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Fire as a stimulant of shrub recruitment in northwestern Patagonian (Argentina) grasslands

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Abstract One strategy of plant survival during post-fire succession is to persist and regenerate by recruiting new individuals from a fire-resistant seed bank. The heat, smoke, and charcoal released during plant combustion may act (individually or in combination) as a cue for post-fire seed germination. *Fabiana imbricata* is a shrub that forms persistent seed banks in the northwestern Patagonian grasslands and shows a high recruitment from seeds during post-fire succession. Mathematical models showed that this species is advancing over the grasslands in response to fires. To corroborate these findings, we studied the role of fire on *F. imbricata* seed germination. In order to achieve this, a factorial experiment was designed in laboratory conditions to study the effect of heat, charcoal, smoke, scarification, and their interactions on *F. imbricata* seed germination. Seeds treated with the higher temperatures required a longer period of time to germinate, thus, significantly affecting the mean germination time. Total germination percentages in *F. imbricata* were significantly enhanced by smoke and scarification, but the interaction of heat, smoke, and scarification was more important than the effect of each fire factor alone. The positive response to fire cues exhibited by *F. imbricata* indicates that this species would have an adaptive advantage to colonize these grasslands if fire frequency increased, as predicted for this environment. Hence, fire will contribute to the grassland encroachment by this species and, therefore, to the loss of biodiversity and productivity of northwestern Patagonian grasslands.

Keywords *Fabiana imbricata* · Fire · Grassland · Dormancy · Germination · Smoke

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Introduction

Disturbances are one of the major causes of fluctuation in ecosystem structure and functioning because they act in promoting environmental heterogeneity and resources releasing (Pickett and White 1985). Grazing and fire are among the main disturbances that affect semiarid grasslands (Oesterheld et al. 1999) and also produce changes in vegetation structure, such as the increase of shrub density (Schlesinger et al. 1990). Grasslands could be totally replaced by shrubs as a consequence of encroachment processes (Van Auken 2000), and this, in turn, could have a negative effect on biodiversity.

Fire is a physicochemical disturbance that has the capacity to remove large amounts of biomass from a system, making it an important agent in structuring communities, since the new openings created provide a potential trigger for vegetation change (Bond and Van Wilgen 1996). Even though fire is an important factor in regulating the balance between woody vegetation and grasses (Bond and Keeley 2005; Bond et al. 2004), the relation between fires and shrub encroachment does not follow a general pattern. In many cases, fire suppression and grazing had favored the advance of shrubs over the grasslands like in North American semiarid grasslands (Van Auken 2000); the northeast of Swaziland, South Africa (Roques et al. 2001), the Californian coastal chaparral, (Lloret and Zedler 1991) and the Chihuahuan Desert (Drewa 2003). However, Heisler et al. (2004) had found that in North American mesic grasslands frequent fires had favored the encroachment of the shrub species *Cornus drummondii* by stimulating the resprouting of this species and by eliminating grass competition. In northwestern Italy, *Betula pendula* shrubland greatly expanded after fires, while grass cover decreased, even in places where fire frequency was high (Borghesio 2009). Fires can also stimulate shrub recruitment by creating favorable micro-sites that allowed shrub germination (Franzese et al. 2009). Therefore, the effect of fire will depend on the specific response of each individual spe-

cies to fire, the species phenology and longevity, and on the characteristics of the fire such as intensity, frequency, and season (Bond and Midgley 2001).

In Mediterranean fire-prone ecosystems, during post-fire succession, plant species persist and regenerate by resprouting, by recruiting new individuals from a seed bank, or by both strategies (Paula et al. 2009; Paula and Pausas 2008). The heat, smoke, ashes, charcoal, and nitrogenous compounds released during plant combustion may act, individually or in combination, as a cue for post-fire seed germination (Paula et al. 2006) of dormant seeds from the seed bank (Keeley and Fotheringham 2000). Heat can stimulate germination by heat-shock, which produces the disruption of the impermeable tissues or alters the seed coat of hard-seeded species allowing water imbibition or oxygen uptake (Keeley and Fotheringham 2000). Smoke and charcoal showed to increase germination (Crosti et al. 2006; Keeley and Pizzorno 1986) and this may be related with a chemical effect of the substances contained in these fire-related products (Keeley and Fotheringham 2000). A butenolide compound from smoke (3-methyl-2Hfuro[2,3-c]pyran-2-one), derived from the combustion of cellulose, is among the responsible agents for the smoke effect (Flematti et al. 2004). For these fire-related cues to have an effect, the presence of a persistent seed bank or the production of heat-resistant seeds is required just before a fire occurs (Paula and Pausas 2008).

