

Litter burning does not equally affect seedling emergence of native and alien species of the Mediterranean-type Chilean matorral

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Abstract. Central Chile differs from other areas with Mediterranean-type climate by the scarcity of natural wildfires. The Chilean matorral is highly invaded by alien plant species from other Mediterranean zones of the world, where natural, recurrent wildfires have been one of their ecological features at least since the Pliocene. This suggests that anthropogenic fires in Chile might favour alien plant recruitment, increasing the invasive process. We assessed the effect of litter burning on the emergence of alien and native species from the soil seedbank of a matorral of central Chile. Soil samples were taken from three types of microhabitats: (i) closed matorral; (ii) beneath the canopy of shrubs and trees from an open matorral; (iii) grassland. Each sample was split in two subsamples. One subsample was exposed to fire by burning the litter taken from its corresponding microhabitat, and the other subsample was left unburned and used as a control. Fire intensity, determined by the fuel type, affected more markedly the native seedbank survival than the alien one. The low-intensity fire produced by grassland litter did not significantly affect the emergence of native herbs but increased alien species richness. The high-intensity and the very high-intensity fires produced by litter burning from beneath the canopy of the closed and the open matorral, respectively, negatively affected the seedling emergence of both native and alien species, but did so in a more pronounced manner to native species. Therefore, anthropogenic fires in central Chile may promote the invasion of alien plants with favourable traits (i.e. heat-shock resistance of seeds) that are not present in the native flora.

Additional keywords: exotic plants, fuel heterogeneity, heat, Mediterranean shrublands, smoke.

Introduction

According to Byers (2002), anthropogenic disturbances may suddenly put previously well-adapted native species into a competitive disadvantage with non-native species ('alteration of selection regimes' hypothesis). Fire is generally considered as a key driver of alien plant invasion in many ecosystems (D'Antonio 2000). Fire can indirectly promote alien success either by increasing availability of resources or by reducing competition with indigenous species (Prieur-Richard and Lavorel 2000). Direct positive effects of fire on plant invasion might be related to a higher resistance of alien species to fire compared with native ones, explained by the presence of favourable functional traits on invasives (e.g. seeds resistant to fire). Prieur-Richard and Lavorel (2000) hypothesised that changes in disturbance type or regime may favour exotics with certain adaptive biological traits that are not present in the native flora (see also McIntyre *et al.* 1995). In this sense, the invasibility potential of alien species from fire-prone biomes in a non-fire-prone region would be enhanced after the occurrence of a wildfire.

Fire is currently one of the most important disturbance agents on the Mediterranean-type Chilean matorral, where 5000 ha of native matorral are burnt every year (Corporación Nacional Forestal, Chile (CONAF), see <http://www.conaf.cl>, accessed

10 October 2006). However, these fires are not naturally ignited, but caused directly or indirectly by human activities. Unlike other Mediterranean-type ecosystems, convective thunderstorms and lightning are very rare during the summer in central Chile, and this absence of natural fires might explain why native woody plants do not show reproductive adaptations to fire, like heat- or smoke-stimulated germination (Muñoz and Fuentes 1989; Gómez-González *et al.* 2008), as they do in other Mediterranean-type ecosystems (Brown 1993; Dixon *et al.* 1995; Keeley 1995). Indeed, it has been found that seedbanks of native woody species are almost completely destroyed during high-severity fires (Muñoz and Fuentes 1989; Segura *et al.* 1998), whereas in the other Mediterranean-type ecosystems, soil seedbanks resist severe fires, leading to increased post-fire recruitment (Keeley 1995). Although resprouting ability is a common characteristic among woody species of this system (Araya and Ávila 1981), the absence of other functional traits related to fire such as seed persistence delays the recovery of the former closed canopy after recurrent fires.

Since the onset of Spanish colonisation (1536–42), the Chilean matorral has been highly invaded by alien plant species coming from the Mediterranean Basin. The majority (~70%) of the alien flora of central Chile is from Eurasia and North Africa



Fig. 1. Spatial pattern of seedling recruitment after a fire in a typical coastal matorral of central Chile.

(Arroyo *et al.* 2000), areas that are characterised by a long history of natural fires and human disturbances. This suggests that in the Chilean matorral, alien plants could have advantages for recruitment after fire compared with native species, thus enhancing the invasive process. However, there is contradictory evidence about the role of fire in the invasibility of the Chilean matorral. Although some studies have reported increases in the abundance of alien species after fires (e.g. Ávila *et al.* 1981; Sax 2002), others have reported non-significant effects (e.g. Keeley and Johnson 1977; Holmgren *et al.* 2000). This controversy could be related to differences between sites in relation to pre-fire alien seedbank or to post-fire processes such as propagule pressure and herbivory. In this regard, the study of the emergence from the soil seedbank after an experimental fire could be a useful approach to unravel the relationship between fire and alien plant invasion.

