual species may be very abundant during the first year after fire in the chaparral, later, these sites are free of exotic species because the closed canopy of shrubs is not favorable for the regeneration of the invasive species, and also because chaparral fires are of high intensity, destroying most of the exotic seeds buried in the soil (Keeley et al. 2003). However, in the Cape Fynbos of South Africa fires favor the invasion of exotic woody plants, which dominate native vegetation creating positive feedback with fire that maintain their dominance over time (Jones 1963, Kruger & Bigalke 1984, Richardson et al. 1994).

Central Chile stands out from the other Mediterranean-type climate regions of the world because lightning fires, with ignitions resulting from thunderstorms, are not present as they are in other areas with similar climates (Rundel 1998). In this region, fires occur during the dry summer months, and are almost exclusively originated by humans, becoming one of the most important disturbances in central Chile (Montenegro et al. 2002). During the last centuries, central Chile matorrals have withstood large changes due to the increasing occurrence of fire (Fuentes 1990, Aronson et al. 1998, Holmgren 2002, Montenegro et al. 2002, Figueroa et al. 2009). As recurring man-made fires are historically recent in central Chile, native plants are not expected to display adaptations to fire (Muñoz & Fuentes 1989, Montenegro et al. 2002, Gómez-González et al. 2008, Contreras et al. 2011). In contrast, exotic species, many of which come from regions where fire is natural or is a millenary practice, may present adaptations to respond to triggers related to it, showing an advantage to recruit rapidly after fires (Naveh 1975, Groves 1986, di Castri 1989). However, results of studies of the effects of fire on plant invasion in the Chilean matorral are contradictory. For instance, Sax (2002) found that alien naturalized species were favored in recently burned sites in the coastal matorral, while Holmgren et al.

(2000) found no effects of fire on alien species abundance in one matorral community of the Andean foothills. This controversy could be related to differences in fire intensity, which clearly affect the regeneration capacity of the burned vegetation (Segura et al. 1998, Gómez-González & Cavieres 2009), and to differences among sites in pre-fire seed banks, which are in turn related to the fire history of the sites themselves (Figueroa et al. 2009, Gómez-González et al. 2011).

Recent studies have experimentally evaluated the effect of fire related cues such as heat and smoke as causes for the expansion of exotic and native plant species in the matorral of central Chile, which are stored in the soil's seed bank (Figueroa et al. 2009, Gómez-González & Cavieres 2009). Contrary to expectations, fire did not increase the seedling density of exotic species over native, although some species-specific positive responses to low-intensity fire were observed on some exotic herbs (e.g., *Poa annua* L.). Indeed, fire related cues facilitate the emergence of a few common native species (*Bromus berteroanus* Colla) and the germination of colonizer native woody species (Gómez-González et al. 2008, Figueroa et al. 2009). Nevertheless, these studies have been conducted with samples taken from sites located in areas with a high recurrence of intense fires such as the coastal foothills and the central valley where the human population density is the highest along the Mediterranean-type climate zone (CONAF 2003). However, very little is known about the potential effects of fire on promoting the germination from the soil seed bank of exotic over native species in areas that have not withstood fires for several decades. As mentioned, fire history can strongly influence species response to fire (Dwire & Kauffman 2003). Hence, the aim of this study is to evaluate the effects of heat shock, plant-originated smoke, and both combined on the emergence of easily germinating native and exotic herbs from soil samples obtained in a protected matorral area of central Chile (San Carlos de Apoquindo, Santiago Province) which has been free of fire for at least the last 50 years. It is hypothesized that in matorral sites that have been free of fires for decades will have a lower proportion of exotic species with fire-related cues than matorral sites subjected to recurrent fires. To test this hypothesis, the results for this study site are compared with those reported for a site affected by small-size annual fires in central Chile (Figueroa et al. 2009).

## METHODS

### *Soil collection site*

Soil samples were collected in San Carlos de Apoquindo (33°27' S, 70°42' W), which is located in the foothills of the Andes Mountain Range, Santiago Province (Fig. 1). San Carlos has a Mediterranean-type climate, with a cool rainy winter and a summer drought period of 6 to 7 months (October to March). Mean annual precipitation is 376 mm, falling mostly as rain during winter (> 70%), with sporadic snowfall. Mean minimum temperature is 10 °C, while mean maximum temperature is 23 °C. Soil is derived from volcanic rocks, and its uppermost stratum consists of a thin layer of fine clayish sand.