Many species restrict seedling recruitment to the immediate post-fire years, arising from previously dormant soil-stored seed banks. These traits are adaptive in fire-prone environments and are a key to providing resilience to specific fire regimes (Keeley et al. 2011). The positive effects of fire-cues on seed germination can be interpreted as adaptations to ensure post-fire recruitment. Consequently, all species that have mechanisms improving chances of successful seedling establishment can have an evolutionary advantage (Crosti et al. 2006). Heat is not a cue specific to fire, as soil heating may also trigger germination of the same species on unburned sites with open, bare mineral soil in summer. Smoke, on the other hand, appears to be a highly specific germination cue, and it is indicative of a rather specific fire adaptation (Pausas and Keeley 2009).

In the last 20 years, many studies concerning the role of fire effects on seed germination have been carried out in fire-prone ecosystems with Mediterranean-type climate (autumn–winter precipitation), such as Australia (Crosti et al. 2006; Tieu et al. 2001), South Africa (Brown et al. 2003), California (Keeley and Fotheringham 1998), the Mediterranean Basin (Moreira et al. 2010), and Chile (Figueroa et al. 2009; Gómez-González et al. 2008). In northwestern (NW) Argentinian Patagonia, there are few studies on fire cues related to vegetation recruitment (Franzese and Ghermandi 2011; Gonzalez and Ghermandi 2012) notwithstanding the fact that fire, along with grazing, is the main disturbance that affects this region (Gittins et al. 2011). Human

interventions, as well as the ENSO phenomenon, have changed the fire regime in this region during the last 100 years (Kitzberger et al. 2005). Southern South America is one of the extra-tropical regions most affected by El Niño (EN) and La Niña (LN) events of the ENSO (Grimm et al. 2000). During EN years, temperatures and precipitation values are in general higher than the normal means and during LN years in general the opposite pattern occurs (Daniels and Veblen 2000; Grimm et al. 2000). Therefore, EN years favor the accumulation of vegetation fuel, which dries off during subsequent LN years. This favors the occurrence and spread of severe and extensive fires (Ghermandi et al. 2004), which are likely to have an important role here (Ghermandi et al. 2010), since some climate change forecasts predict an increase in the frequency and in the amplitude of the ENSO phenomenon (Stevenson et al. 2012).

Patagonian grasslands are under an intense and continuous regime of sheep and livestock grazing. This has produced a decrease of the total vegetation cover, a huge reduction of palatable grasses cover, and it has favored shrub encroachment processes (León and Aguilar 1985). According to this, perennial grasses can be replaced by *Mulinum spinosum* or *Senecio* spp. shrubs and by *Acaena* spp. sub-shrubs (Bertiller and Bisigato 1998) in overgrazed paddocks of Patagonian ranches.

Fabiana imbricata Ruiz et Pavon (Solanaceae) is a native shrub characteristic of the ecotone between woody ecosystems and steppes in northwestern Patagonia (Argentina). This species is very important in the grassland dynamics because its encroachment related to fire (de Torres Curth et al. 2012) can change vegetation physiognomy and ecosystem processes. The spatial configuration of *F. imbricata* is related to fire, soil topography, and hydrography (Oddi et al. 2010). This species forms even-aged stands where no new recruitment is observed in the absence of extreme disturbances (Ghermandi et al. 2010). Although cattle or sheep do not consume this species, overgrazing disturbance alone does not show to favor its recruitment. Emergence and seedling growth of *F. imbricata* was not observed at all during 9 years after experimental mechanical clearing of grassland biomass, despite the fact that viable seeds were present in the soil seed bank, even if favorable environmental conditions occurred (Ghermandi et al. 2013). Germination at 20°C/24 h light was found to be very low (3%) and seeds did not germinate at lower temperatures or in darkness (Fischer et al. 2011). However, and even though this species does not resprout after fires, it shows a high recruitment from seeds during post-fire succession (Ghermandi et al. 2004, 2010). Mathematical models that analyze *F. imbricata* population dynamics at different fire frequencies and at different values of precipitation indicate that *F. imbricata* population is advancing over the grassland and that it grows at a wide range of fire frequencies, reaching its maximum with a fire frequency of once every 6–10 years (de Torres Curth

et al. 2012; Ghermandi et al. 2010). According to this, fire followed by a wet spring seems to be the best scenario for *F. imbricata* recruitment (Ghermandi et al. 2010). Fire frequency in this region is about once every 30 years, and it is expected to increase because of the ENSO phenomena previously described, which would imply more recruitment windows for *F. imbricata*. As it is a non-palatable species for livestock, this could be a major problem in this region, as northwestern (NW) Patagonian grasslands are one of the main natural resources in the region and the main economic source for the support of extensive livestock production.

The objective of this work is to evaluate if fire has a direct effect on *F. imbricata* recruitment, focusing on the effect of smoke, heat, charcoal, and their interactions on seed germination. We have hypothesized that fire-related factors will stimulate *F. imbricata* seed germination. If this is so, fires will contribute here to the grassland encroachment as mathematical models stated.