The Chilean matorral is characterised by multispecific shrub clumps that are surrounded by open grasslands. Fuel phytomass is hence unevenly distributed in space, and consequently, fires have patchy effects, generating mosaics of fire-consumed shrubs surrounded by lightly burned open areas (Segura *et al.* 1998). This patchiness may affect post-fire seedling recruitment, because a high density of seedlings has only been observed in open areas among the skeletons of burned shrubs in the field (Fig. 1). This suggests that fire in open grasslands reaches low intensity, whereas fire beneath shrub canopies must be more severe. In Australia, for example, although fires in grassland can reach maximum soil temperatures of $\sim 60^{\circ}\text{C}$ during 10 min, fires in *Eucalyptus* forests produce soil temperatures $\sim 120^{\circ}\text{C}$ during ~ 30 min (Bradstock *et al.* 1992). Nevertheless, there is no

information about how the natural fuel heterogeneity occurring in the Chilean matorral could affect post-fire plant recruitment via its effects on fire intensity.

Our main objective was to assess the effect of burning the accumulated litter biomass in different microhabitats of a central Chilean matorral on the seedling emergence from the soil seedbank of native and alien species. We hypothesise that the characteristic light litter biomass of open grassland patches in the matorral will produce low-intensity fires that would have little effect on the emergence of either native or alien species from the seedbank. However, the larger amount of fuel accumulated in the litter beneath shrub canopies will produce fires of higher intensities that could have comparatively more harmful effects on the native seedbank.

Materials and methods

Study site

To test our hypothesis, we selected a typical matorral in the locality of San Carlos de Apoquindo ($33^{\circ}27'\text{S}$, $70^{\circ}42'\text{W}$, province of Santiago). This site is located in the foothills of the Andes (990–1104 m above sea level). The climate is Mediterranean-type, characterised by rainy winters and long dry summer periods. Annual rainfall ranges from 300 to 500 mm. Mean annual temperature in the study area is 18°C , with maximum temperatures above 30°C during the summer and minimum temperatures below 0°C during the winter (di Castri and Hajek 1976). Soil is derived from volcanic rock and its uppermost stratum is formed by a thin layer of fine-grained ash. Vegetation is dominated

by native shrub species such as *Lithraea caustica*, *Quillaja saponaria*, *Baccharis* spp. and *Acacia caven*, whereas the herbaceous layer is dominated by native annuals such as *Bromus berterioanus*, and the alien annuals *Vulpia* spp. and *Erodium cicutarium* (Figueroa *et al.* 2004). Like in many other areas of the central Chilean matorral, there is a strong spatial segregation of the vegetation. While on gentle south-facing slopes, a closed matorral with a continuous canopy can be observed, an open matorral develops on north-facing slopes and flat areas with annual forbs and grasses growing profusely among clumps of shrubs and trees. Further characteristics about the study site (e.g. species composition, species phenology, disturbance history) are detailed in Figueroa *et al.* (2004).

Soil sampling design

To evaluate the effects of possible fire intensities occurring on a single area, we took soil samples from three different microhabitats: (1) beneath the canopy of a closed matorral, characterised by high quantities of woody debris and leaf litter, and high soil humidity beneath the continuous canopy; (2) beneath the canopy of shrub and tree clumps of an open matorral on a flat area, characterised by high quantities of woody debris and leaf litter, but low soil humidity due to canopy openness; and (3) from grasslands surrounding the shrubs and trees of the open matorral, dominated by a dry and light leaf litter derived mostly from the herbaceous species.

In the closed matorral, a 40-m linear transect was laid out following the slope, where a soil sample was taken every 2 m. Another 40-m linear transect was laid out in the open matorral. Along this last transect, two soil samples were taken every 2 m, one in the grassland outside the canopies and the other beneath the canopy of the nearest shrub and tree clump. Soil samples were taken with a 5-cm diameter and 10-cm depth metallic bore. We considered only the top 10 cm of soil because it is within this soil depth that most of the viable seeds are found (Jiménez and Armesto 1992). Apart from the soil samples, we also collected 300 cm² of the litter that covered each soil sample in the field. These litter samples were weighed to determine the average fuel mass (*Fm*) to be used in fire treatments. Additionally, six soil samples were randomly taken from each microhabitat, to determine the gravimetric soil moisture, Θ , as

$$\Theta = (\text{weight of wet soil} - \text{weight of dry soil}) / \text{weight of dry soil}$$

Sampling was performed in early March 2005, after almost all species had dispersed their seeds and before autumn rains occurred. At the end of the summer season, there is a great amount of dry phytomass and the risk of fire ignition is very high.

Experimental litter burning

Most fires in the Mediterranean zone of central Chile are surface fires (CONAF, <http://www.conaf.cl>). Surface fires spread through the fuel provided by the litter. To assess the effect of litter burning on seedling emergence of both native and alien species, a series of small-scale experimental burns were conducted in an open greenhouse in the Universidad de Concepción. Our experiment tried to simulate the effect of a surface fire in a typically

heterogeneous matorral by burning the different kinds of litter produced by the three main types of microhabitats within the Chilean matorral. In open grasslands, litter was composed of dead grasses and forbs, whereas beneath canopies of both closed and open matorral, litter was formed by dead leaves, twigs and branches of the most common woody species (e.g. *Lithraea caustica*, *Quillaja saponaria* and *Acacia caven*). Each of the 60 collected soils samples (20 samples per microhabitat) was homogenised and split in two subsamples of the same volume. One subsample was put in a clay pot surrounded by bricks, topped by its corresponding portion of litter, and then set alight with a blowtorch and left to burn, while the other subsample was left as a control.