Vegetation at the study site is dominated by sclerophyllous evergreen shrubs, and annual herb species. Among the dominant woody species, the most frequent are shrubs such as *Quillaja saponaria* Mol., *Lithrea caustica* Mol., *Baccharis* spp. and *Colliguaja odorifera* Mol. Among dominant herbaceous species are exotic forbs such as *Anthriscus caucalis* M. Bieb. *Erodium* spp., and annual grasses such as *Vulpia bromides* S.F. Gray, *Bromus berteroanus,* as well as native perennials of the genera *Conyza* and *Gamochaeta* (Figueroa et al. 2004).

### *Soil collection and fire-related treatments applied*

Soil samples were collected in an area characterized for vegetation not affected by fire, at least during the last 50 years, which is dominated by *Quillaja saponaria* and

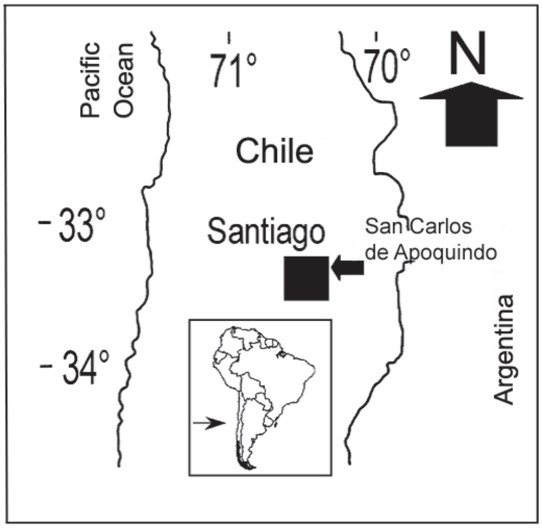

*Fig. 1:* Geographical location of the soil collection site at San Carlos de Apoquindo, Santiago Province, central Chile.

Ubicación geográfica de los sitios de colecta de suelo en San Carlos de Apoquindo, Provincia de Santiago, Chile central.

*Lithrea caustica* (Figueroa et al. 2004). During February 2003, after the peak of the seed-dispersal period and when fires are more frequent in central Chile (CONAF 2003), two linear transects, 200 m each in length, were placed in random directions. At each transect, a soil sample was obtained every five meters. Soil samples were taken with a 5 cm diameter cylindrical metal bore dug to a depth of 5 cm (volume of soil was ca. 100 $cm^3$). We focused on the surface 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. 2004). The 40 samples taken at each transect were maintained separate to analyze whether variation was random within the site. For comparative purposes, this experimental design was similar to that of recent studies undertaken in the region (Gómez-González et al. 2008, Gómez-González & Cavieres 2009, Figueroa et al. 2009) and that of other Mediterranean-type climate regions (Valbuena & Trabaud 2001).

Immediately after collection, all samples were dried and stored under laboratory conditions for two weeks. Of each transect, ten samples were randomly chosen, and one of the following treatments was applied: (1) Heat-shock treatment, 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 reproduce a hot burn for a short time, which has been recorded in the matorral of central Chile (Muñoz & Fuentes 1989). (2) Wood-fueled smoke treatment, applied in a sealed 1.7 x 1.7 x 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 *Lithrea caustica* and *Quillaja saponaria* (50:50), species chosen on account of their dominance in chosen sites in San Carlos. (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 four hours between treatments. (4) Control treatment, corresponding to samples not subjected to treatment. These treatments were applied to assess the effects of heat, smoke or a combination of both on the emergence of native and exotic species.

### *Germination essays*

Seedling emergence from the 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. Soil samples were later watered at field capacity and additional irrigation of the soil samples was performed daily. Soil samples were 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 seedling emerged per species per $m^2$ of soil was determined for each treatment and control. The seeds which were dormancy or unviable before and after of the treatments were not recorded. In cases where identification of seedlings at the species level was dubious, they were grown until flowering and then identified. Species nomenclature follows Marticorena & Quezada (1985).

### *Data analyses*

The effect of heat, smoke, and their combination on the total number of species and seedlings emerged, the number of native and the number exotic species and seedlings emerged per sample, were obtained with ANOVAs. 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 transects was considered a random factor. To assess differences on the total density of emerged native and exotic species and seedlings, the raw seed densities were transformed to ln (x+1). We considered that treatments significantly affected the response variable when $P < 0.05$.