Methods

Study area

The study area is located in the San Ramón ranch, located 30 km east of San Carlos de Bariloche city, (41° 03' 19" S, 71° 01' 50" W), Río Negro province, Argentina (Fig. 1). This 23,846-ha ranch is situated in the Andean foothills and its main economic activity is livestock production. The climate is cold-temperate with a Mediterranean-type precipitation regime (60 % of the annual rain concentrated between May and August). Mean annual precipitation is about 580 mm and the mean annual temperature is 8.6 °C. Frequently, strong westerly winds blow the entire year and especially in summer (mean wind speed can reach 35 km/h) (San Ramón meteorological station, unpublished data). Vegetation belongs to the Sub Andean District of the Phytogeographical Patagonian Province (Cabrera 1971). Vegetation is characterized by a grassland steppe dominated by *Pappostipa speciosa* in the lowlands and by *Festuca pallescens* in the uplands (Boelcke 1957). Native shrubs such as *Senecio bracteolatus* and *Mulinum spinosum* are present, having a scattered arrangement (Ghermandi et al. 2004), and others, like *F. imbricata* and *Discaria articulata*, are present forming dense shrublands (Anchorena and Cingolani 2002). Northwestern Patagonian grasslands are the most productive of the region, being widely used for forestry and stockbreeding. Grazing and fire are the more frequent grassland disturbances that strongly influence vegetation dynamics in this area. For example, in January 1999, a wildfire burned 17,500 ha (60 % of the total ranch area) (Ayesa and Barrios 1999), and quickly spread because of an exceptional 1998–1999 drought that was caused by a strong La Niña event (National Weather Service, Climate Prediction Center), (Ghermandi et al. 2004).

Species description

Fabiana imbricata Ruiz et Pavón (Solanaceae) is an evergreen shrub geographically distributed from Mendoza to the center of Chubut in Argentina, and from Atacama to Valdivia in Chile. In NW Patagonian ecotone (Argentina) is frequently found in rocky substrates, and also in drainage lines and streams (Anchorena and Cingolani 2002). *F. imbricata* is characterized by a longevity of approximately 150 years (Oddi et al. 2010) reaching a height of 4 m (e.g., FJ Oddi, CONICET, Bariloche, Argentina pers. comm.). The fruit is a septicidal capsule that contains many seeds of 0.80–1.20 mm, having a reticulate seed coat. Seed production per mature plant was estimated at 200,000 (Ruete 2006). The flowering period extends from September to January and seeds mature from March to April. This species does not resprout after fires, but it shows a high post-fire recruitment from seeds.

Seed collection and treatments

At the end of the 2009–2010 summer, we collected mature seeds from randomly chosen *F. imbricata* individuals selected from different shrublands. These seeds were then stored in paper bags at room temperature in the laboratory until the treatments were applied in the autumn of 2010. Healthy seeds were separated using a stereoscopic microscope and viability was tested by the pressure method (Zuluaga et al. 2004).

Seed permeability

The water permeability of the seed coat was investigated by comparing water uptake of unscarified and scarified seeds (Morris et al. 2000). Seed scarification naturally occurs in field conditions after seed dispersion in March–April. Effectively cold and rainy autumns and winters soften the seeds coats by natural stratification occurring in the soil seed bank (personal observation). As harvested seeds did not suffer this natural process and with the objective to fasten experimental times, seed scarification was performed mechanically by abrasion between two sheets of fine-grained sandpaper (Herranz et al. 2006). However, unscarified seeds were also tested to see if scarification is really required to increase water permeability of the seed coat. Scarified and unscarified seeds were weighed and then placed in Petri dishes, imbibed in deionized water, and then placed in a germination chamber. After that, water absorption was measured gravimetrically by reweighting the seeds 4 and 24 h later and the results were reported as percent fresh weight. Each treatment consists of ten replicates of 100 seeds of each one.