The evolution of soil temperature during each fire treatment was registered at 2.5-cm soil depth in 2 of the 20 samples using two copper–constantan thermocouples. For each fire treatment, we obtained the maximum average temperature reached (T_{max}) and the residence time above 80°, 100° and 120°C. T_{max} and residence time are two variables related to fire intensity and they are useful to compare our results with those obtained in experimental fires performed in other Mediterranean-type ecosystems.

Germination assays

After fire, all samples (control and burnt) were spread in 20 × 12 × 2 cm plastic trays and placed in a greenhouse. Trays were then watered and checked for seedling emergence on a daily basis. After 90 days, soil samples were disturbed by turning the soil, so as to stimulate further seedling emergence. The germination assay started in April 2005 (autumn) and ended in October 2005 (spring), when no more seedlings emerged. The number of emerged seedlings per square metre of soil was determined for each species. We considered the germination method the best approach to assess the effect of fire on seedling emergence because the visual count of seeds could cause spurious results owing to the inability to distinguish tiny black seeds in burnt soil samples.

To properly identify all the species, several seedlings per species were grown until flowering. Nomenclature of plant taxa follows Marticorena and Quezada (1985).

Statistical analyses

Differences in mean fuel phytomass (*Fm*) and gravimetric soil moisture (Θ) between pairs of microhabitats were evaluated by means of *t*-tests. *Fm* data were log-transformed ($\log[x + 1]$), whereas Θ data were transformed by an inverse square-root transformation ($1/\sqrt{x}$) before analyses. Wilcoxon tests for paired samples were used to compare the emergence of native and alien seedlings from the pairs of burnt and control soil subsamples within each microhabitat. Dependent variables assessed were: total species richness, species richness of natives and aliens, total seedling density, seedling density of natives and aliens, relative seedling density of aliens, and percentage of alien species. To evaluate the species-specific responses to fire, for each species we use proportion tests to compare the proportion of seedlings emerged in both treatments.

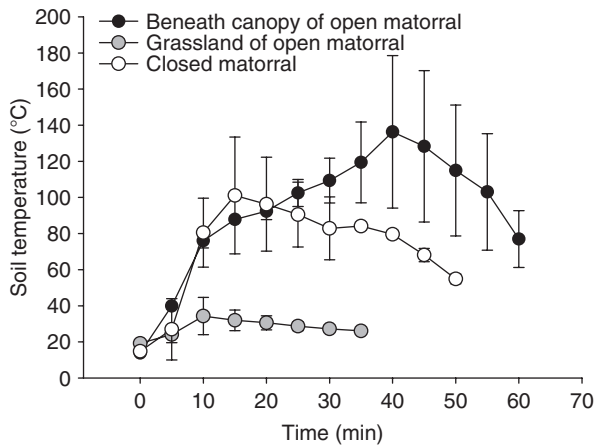


Fig. 2. Soil temperatures reached during the burning of the three different kinds of litter from each microhabitat type. Mean temperatures (± 2 s.e., error bars) are shown ($n = 2$).

Results

Fuel and soil characteristics during fire treatments

The average fuel phytomass ($F_m \pm 2$ s.e.) used for fire experiments was very similar for the two microhabitats beneath canopies (closed matorral 90.9 ± 22.67 g, and open matorral 96.15 ± 13.87 g, $t = -1.11$, $P = 0.274$). In contrast, those fuel mass values (beneath canopies) were significantly higher than that of the grassland (31.29 ± 5.30 g, $t = 5.84$, $P < 0.0001$ for closed matorral and $t = 9.69$, $P < 0.0001$ for open matorral).

Mean soil water content ($\Theta \pm 2$ s.e.) was significantly higher in soil samples coming from the closed matorral (0.071 ± 0.022) than in those from the grassland (0.017 ± 0.005 , $t = -7.10$, $P < 0.0001$) and the open matorral (0.027 ± 0.003 , $t = -4.48$, $P = 0.001$).

Soil temperature kinetics during the fire treatment also differed depending on the litter type (Fig. 2). For grassland litter, T_{max} only reached 35°C , with temperatures $\sim 30^\circ\text{C}$ lasting for 30 min. In contrast, the litter from the closed matorral produced $T_{max} = 101^\circ\text{C}$, with temperatures above 100°C for only 3 min, and above 80°C for 25 min. Despite the similarity in the fuel mass beneath canopies of the closed and open matorral, the fire intensity generated by the litter of the closed matorral was lower than that of the open matorral. In the case of the open matorral, T_{max} reached 137°C , with an average temperature of 120°C lasting for 10 min. Temperatures above 100°C occurred during 35 min and above 80°C during 40 min. They were thus classified as ‘low-intensity fire’ (LF), ‘high-intensity fire’ (HF) and ‘very high-intensity fire’ (VHF) for grassland, closed matorral and open matorral (beneath canopy), respectively.