Inference for proportions ($\alpha < 0.05$) were performed to compare proportion of species with fire-related cues (exotic, native and both combined) between a fire-free site (this study) vs. the site subjected to recurrent fires (data from Figueroa et al. 2009).

## RESULTS

Twenty-seven species, representing 13 families, emerged from the soil samples (Table 1). The most abundant families were Asteraceae and Poaceae. All of the emerged species were herbs, and approximately 66.6 % (18 species) were exotic. We did not find emergence of exotic or native woody plants, possibly due to limited seeds in the soil (Figueroa et al. 2004).

Considering all the treatments applied, the species that emerged with the highest abundance were of exotic origin, such as the forbs *Anthriscus caucalis*, *Aphanes arvensis* L., and the annual grasses *Vulpia bromoides* and *Poa annua* (Table 1). The native species that emerged with the highest abundance considering all treatments were the forbs *Soliva sessilis* Ruiz et Pavón, *Oxalis micrantha* Bertero ex Colla and *Gamochaeta coarctata* (Willdenow) Kerguélen and the annual grass *Bromus berteroanus* (Table 1).

For both exotic and native species, the mean number of species that emerged from the soil samples did not differ significantly with respect to the control for any of the treatments applied (Table 2). Likewise, the density of exotic and native seedlings that emerged from the soil samples did not differ significantly with respect to the control for any of the treatments applied (Table 2). Thus, at a first glance, fire-related germination cues did not affect the emergence of native with respect to exotic species from the soil seed bank (Table 2).

Nevertheless, interesting species-specific responses were observed; three exotics and

TABLE 1

Mean exotic 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/ number of pots with emerged seedlings. F and P values are from ANOVAs (d.f. = 3, 76). Responses compared the control treatment (Holm-Sidak method). 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 annual herbs except *Centaurea melitensis*, *Gamochaeta coarctata*, *Leontodon saxitalis* (perennial herbs). Different letters indicate significant differences ($P < 0.05$).

Densidad promedio de plantas exóticas (Número de plántulas emergentes $m^{-2}$) con respecto a diferentes tratamientos aplicados a muestras de suelo de Chile central. En paréntesis se indica ± 1 error estándar/número de bandejas con plántulas emergentes. Valor de F y P son de las ANDEVAs (g.l.= 3, 76). Respuestas comparadas al tratamiento control (método de Holm-Sidak). 1: promovida por calor; 2: promovida por humo; promovida por calor y humo combinado; 4: inhibida por calor; 5: inhibida por humo; 6: inhibida por calor y humo combinado; -: indiferente. Todas las especies son hierbas anuales excepto *Centaurea melitensis*, *Gamochaeta coarctata*, *Leontodon saxitalis* (hierbas perennes). Las letras diferentes indican diferencias significativas ($P < 0.05$).

| Species | Origin | Control | Heat | Smoke | Heat-Smoke | F | P | Responses |
|---|---|---|---|---|---|---|---|---|
| *Anthriscus caucalis* | Exotic | 488 (204/8)$^{a}$ | 426 (107/17)$^{a}$ | 691 (155/16)$^{b}$ | 795 (160/18)$^{b}$ | 4.8 | 0.004 | 2, 3 |
| *Aphanes arvensis* | Exotic | 155 (124/5)$^{a}$ | 133 (70/8)$^{a}$ | 43 (38/2)$^{a}$ | 13 (9/2)$^{b}$ | 2.5 | 0.05 | 6 |
| *Avena barbata* | Exotic | 0$^{a}$ | 3 (3/1)$^{a}$ | 20 (8/5)$^{b}$ | 0$^{a}$ | 4.8 | 0.004 | 2 |
| *Bromus berteroanus* | Native | 43 (17/7)$^{a}$ | 58 (19/9)$^{a}$ | 5 (3/2)$^{b}$ | 10 (5/4)$^{a}$ | 3.0 | 0.03 | 5 |
| *Achillea mellifolium* | Exotic | 0 | 0 | 3 (3/1) | 0 | 2.1 | 0.1 | - |
| *Amsinckia hispida* | Native | 0 | 5 (5/1) | 3 (3/1) | 18 (10/3) | 1.5 | 0.2 | - |
| *Bowlesia incana* | Native | 8 (8/1) | 58 (45/5) | 33 (22/5) | 25 (17/2) | 1.0 | 0.3 | - |
| *Capsela bursa-pastoris* | Exotic | 3 (3/1) | 8 (8/1) | 20 (12/3) | 0 | 1.5 | 0.2 | - |
| *Cardamine hirsuta* | Exotic | 38 (21/5) | 38 (23/4) | 183 (87/9) | 50 (21/8) | 1.5 | 0.2 | - |
| *Centaurea melitensis* | Exotic | 0 | 5 (5/1) | 0 | 0 | 1 | 0.4 | - |
| *Erodium bothrys* | Exotic | 0 | 0 | 0 | 35 (33/2) | 2.2 | 0.1 | - |
| *Erodium cicutarium* | Exotic | 23 (23/1) | 0 | 20 (13/3) | 35 (33/2) | 0.8 | 0.4 | - |
| *Erodium moschatum* | Exotic | 25 (13/4) | 75 (31/8) | 15 (10/3) | 32 (16/4) | 1.5 | 0.2 | - |
| *Gamochaeta coarctata* | Native | 58 (25/6) | 38 (18/5) | 53 (26/6) | 15 (6/5) | 0.2 | 0.9 | - |
| *Galium aparine* | Exotic | 0 | 0 | 0 | 3 (3/1) | 0.8 | 0.4 | - |
| *Leontodon saxatilis* | Exotic | 30 (16/4) | 40 (28/2) | 8 (8/1) | 8 (8/1) | 0.8 | 0.4 | - |