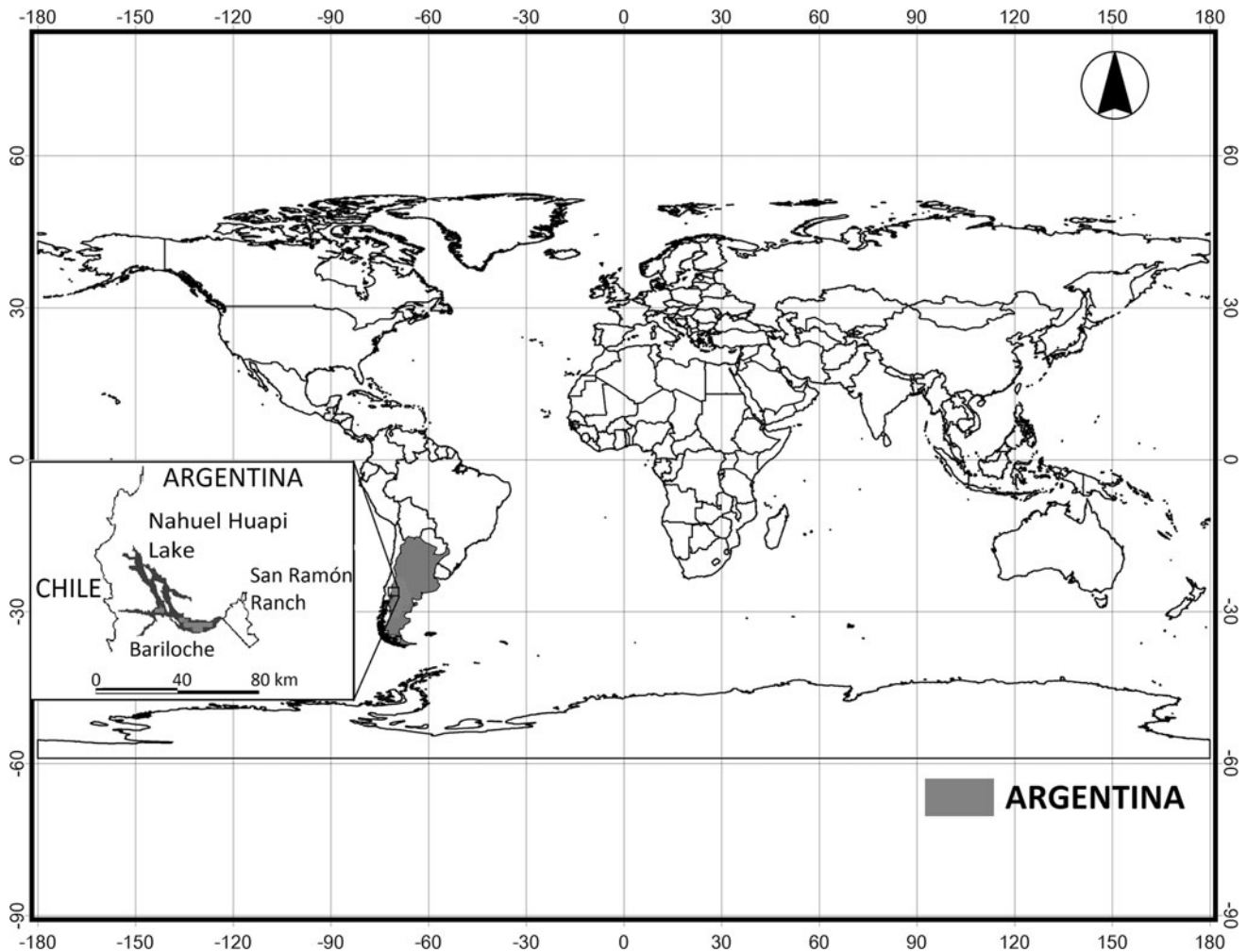


Fig. 1 Location of the study site

Scarification, heat, charcoal, and smoke treatments

A factorial experiment was designed to test the effect of scarification, heat, smoke, charcoal, and their interactions on *F. imbricata* seed germination. Scarification was included in the test to test if the seed coat is imposing some kind of dormancy. The factorial experiment resulted in a design that had four factors: smoke with two levels (smoked–unsmoked), charcoal with two levels (with charcoal–without charcoal), heat with five levels (unheated, 60 °C for 5 min, 60 °C for 10 min, 90 °C for 5 min and 90 °C for 10 min), and scarification with two levels (scarified–unscarified). Unheated seed were maintained at 20 °C (room temperature). The interaction charcoal \times smoke \times heat \times scarification was excluded from the design. Seed scarification was performed as described before. The heat levels selected were within the temperature range that seeds buried in the most superficial soil layers experience during grassland fires (Wright and Bailey 1982). Higher temperatures, which correspond to the temperatures observed during a fire

over the soil surface, were not tested because they were found to be lethal for this species (Ghermandi et al. 2013). For heat treatments, dry seeds were placed in Petri dishes and then put into a laboratory oven during variable periods depending on each treatment. After heat treatment, seeds were equilibrated at room temperature prior to incubation. For smoke treatments, a special device was used to produce smoke by the slow controlled combustion of grassland dry biomass. This device consists of a 200-l drum containing an interior grill for the biomass burning. The smoke was conducted by a galvanized pipe and then cooled and channeled to a 100-cm³ hermetic box by a plastic tube (adapted from Tieu et al. 2001). The seeds were placed in open Petri dishes and inside the box and afterwards exposed to smoke for 10 min. For the charcoal treatments, a 10 g/l solution of pulverized charcoal (Buhk and Hensen 2006) was obtained by the combustion of grassland dry biomass. Deionized water was added to the pulverized charcoal to obtain the required concentration of the solution.