Fire effects on species richness and seedling density

Although the burning of litter on grassland soil samples did not affect significantly the native species richness that emerged from the soil seedbank, it significantly increased the number of alien species (Fig. 3a). Thus, the LF that occurred on grassland samples increased the percentage of alien species from 26% in control samples to 36% in fire-treated samples

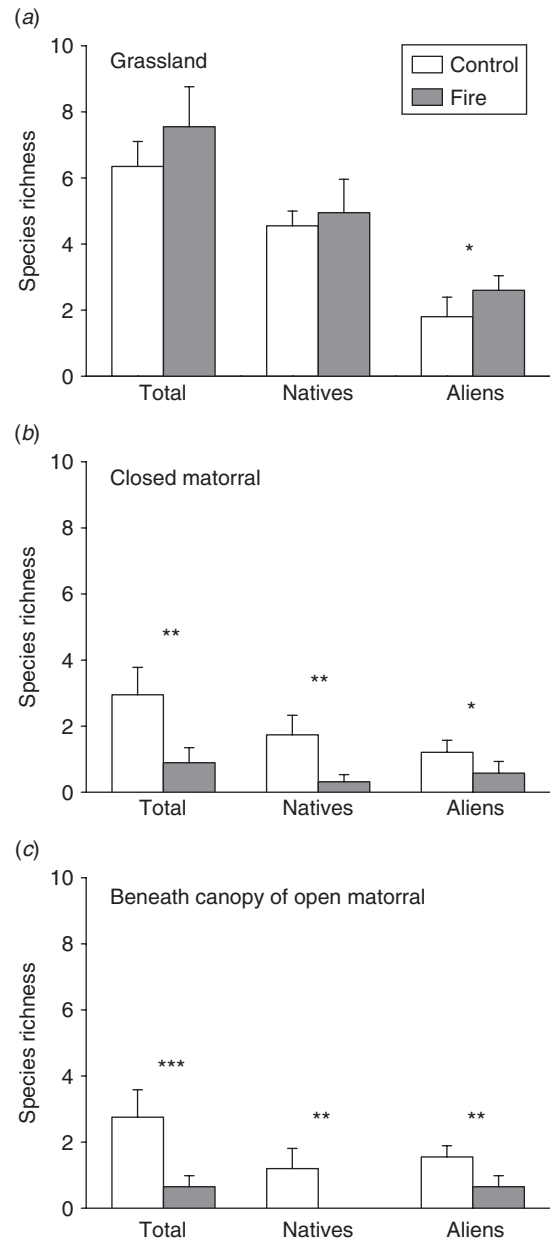


Fig. 3. Effect of litter burning on the number of species emerged from the soil seedbank in the three different microhabitats of the matorral of San Carlos de Apoquindo. Mean values (± 2 s.e., error bars) are shown ($n = 20$). Asterisks indicate significant differences between treatments ($*P < 0.05$; $**P < 0.01$; $***P < 0.001$; Wilcoxon rank-sum tests).

(Table 1). In addition, LF did not affect the seedling density of both native ($P = 0.287$; Wilcoxon rank-sum test) and alien ($P = 0.171$; Wilcoxon rank-sum test) species (Fig. 4a).

Contrastingly, the burning of litter from the closed matorral significantly decreased species richness, and this reduction was slightly higher for native than for alien species (Fig. 3b). This HF also reduced the seedling density of both native and alien species (Fig. 4b). Likewise, the VHF that occurred on soil samples from the open matorral caused a higher decrease in the

Table 1. Effect of litter burning on the species percentage and the relative density of seedlings of alien species emerged from the soil seedbank in different microhabitats of the matorral of San Carlos de Apoquindo

CM, closed matorral (continuous canopy); B-OM, beneath canopy of the open matorral; G-OM, grassland of the open matorral. Mean values \pm 2 s.e. (in parentheses) are shown, $n = 20$. P values in bold indicate significant differences between treatments (significance level < 0.05 ; Wilcoxon rank-sum tests)

Variable	Microhabitat type	Control	Fire	P
Species percentage	CM	45.25 (5.9)	59.95 (13.2)	0.602
	B-OM	68.57 (6.2)	100	0.001
	G-OM	25.86 (3.5)	35.87 (2.5)	0.004
Relative seedling density	CM	0.52 (0.07)	0.61 (0.14)	0.218
	B-OM	0.75 (0.06)	1	0.001
	G-OM	0.23 (0.04)	0.28 (0.05)	0.306

number of natives than alien species (Fig. 3c). As a consequence, the percentage of alien species increased from 68 to 100% after the VHF treatment (Table 1). Seedling density of both native and alien species was also significantly reduced by this VHF (Fig. 4c). As after the VHF treatment no single native seedling emerged (Fig. 4c), the proportion of alien seedlings emerged increased from 0.75 to 1 (Table 1).