TABLE 1. Continuation

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Lophochloa cristata* | Exotic | 3 (3/1) | 0 | 0 | 0 | 0.8 | 0.4 | - |
| *Logfia gallica* | Exotic | 31 (7/2) | 0 | 0 | 0 | 2.1 | 0.1 | - |
| *Madia sativa* | Native | 0 | 3 (3/1) | 0 | 0 | 0.8 | 0.4 | - |
| *Mentha* sp. | Native | 5 (5/1) | 3 (3/1) | 0 | 5 (5/1) | 0.3 | 0.8 | - |
| *Oxalis micrantha* | Native | 50 (22/8) | 15 (9/3) | 38 (19/5) | 50 (34/2) | 1.5 | 0.2 | - |
| *Poa anua* | Exotic | 70 (39/3) | 45 (33/2) | 28 (20/3) | 48 (23/5) | 0.3 | 0.8 | - |
| *Stellaria media* | Native | 28 (11/6) | 18 (8/5) | 35 (16/6) | 35 (13/6) | 0.1 | 0.9 | - |
| *Soliva sessile* | Native | 153 (77/6) | 148 (82/8) | 33 (14/5) | 75 (37/8) | 0.5 | 0.7 | - |
| *Trifolium glomeratum* | Exotic | 33 (25/4) | 100 (43/11) | 50 (28/7) | 78 (27/8) | 2.2 | 0.1 | - |
| *Urtica ureas* | Exotic | 0 | 0 | 0 | 3 (3/1) | 0.9 | 0.4 | - |
| *Vulpia bromoides* | Exotic | 190 (54/14) | 263 (67/13) | 255 (66/13) | 185 (53/14) | 0 | 1 | - |

one native species showed differences in their emergence after the application of fire-related cues. The native grass *Bromus berteroanus* significantly decreased its emergence compared to the control after smoke treatment (Table 1). In contrast, the exotic *Anthriscus caucalis* significantly increased its emergence after the smoke and heat-smoke treatment (Table 1). Likewise, the exotic *Avena barbata* increased its emergence after the smoke treatment compared to control, and the exotic *Aphanes arvensis* significantly decreased its emergence after the smoke treatment (Table 1). In the remaining 23 species recorded, of which ca. 65 % were exotic, seedling emergence was not significantly affected by any of the treatments (Table 1). The analyses carried out found no significant block effect (P > 0.05).

Finally, the proportion of fire-sensitive species did not differ significantly between the fire-free site vs. the sites subjected to recurrent fires neither for exotic (Fig. 2A), native (Fig. 2B) or both species-type combined (Fig. 2C).