As a result of the different combination of scarification, heat, smoke, and charcoal, a total of 30 treatments was obtained. The control was the one that did not receive any treatment (unscarified, unsmoked, unheated, and without charcoal). After the treatments, seeds were placed in sterilized Petri dishes over Whatman number 1 filter paper moistened with 4 ml of deionized water to allow seed imbibition. Carbendazim ($2 \text{ cm}^3/\text{l}$) was also applied to avoid fungi proliferation and the Petri dishes were then wrapped with plastic film to avoid water evaporation. After this, the Petri dishes were randomly placed and incubated in germination chambers with a controlled environment. The chamber was set to reach the same environmental conditions of the germination season (Baskin and Baskin 1998; Soriano 1960), which in the case of *F. imbricata* is the spring. Therefore, the chamber was set to have in each 24-h cycle, 12 h of light at a temperature of $19 \text{ }^\circ\text{C}$ and 12 h of darkness at $5 \text{ }^\circ\text{C}$, being used as light sources 18-W fluorescent Gro-lux lamps. These lamps have the advantage of producing a uniformly distributed lighting over large surfaces, and at the same time, producing no heating of the chamber environment. Each treatment had ten seeds and was repeated ten times.

Germination criteria

Seed germination was monitored once a week until the end of the experiment, 3 months later. At each count, the germinated seeds (those with radicle emergence $>1 \text{ mm}$, determined under a magnifying lens) were scored and removed from the Petri dishes.

Data analysis

Data from the imbibition test were tested in a one-way ANOVA directly as imbibition percentages, because they fit normality and homoscedasticity assumptions and the post hoc Tukey HSD test was calculated at $p < 0.05$.

To confirm any significant differences in seed germination between treatments, a factorial analysis of deviance was performed using a generalized linear model (GLM) with a binomial distribution. Not including the fourth interaction, the model resulted as follows:

Model $< - \text{glm} \quad (y \sim \text{scarification} \times \text{smoke} \times \text{heat} + \text{scarification} \times \text{charcoal} \times \text{heat}, \text{binomial})$.

To test the differences between the means of the treatments, a post hoc Tukey HSD test was performed at $p < 0.05$, using the R package multcomp.

Mean germination time

Mean germination time (MGT) was calculated for each treatment as

$$\text{MGT (days)} = \frac{\sum t_i n_i}{\sum n_i}$$

where n_i is the number of seeds germinated each day, and t is the number of days starting from the date of sowing (Bewley and Black 1994). For statistical analysis, MGT was calculated for those treatments exhibiting some germination in at least five replicates. A factorial ANOVA was performed to test significant differences in MGT (also excluding the fourth interaction), as they fit normality and homoscedasticity assumptions. The post hoc Tukey HSD test was calculated at $p < 0.05$. All data analyses described before were performed using the free R software, 2.13.1.

Results

Seed permeability

The percentage of increase in fresh weight was similar for scarified and unscarified seeds (Fig. 2; $p < 0.05$). After 4 h of water imbibition, the weight of 100 seeds went from an initial weight of $10.10 \pm 0.80 \text{ mg}$ (mean \pm SE) to $17 \pm 1.20 \text{ mg}$ for unscarified seeds and from 9.90 ± 0.85 to $15.50 \pm 2.10 \text{ mg}$ for scarified seeds. After 24 h of water imbibition, the fresh weight went to $30.50 \pm 2.10 \text{ mg}$ for unscarified seeds and to $28.20 \pm 1.30 \text{ mg}$ for scarified seeds, almost threefold the initial weight.

Scarification, heat, charcoal, and smoke effects on germination

Germination started between day 7 and 10 and continued beyond day 80. At the end of the experiment, seeds from the control exhibited $4 \pm 3 \%$ (mean \pm SE) of final germination (Fig. 3a). Scarification and smoke had a significant effect on final seed germination and char-

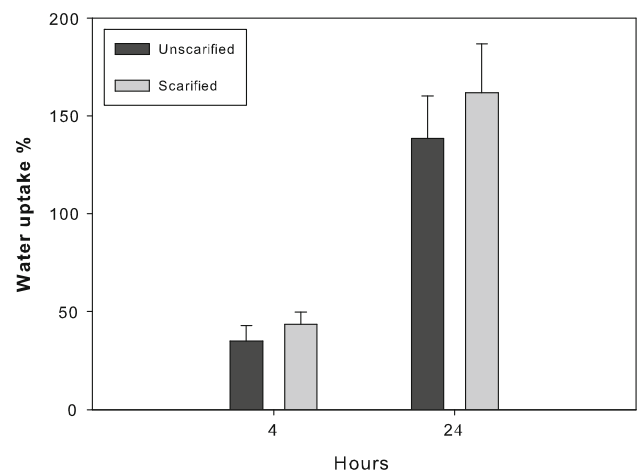


Fig. 2 Water uptake after 4 and 24 h for scarified and unscarified seeds. Bars indicate mean \pm SE