Species-specific responses to fire

In grassland soil samples, most of the native and alien species did not change considerably the proportion of seedlings emerging after LF (Table 2). Although the LF exposure lowered the emergence of some species (e.g. the native *Gamochaeta simplicicaulis* and the alien *Logfia gallica*), they still maintained a considerable amount of seedlings in fire-treated samples (Table 2). However, species such as the natives *Clarkia tenella*, *Helenium aromaticum*, *Calamagrostis gayana* and *Bromus bertoanus*, as well as the alien *Vulpia myuros*, showed higher seedling emergence in samples exposed to LF than in controls (Table 2), suggesting that fire might stimulate germination in these species when fire severity is low.

The native species *Plagiobothrys myosotoides* and *H. aromaticum*, which were very abundant in control samples from the closed matorral, did not resist the HF conditions of the burnt samples (Table 2). However, the proportion of seedlings of natives *Moscharia pinnatifida*, *G. simplicicaulis* and *Clarkia tenella* that emerged after HF treatment did not change (Table 2). Hence, these three latter species can be considered as resistant to HF. The same resistance to HF was found for the alien species *Anthriscus caucalis* and *L. gallica* (Table 2). Finally, the alien species *Trifolium pratense* showed an even higher seedling emergence in the HF-exposed samples than in the control ones (Table 2).

No native seedlings emerged from the soil samples exposed to VHF, where soil reached the highest temperatures (Table 2). Native species that were abundant in control trays (e.g. *Soliva sessilis* and *G. simplicicaulis*) did not resist the VHF regime (Table 2). In contrast, the majority of the alien species survived (except *Galium aparine* and *Erodium cicutarium*). Again, the alien *T. pratense* had increased seedling emergence also

after these VHF conditions, suggesting that germination in this species could be stimulated by high temperatures.

Discussion

Although some seeds of a few native species survived the HF determined by the burning of litter from beneath closed matorral (e.g. *Gamochaeta simplicicaulis*, *Moscharia pinnatifida* and *Clarkia tenella*), this treatment was comparatively more harmful for seeds of native species than for those of aliens, suggesting that fire might create an advantage for alien recruitment in this microhabitat. In the open matorral, the litter beneath the canopy was drier, thus reaching in its combustion a very high temperature (VHF). In this case, soil temperatures surpassed 120°C during a relatively long time (10 min), destroying the seedbank of all the native species. Only seeds of some alien species did survive this severe fire treatment. For example, the alien species *Anthriscus caucalis* and *Trifolium pratense* maintained an important amount of viable seeds after VHF. These species constituted 71% of all seeds emerged in burnt samples from the closed matorral and 81.6% in samples from the open matorral. Indeed, *T. pratense* enhanced its proportion of emerged seedlings when the intensity of fire was very high (VHF). This indicates that, after a wildfire in the matorral, these alien species could monopolise the spaces beneath canopies and out-compete the post-fire dispersed native species. In fact, in coastal matorral areas, stands dominated by *A. caucalis* and *Trifolium* spp. have been observed in black patches produced by high-intensity fires (S. Gómez-González, pers. obs.). Contrastingly, the LF did not change the number of native species that emerged from the soil seedbank, but increased the alien species richness. This could be due to seed germination of some alien species (e.g. *Vulpia myuros*) stimulated by moderate heat or by chemical compounds from ash or smoke, or both.

Heterogeneity in fire severity may play an important ecological role in this system (Knapp and Keeley 2006). In our experiment, after the low-intensity fire regime the number of alien species that emerged was higher than in the control trays. However, although the absolute number of alien species