## DISCUSSION

The low proportion of fire-sensitive species recorded in this fire-free matorral is not statistically different from the proportion of fire-sensitive species found in a matorral subjected to periodic fires (Figueroa et al. 2009); thus, we do not find evidence to support our general hypothesis. The fire-associated triggers analyzed in this study (heat, smoke, and the combination of both), did not increase the mean number of exotic over native species, or the density of exotic over native seedlings that emerged from soil samples taken from a Chilean matorral that has not been affected by fire over the last 50 years. Although, it is hard to evaluate plant establishment by using post-fire emergence only (Daws et al. 2007), our results are consistent with those found by Keeley & Johnson (1977) and Holmgren et al. (2000), where they suggest that fire has no direct effect on the abundance and composition in the vegetation of central Chile. The aforementioned studies showed evidence that the establishment of exotic (e.g., *Lophocloa cristata* (L.) N. Hylander, *Erodium cicutarium* (L.) L'Hér. ex Aiton , *Medicago polymorpha* L.), and native plants (e.g., *Bromus berteroanus*, *Amsinckia hispida* (Ruiz et Pavón) I. M. Johnst.) is not stimulated by fire. It is worth mentioning that our soil samples were collected in the same site where the study by Holmgren et al. (2000) was carried out, although the fire intensity probably was lower than the heat treatments used in the present study.

Although there are studies that provide evidence that fire seems to change exotic

*Fig. 2:* Proportion of fire-sensitive species in a fire-free matorral vs. a matorral affected by recurrent fires, for exotic (A), native (B) and both species combined (C). Significant differences between sites were not found (Inference for proportions, $\alpha > 0.05$).

Proporción de especies sensibles al fuego en un matorral libre de fuegos vs. un matorral afectado por fuego en especies nativas, exóticas y ambas combinadas. No se encontraron diferencias significativas entre sitios (Inference for proportions, $\alpha > 0.05$).

TABLE 2

Mean species number (Number emerged species m$^{-2}$) and mean seedling number (Number emerged seedlings m$^{-2}$) with regard to different treatments applied to soil samples from central Chile matorral. In parentheses is indicated ± SE/number of pots with emerged seedlings. F and P values are from ANOVAs (d.f. = 3, 76). Responses compared the control treatment (Holm-Sidak method). 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.

Número promedio de especies (Número de especies emergentes m$^{-2}$) y número promedio de plántulas (Número de plántulas emergentes m$^{-2}$) con respecto a diferentes tratamientos aplicados a muestras de suelo de un matorral de Chile central. En paréntesis se indica ± EE/número de bandejas con plántulas emergentes. Los valores de F y P son de las ANDEVAs (g.l. = 3, 76). Respuestas comparadas al tratamiento control (método de Holm-Sidak). 1: promovida por calor; 2: promovida por humo; promovida por calor y humo combinado; 4: inhibida por calor; 5: inhibida por humo; 6: inhibida por calor y humo combinado; -: indiferente.

| Dependent variables | Control | Heat | Smoke | Heat-Smoke | F | P | Response |
|---|---|---|---|---|---|---|---|
| Number of exotic seedlings | 1063 (266/20) | 1136 (172/20) | 1333 (235/20) | 1283 (199/20) | 1.5 | 0.2 | - |
| Number of native seedlings | 343 (84/17) | 343 (84/20) | 198 (40/15) | 233 (43/18) | 1 | 0.3 | - |
| Number of exotic species | 2.6 (0.3/20) | 3.5 (0.4/20) | 3.3 (0.3/20) | 3.3 (0.3/20) | 0.8 | 0.4 | - |
| Number of native species | 1.8 (0.3/17) | 1.9 (0.2/19) | 1.5 (0.3/15) | 1.6 (0.2/18) | 0.6 | 0.6 | - |
| Total of seedlings | 1405 (283/20) | 1479 (185/20) | 1530 (236/20) | 1515 (202/20) | 0.5 | 0.6 | - |
| Total of species | 4.4 (0.5/20) | 5.4 (0.5/20) | 4.8 (0.4/20) | 4.9 (0.3/20) | 0.6 | 0.6 | - |

plant abundance (Gómez-González et al. 2011), heat-shock can increase the emergence of some native herbs (e.g., *Calamagrostis gallana, Helenium aromaticum* (Hook.) Bailey in Gómez-González & Cavieres 2009), some exotic herbs (e.g., *Hordeum marinum* Hudson, and *Trifolium pratense* L. in Gómez-González & Cavieres 2009), and some woody species (e.g., *Muhelembeckia hastulata* (J. E. Sm.) Johnst. in Muñoz & Fuentes 1989) in central Chile, most of these species were not present in the soil samples collected at our study site. For other previously reported heat-shock stimulated species, such as the exotic species *Lofgia gallica* (L.) Coss. et Germ. (Gómez-Gonzalez & Cavieres 2009), we found a dissimilar response to heat-shock application. Perhaps the temperature treatment applied in our study (100 °C for 10 min) is greater than the stimulating temperature for fire-associated exotic and native species, as indicated in the study by Gómez-González & Cavieres (2009). These authors found that in central Chile fire promotes exotic over native plants only for low-intensity fires (c.a. 30 °C for 30 min). High- and very high-intensity fires (average temperature of 120 °C for 10 min and maximum temperature of 137 °C) decreased the richness and seedling emergence of both exotic and native herbs, although this decrease was sharper for native species, increasing the relative proportion of exotics (Gómez-González & Cavieres 2009).