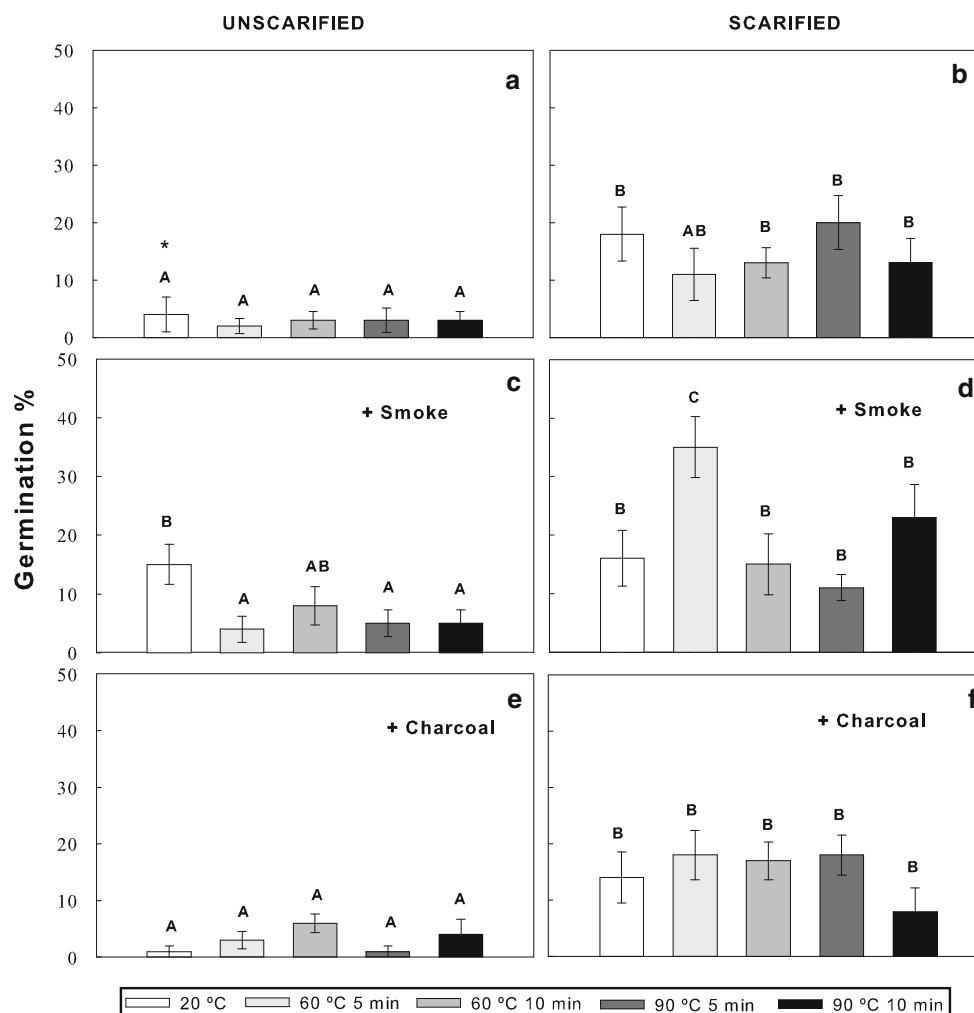


Fig. 3 Effect of heat (a), heat + scarification (b), heat + smoke (c), heat + smoke + scarification (d), heat + charcoal (e), and heat + charcoal + scarification (f) on final germination. Bars indicate mean \pm SE. Different uppercase letters indicate significant differences between all treatments according to Tukey post hoc at $p < 0.05$. *Control seeds

coal and heat had no significant effect (Table 1). In general, scarified seeds (Fig. 3b, d, f) showed higher germination percentages than unscarified seeds (Fig. 3a, c, e) and smoked seeds (Fig. 3c, d) showed higher germination percentages than unsmoked seeds (Fig. 3; $p < 0.01$). There was a significant interaction between scarification \times smoke and also between scarification \times smoke \times heat (Table 1). This means that scarified and unscarified seeds respond differently to the application of smoke and also that this varies with the level of heat applied. In general, smoke enhanced the germination of both unscarified and scarified seeds, but this enhancement was proportionally higher for scarified seeds (Fig. 4). Analysis of the interaction between scarification \times heat \times smoke showed that heat had a stimulatory effect on scarified seeds but not on unscarified seeds, and also that the effect depends on the level of heat applied, and on the smoke treatment. Scarified

smoked seeds show the best germination between all treatments, but this enhancement was proportionally higher for seeds that were heated at 60 °C for 5 min (Table 1; Fig. 3d). This combination was the one that showed the best germination between all treatments. Other interactions were not significant.