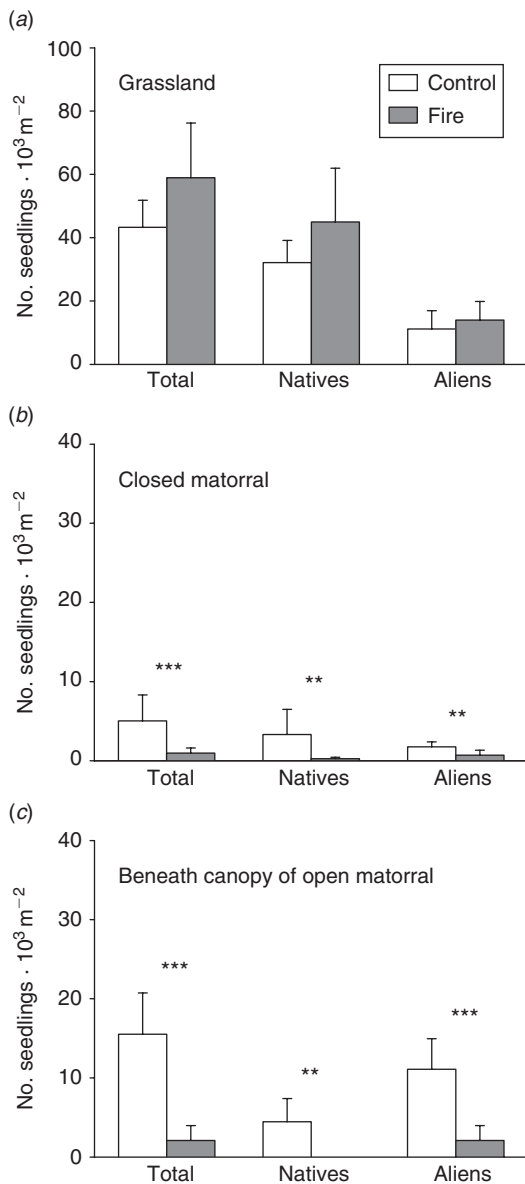


Fig. 4. Effect of litter burning on the density of seedlings emerged from the soil seedbank in the three different microhabitats of the matorral of San Carlos de Apoquindo. Mean values (± 2 s.e., error bars) are shown ($n = 20$). Asterisks indicate significant differences between treatments (** $P < 0.01$; *** $P < 0.001$; Wilcoxon rank-sum tests).

decreased under high and very high fire regimes, this decrease was comparatively higher for native species. Therefore, the relative abundance of alien species that emerged from the seedbank increased with fire intensity. Hence, it can be stated that fire intensity favours alien invasion through a comparatively higher survival of alien seeds beneath canopies after wildfires. Furthermore, less severely burned patches of grasslands may act as a secondary source of alien propagules to colonise the more severely burned areas beneath canopies. We hence hypothesise that the heterogeneity in fire intensity and burned-patch size might be important variables determining the success of invasion after fire in the Chilean matorral.

Fire intensity is an important factor affecting the success of alien plants in other ecosystems (Keeley *et al.* 2005; Hunter *et al.* 2006). However, its facilitating effects depend on the evolutionary history of disturbance of the invaded community. For example, in Californian chaparral, natural fires have been historically characterised by their high intensity (Keeley 2006). These intense fires destroy the alien seedbanks, but native seeds are adapted to endure such harsh conditions (Keeley *et al.* 2005). By contrast, in the mixed-conifer forest of the western United States, Hunter *et al.* (2006) suggested that the high severity of wildfires may be one of the more important mechanisms for the continued spread of non-native species. According to the 'alteration of selection regimes' hypothesis (Byers 2002), anthropogenic disturbances may suddenly put previously well-adapted native species into a competitive disadvantage against non-native species. This phenomenon could happen after recurrent wildfires in the Chilean matorral by different but non-mutually exclusive mechanisms: (i) comparatively higher seed mortality of native species in severely burned patches, reducing competition in favour of fire-resistant alien plants; (ii) higher alien seedling density occupying the bare ground available; and (iii) competitive advantage for alien species in the post-fire environments due to elevated nitrogen availability (Bidwell *et al.* 2006). Nevertheless, specific studies aimed to test post-fire competitive interactions between native and non-native species are needed to assess the latter hypothesis and separate the relative importance of seed-bank survival from competitive processes in the alien dominance after fires in the Chilean matorral.

In other Mediterranean-type ecosystems, the native vegetation rapidly returns to its original closed-canopy condition after fire, displacing alien species with time since fire (Trabaud 1991; Keeley *et al.* 2003; Dimitrakopoulos *et al.* 2005). In contrast, the post-fire recovery of the native Chilean matorral is very slow (Jiménez and Armesto 1992), suggesting that the exclusion of alien species after fire might be also slow. Most matorral woody species have bird-dispersed seeds. As birds normally use shrubs and trees as perches, most seedling recruitment of matorral woody species occurs beneath the canopy of woody plants (Fuentes *et al.* 1986). As seeds of woody species are not fire-resistant (Muñoz and Fuentes 1989), there is no recruitment of new native individuals in high-severity fire patches beneath canopies (Segura *et al.* 1998). Moreover, seeds of woody species are dispersed at short distances (Fuentes *et al.* 1986), and seedling establishment in open areas is limited by desiccation and herbivory (Fuentes *et al.* 1984). The Chilean matorral thus seems to have lower resilience than fire-adapted shrublands in other Mediterranean-type ecosystems and this could favour the success of alien species for a longer period after fire.

In the Chilean matorral, studies aiming to explore the importance of fire in seed germination have been focussed only on native woody species (Muñoz and Fuentes 1989; Segura *et al.* 1998; Gómez-González *et al.* 2008). These studies concluded that woody natives are not adapted to fire, because germination stimulated by heat or smoke is poorly represented among the species studied. The exceptions were the woody species *Muehlenbeckia hastulata* and *Retanilla trinervia*, which germinated after heat treatment (Muñoz and Fuentes 1989) and they also recruited after low-intensity fires in the field (Segura

Table 2. Total seedlings emerged per treatment and microhabitat type

The numbers in parentheses indicate the percentage of seedlings emerged. *P* values in bold indicate significant differences between treatments (significance level < 0.05; proportions tests)