Plant-derived smoke significantly decreased the seedling density of one native (*B. berteroanus*) and one exotic (*Aphanes arvensis*), both common species in San Carlos de Apoquindo (Figueroa et al. 2004). Conversely, smoke treatment increased the seedling emergence of the exotics *Anthriscus caucalis* and *Avena barbata*. Exotic plants have never been recorded in central Chile as smoke-stimulated plants, with the exception of *Poa annua* in the Lampa matorral (Figueroa et al. 2009). *A. caucalis* is a highly aggressive alien herb in central Chile that inhibits the establishment of native herbs and decreases their survival affecting the composition and diversity of herbaceous stratum of the Chilean matorral (Castro et al. 2010). In addition, heat-shock > 130 °C on the seeds of this species increases the emergence of seedlings (Gómez-González et al. 2009). *A. barbata* is an aggressive annual exotic that colonizes cultivated fields and roadsides (Matthei 1995). Thus, this smoke-stimulated emergence syndrome could facilitate the spread and the post-fire colonization of *A. caucalis* and *A. barbata* in the open sites of the Chilean matorral subject to fire.

The responses to fire cues across multiple populations could be highly variable (Kenny et al. 2001, Thomas et al. 2003, 2007). For central Chile, we have found that *B. berteroanus* was inhibited by smoke (Table 1), whereas Figueroa et al. (2009) regarded this species as promoted by heat and heat and smoke combined. Additionally, Gómez-González & Cavieres (2009) found that this species was stimulated by low severity fires, but negatively affected by high-severity fires. Likewise, *E. cicutarium* has been considered inhibited by smoke (Figueroa et al. 2009), while Gómez-González & Cavieres (2009) reported indifference to fire, and in this study we found indifference to smoke and heat (Table 1). *Poa annua* is promoted by heat and smoke according to Figueroa et al. (2009), but here we found that it was indifferent to both factors (Table 1). We do not know the exact reasons for these different responses between populations. One likely explanation could be related to the differences in the experimental design between the studies mentioned above. Alternatively, the lack of recurrent fires in our study site might generate neutral conditions for the establishment of fire-associated plants and hence create different selective scenarios in the responses to fire compared to sites where fires are recurrent (Cowling 1987, Parker & Kelly 1989, Thomas et al. 2007). However, given the lack of studies addressing this issue on species present in Chile, a discussion on this matter would be speculative.

In the Chilean matorral there is little similarity between the seed bank and the above-ground vegetation (Jiménez & Armesto 1992, Figueroa et al. 2004). The evidence shows that in the matorral there are very few viable seeds of native woody species in the soil seed bank. The disturbance regimens imposed by humans, including fire, have probably caused this pattern (Aronson et al. 1998). Periodic fires could be involved in the high replacement of woody species by exotic annuals observed in early successional post-fire sites of the Chilean matorral (Altieri & Rodríguez 1974, Avila et al. 1981, Sax 2002, Gómez-González et al. 2008). Human-caused recurrent fires have been present in the Chilean matorral since the first indigenous settlements, several thousand years ago (Aravena et al. 2003) and such a time-span could be enough for adaptive responses to fire in species with short life-cycles (i.e. annual herbs). Nonetheless, fire has to be a permanent selection agent to promote a particular response, and therefore fire frequency may become an important factor in selective responses (Arianoutsou 1998). Also, high- and low-intensity human-provoked fires can produce ecologically different effects in the Chilean matorral (Segura et al. 1998). Thus, differences in the frequency and intensity at which different populations of the same species are exposed to fire may be involved in the non-consistent responses to fire-related germination cues (Thomas et al. 2007). This topic deserves further exploration to generate more general pictures of the role of fire on the invasion process and community structure in the Chilean matorral. To identify the causes underlying the observed variation in the responses to fire cues across populations, studies on the genetic heritability of fire related cues as well as on their adaptive advantage on different selective scenarios are needed.

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