Mean germination time

Scarification, smoke, and charcoal had no effect on mean germination time. However, MGT was significantly affected by heat treatments ($p < 0.001$; $F = 66.63$; $df = 4$). Longer time exposures to heat seem to increase MGT, and those seeds heated at 90 °C for 10 min required a longer period of time to germinate (Table 2). There was no interaction effect between any factors on MGT.

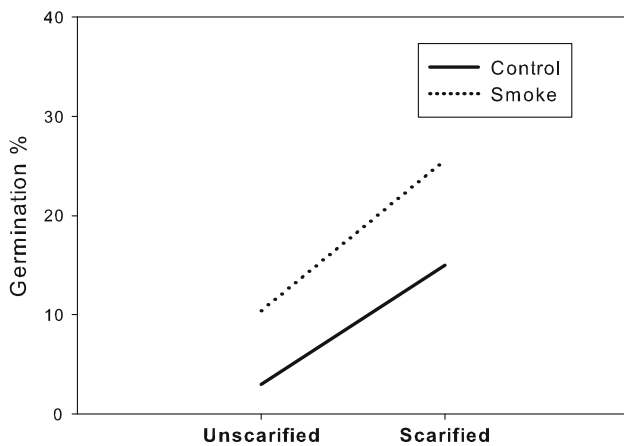
Table 1 GLM factorial analysis of deviance

	Estimate	SE	Z	Pr(> z)
Scarification	1.662	0.573	2.901	0.004**
Smoke	1.443	0.582	2.480	0.013*
Heat 60 °C-10 min	-0.298	0.777	-0.383	0.701
Heat 60 °C-5 min	-0.714	0.878	-0.813	0.416
Heat 90 °C-10 min	-0.298	0.777	-0.383	0.701
Heat 90 °C-5 min	-0.298	0.777	-0.383	0.701
Charcoal	-1.417	1.127	-1.258	0.208
Scarification × smoke	-1.585	0.694	-2.286	0.022*
Scarification × smoke × heat*	2.343	1.182	1.982	0.037*

Main effects of the level of each factor and the significant interactions. To simplify the table, interactions that were not significant are not showed

*Level of significance >95 %

**Level of significance >99.5 %

**Fig. 4** Interaction between scarification × smoke factors**Table 2** Mean germination time

Heat	MGT (days) SE
60 °C-5 min	23.08 ± 2.20 A
Unheated	23.34 ± 2.13 A
90 °C-5 min	24.45 ± 2.10 A
60 °C-10 min	26.07 ± 1.98 AB
90 °C-10 min	32.43 ± 2.24 B

Different uppercase letters indicate significant differences in mean germination time (MGT) at $p < 0.05$ (Tukey)

Discussion

In agreement with the mathematical models that indicate that *F. imbricata* shrublands are growing in relation to fire (de Torres Curth et al. 2012; Ghermandi et al. 2010), fire cues stimulated the germination of *F. imbricata*, indicating a direct effect of fire in the species recruitment by stimulating germination and/or releasing dormancy. The permeability to water that *F. imbricata*

seeds showed indicates that the seed coat is not imposing physical dormancy by restricting water uptake. However, the scant germination exhibited by the control seeds and the positive effect of scarification indicate that the seed coat is imposing some other kind of dormancy. In addition to the restriction of water uptake, Bewley and Black (1994) proposed other mechanisms by which the seed coat can impose dormancy on a seed, such as mechanical restriction of germination of the embryo, prevention of the exit of inhibitors from the embryo, presence of chemical inhibitors, and restriction of oxygen uptake. Probably one or more of these mechanisms are restricting *F. imbricata* germination, and this explains why seed scarification results in higher percentages of germination. Dormancy is important to avoid germination under inadequate environmental conditions (Finch-Savage and Leubner-Metzger 2006), especially in harsh and variable environments (Venable and Brown 1988), like these semiarid grasslands, to avoid the loss of individuals. Therefore, this trait would be important for this species to ensure germination when favorable conditions occurred after a fire, like the opening of a gap in the vegetation.

Fabiana imbricata seeds tolerated the temperatures tested here, which are between the most common temperatures that seeds buried in the superficial soil layers experience during grassland fires (Wright and Bailey 1982). Even though heat alone did not stimulate germination, it had an important role in stimulating germination when interacting with smoke. This may indicate that once dormancy is overcome, heat has a stimulating effect on final seed germination. Smoke was also an important stimulant for *F. imbricata* germination, yet the most important effect also occurred when interacting with scarification and heat. Hence, the interaction of heat, smoke, and scarification appear to be more important than the effect of each fire factor alone. Fire-related cues are present and act simultaneously in field conditions. Therefore, the high recruitment of *F. imbricata* observed in the field during post-fire succession (Ghermandi et al. 2004, 2010) could be explained in part by the simultaneous action of these

fire-related cues. Therefore, our findings and the previous evidence support our hypothesis about the role that fire-related factors have in the germination of *F. imbricata*.