Species	Closed matorral			Open matorral			Grassland		
	Control	Fire	<i>P</i>	Beneath canopy Control	Beneath canopy Fire	<i>P</i>	Control	Fire	<i>P</i>
Native species									
<i>Gamochaeta simplicicaulis</i>	31 (18)	4 (12.9)	0.41	15 (6)	0	–	69 (11.9)	44 (5.6)	0.00
<i>Clarkia tenella</i>	2 (1.2)	1 (3.2)	0.40	2 (0.8)	0	–	107 (18.5)	181 (23.1)	0.04
<i>Moscharia pinnatifida</i>	2 (1.2)	1 (3.2)	0.37	–	–	–	–	–	–
<i>Calandrinia compressa</i>	0	1 (3.2)	0.02	–	–	–	3 (0.5)	2 (0.3)	0.56
<i>Helenium aromaticum</i>	26 (15.2)	0	–	3 (1.2)	0	–	61 (10.6)	152 (19.4)	0.00
<i>Calamagrostis gallana</i>	4 (2.3)	0	–	14 (5.6)	0	–	6 (1)	22 (2.8)	0.02
<i>Soliva sessilis</i>	4 (2.3)	0	–	15 (6)	0	–	40 (6.9)	39 (5)	0.14
<i>Bowlesia incana</i>	1 (0.6)	0	–	1 (0.4)	0	–	3 (0.5)	3 (0.4)	0.78
<i>Plagiobothrys myosotoides</i>	25 (14.6)	0	–	–	–	–	–	–	–
<i>Pectocarya linearis</i>	2 (1.2)	0	–	–	–	–	113 (19.6)	73 (9.3)	0.00
<i>Chaetanthera linearis</i>	1 (0.6)	0	–	–	–	–	5 (0.9)	14 (1.8)	0.16
<i>Madia chilensis</i>	–	–	–	3 (1.2)	0	–	20 (3.5)	41 (5.2)	0.13
<i>Bromus berterianus</i>	–	–	–	12 (4.8)	0	–	2 (0.3)	13 (1.7)	0.01
<i>Nassella gibba</i>	–	–	–	2 (0.8)	0	–	–	–	–
<i>Amsinckia calycina</i>	–	–	–	–	–	–	3 (0.5)	8 (1)	0.30
<i>Plagiobothrys procumbens</i>	–	–	–	–	–	–	1 (0.2)	2 (0.3)	0.72
<i>Rhodophiala</i> sp.	–	–	–	–	–	–	0 (0)	2 (0.3)	0.18
<i>Quillaja saponaria</i>	–	–	–	–	–	–	0 (0)	3 (0.4)	0.13
<i>Lithraea caustica</i>	3 (1.8)	0	–	–	–	–	0 (0)	1 (0.1)	0.45
<i>Acacia caven</i>	1 (0.6)	0	–	–	–	–	0 (0)	2 (0.3)	0.18
Alien species									
<i>Anthriscus caucalis</i>	57 (33.3)	14 (45.2)	0.23	120 (47.8)	6 (15.8)	0.00	6 (1)	4 (0.5)	0.23
<i>Trifolium pratense</i>	1 (0.6)	8 (25.8)	0.00	1 (0.4)	25 (65.8)	0.00	7 (1.2)	5 (0.6)	0.23
<i>Hordeum marinum</i>	0	1 (3.2)	0.02	17 (6.8)	4 (10.5)	0.41	13 (2.2)	16 (2)	0.80
<i>Lofgia gallica</i>	7 (4.1)	1 (3.2)	0.81	–	–	–	12 (2.1)	4 (0.5)	0.01
<i>Plantago lanceolata</i>	1 (0.6)	0	–	–	–	–	–	–	–
<i>Cerastium glomeratum</i>	3 (1.8)	0	–	–	–	–	2 (0.3)	5 (0.6)	0.42
<i>Centaurea melitensis</i>	–	–	–	19 (7.6)	1 (2.6)	0.26	41 (7.1)	44 (5.6)	0.26
<i>Vulpia myuros</i>	–	–	–	23 (9.2)	2 (5.3)	0.43	7 (1.2)	40 (5.1)	0.00
<i>Erodium cicutarium</i>	–	–	–	1 (0.4)	0	–	49 (8.5)	55 (7)	0.30
<i>Galium aparine</i>	–	–	–	3 (1.2)	0	–	2 (0.3)	2 (0.2)	0.72
<i>Galium murale</i>	–	–	–	–	–	–	5 (0.9)	5 (0.6)	0.52
<i>Erodium malacoides</i>	–	–	–	–	–	–	1 (0.2)	1 (0.1)	0.63
Total									
Native seedlings	102	7		66	0		433	602	1210
Alien seedlings	69	24		185	38		145	181	642
All species seedlings	171	31		251	38		578	783	1852

et al. 1998). Other pioneering species such as *Acacia caven* and *Baccharis vernalis* also responded positively to smoke treatments (Gómez-González et al. 2008). In the present study, some native herb species endured high temperatures in our experiments. For example, seeds of the annuals *G. simplicicaulis*, *M. pinnatifida* and *Clarkia tenella* survived to temperatures above 100°C during a few minutes. Other native species, such as *Helenium aromaticum*, *Calamagrostis gayana*, *Bromus berterianus* and *Clarkia tenella*, increased the proportion of seedlings that emerged after the low-intensity fire caused by grassland litter. The maximum soil temperature reached there was only 35°C. Given that in the summer periods soils reach higher temperatures, seed germination cued by heat seems not to be the mechanism for enhanced seed germination in this case.