As mentioned before, this species produces an extremely high number of seeds (Ruete 2006), which accumulate in the soil seed bank and remain viable for years (Gonzalez and Ghermandi 2008). Therefore, any small change in the germination percentage of this species will have a high impact in the field. The persistent seed banks will also have an ecological significance, because seeds can remain dormant and germinate when favorable conditions occur after a fire. It will also give to the species an adaptive advantage, which consists of increasing the chances to persist in the ecosystem. The relationship between the ability of a particular species to persist in the ecosystem with the fire regime is very important, and species which recruit from seeds after a fire would be able to persist if they reach sexual maturity before the next fire occurs (Bond and Midgley 2003; Clarke and Dorji 2008). *F. imbricata* reaches sexual maturity at approximately 6 years of age (Ghermandi et al. 2010) and fire frequency in this region is approximately once every 30 years. Therefore, under the current fire regime or even if fire frequency increases, this species can ensure its persistence in the ecosystem.

The two dominant species of these grasslands are the grasses *P. speciosa* and *F. palleescens*. The shrubs *M. spinosum* and *S. bracteolatus* are present in low density and are scattered within the grassland matrix. After exposure to fire cues, seeds from *M. spinosum* were killed and germination of *S. bracteolatus* seeds was inhibited (Gonzalez and Ghermandi 2012). *P. speciosa* seeds were shown to increase germination after being exposed to smoke alone (Franzese and Ghermandi 2012) but when the seeds were exposed to a combination of heat and smoke, germination was inhibited (Gonzalez and Ghermandi 2012). Moreover, when this species was subjected to experimental burning, seedling growth decreased (Franzese and Ghermandi 2012). The germination of *F. palleescens* was not affected by smoke, heat, or the combination of these factors (Gonzalez and Ghermandi 2012), but experimental burning was shown to reduce the germination and seedling growth of this species (Franzese and Ghermandi 2012). Even though *P. speciosa* and *F. palleescens* can resprout after fires, the remaining biomass is very low, and as these species are constantly subjected to grazing, especially by sheep, seedlings and young resprouts can be rapidly eliminated. *F. imbricata* is not affected by grazing, and therefore when suitable conditions for vegetation growth occurred after a fire, emergence and seedling growth occurs very fast, and this species rapidly dominates the vegetation canopy (Ghermandi et al. 2004, 2010). Therefore, after a fire, *F. imbricata* may have a competitive advantage over *P. speciosa*, *S. bracteolatus*, and *F. palleescens* to colonize these grasslands, which are constantly subjected to grazing. This is in accordance with what it was observed in the field in earlier stages of the post-fire succession with the evolution of vegetation cover (Ghermandi et al.

2004). Therefore, fire will not only stimulate *F. imbricata* germination but also (along with grazing) will contribute to eliminate the early competition by the dominant species, allowing *F. imbricata* to recruit successfully. Overgrazing alone does not favor *F. imbricata* encroachment, but fire and grazing together are very likely to have a synergic effect on the recruitment of this species.

The positive response to fire factors, and especially to smoke that *F. imbricata* seeds exhibited, may indicate that this species has an adaptive advantage or that is adapted to fire. Pierce et al. (1995) suggest that due to the response to smoke that species from non-fire-prone environments showed, this cannot be considered as a fire adaptation. More recent studies also support this and question the concept of plant traits adapted to fire (Bradshaw et al. 2011). However, on the other hand, Pausas and Keeley (2009) support the opposite view, saying that this conclusion does not consider the fact that smoke is a complex mixture of thousands of chemicals, many of which occur in diverse ecological settings and stimulate many plant processes. Moreover, even though most species seem to be sensitive to butenolide, only a small subset of Mediterranean-type climate species have the capacity to remain dormant and then cue germination to the immediate post-fire environment (Keeley et al. 2011).

Conclusions

The results obtained here add evidence that fires, possibly along with grazing, are positively contributing here to the grassland encroachment by *F. imbricata* and hence, to reduce the grassland productivity and biodiversity. Management techniques of this ecosystem should start considering fuel regulation, because in this type of grasslands (450–700 mm precipitation), fire depends on fuel accumulation over more than one year (Oesterheld et al. 1999). Thus, grazing and forestry management, which have a high impact in floristic composition and fuel load, could affect directly the occurrence, intensity and severity of fires.

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