Nevertheless, compounds derived from smoke or ash could have promoted the germination of these species. Native species could be then more resistant to fire than previously assumed (Armesto and Gutierrez 1978; Muñoz and Fuentes 1989; Jiménez and Armesto 1992; Segura et al. 1998), suggesting that further investigations are needed to evaluate whether annual native plant species might have recently acquired seed persistence due to long-term pressure by anthropogenic fires. 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 have been enough for adaptive responses to fire being acquired by species with short life-cycles (e.g. annuals). Nevertheless, this deserves further investigation.

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Appendix 1. Life history, geographical origin and status of invasion of the native and alien species emerged from the soil seedbank of the matorral of San Carlos de Apoquindo, Santiago

Status of invasion according to The Global Compendium of Weeds (<http://www.hear.org/gcw/index.html>, accessed April 2007): W, weed; NW, noxious weed; N, naturalised; Ad, adventitious. Life history: A, annual; B, biennial; HP, herbaceous perennial; WP, woody perennial. Origin: E, endemic to Chile

	Life history	Family	Origin	Status of invasion
Natives				
<i>Acacia caven</i> Molina	WP	Mimosaceae	S America	W
<i>Amsinckia calycina</i> (Moris) Chater	A	Boraginaceae	America	W
<i>Bowlesia incana</i> Ruiz and Pav.	A	Apiaceae	S America	W
<i>Bromus berteroaenus</i> Colla	A, HP	Poaceae	S America	W
<i>Calamagrostis gayana</i> (Steud.) Soreng	HP	Poaceae	S America	–
<i>Calandrinia compressa</i> Schrad. ex DC.	A	Portulacaceae	Chile (E)	N
<i>Chaetanthera linearis</i> Poepp. ex Less.	A	Asteraceae	Chile (E)	–
<i>Clarkia tenella</i> (Cav.) F.H. Lewis et M.R. Lewis	A	Onagraceae	S America	–
<i>Gamochaeta simplicicaulis</i> (Willd. ex Spreng.) Cabrera	A	Asteraceae	S America	Ad
<i>Helenium aromaticum</i> (Hook.) L.H. Bailey	A	Asteraceae	America	W
<i>Lithraea caustica</i> Hook. and Arn.	WP	Anacardiaceae	Chile (E)	–
<i>Madia chilensis</i> Reiche	A	Asteraceae	Chile (E)	–
<i>Moscharia pinnatifida</i> Ruiz et Pav.	A	Asteraceae	Chile (E)	–
<i>Nassella gibba</i> (Phil.) M. Muñoz-Schick	HP	Poaceae	S America	–
<i>Pectocarya linearis</i> (Ruiz et Pav.) DC.	A	Boraginaceae	America	–
<i>Plagiobothrys myosotoides</i> (Lehm.) Brand	A	Boraginaceae	America	–
<i>Plagiobothrys procumbens</i> (Colla) A. Gray	A	Boraginaceae	Chile (E)	–
<i>Quillaja saponaria</i> Molina	WP	Rosaceae	Chile (E)	–
<i>Rhodophiala</i> sp.	HP	Amarillidaceae	S America	–
<i>Soliva sessilis</i> Ruiz et Pav.	A	Asteraceae	S America	W
Aliens				
<i>Anthriscus caucalis</i> M. Bieb.	A	Apiaceae	Eurasia	W
<i>Centaurea melitensis</i> L.	A, B	Asteraceae	Mediterranean	W
<i>Cerastium glomeratum</i> Thuill.	A	Caryophyllaceae	Mediterranean	W
<i>Erodium cicutarium</i> (L.) L'Hér. ex Aiton	A, B	Geraniaceae	Eurasia	NW
<i>Erodium malacoides</i> (L.) L'Hér. ex Aiton	A, B	Geraniaceae	Mediterranean	W
<i>Galium aparine</i> L.	A	Rubiaceae	Eurasia	NW
<i>Galium murale</i> (L.) All.	A	Rubiaceae	Europe	W
<i>Hordeum marinum</i> Huds.	A	Poaceae	Mediterranean	W
<i>Logfia gallica</i> (L.) Coss. et Germ.	A	Asteraceae	Europe	W
<i>Plantago lanceolata</i>	A, B	Plantaginaceae	Eurasia	NW
<i>Trifolium pratense</i> L.	B	Fabaceae	Eurasia	W
<i>Vulpia myuros</i> (L.) C. C. Gmel.	A	Poaceae	Eurasia	W