

Disentangling *Fabiana imbricata* (Solanaceae) regeneration: The importance of disturbance and rainfall

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ABSTRACT

In Mediterranean ecosystems, fire influences plant population dynamics and changes plant community structure by affecting germination and establishment of seeder shrubs. *Fabiana imbricata* is a long-lived seeder shrub with a broad distribution in South America. In Northwestern Patagonia grasslands there are many records of *F. imbricata* recruitment after fires. We hypothesized that recruitment is promoted by: 1) soil erosion that exposes deeply buried seeds; 2) direct fire effects such as heat that could break seed dormancy; 3) indirect fire effects (i.e. increase of light availability and elimination of allelopathic substances) and 4) water availability in spring. In field conditions, we tested the effects of shading and soil disturbance on *F. imbricata* recruitment and seed availability and distribution in the soil profile. Under controlled conditions, we investigated the influence of leaf leachate, light, heat and water on seed germination and seedling emergence. Seed germination was inhibited by leachate, and seedling emergence was inhibited by seed heated to 80 °C and 120° for 5 min. *F. imbricata* seedlings only emerged in germination treatments that simulated wet and very wet spring conditions. Fire and postfire wind that favor seed exposure, combined with high precipitation early in the growing season, would be necessary for successful shrub recruitment. When *F. imbricata* shrubland colonizes the grassland, it strongly modifies local vegetation structure, reduces species richness and increases fuel loads. *F. imbricata* is a key species in the ecosystem specially related to fire regime. Information on the postfire regeneration of this species would provide valuable knowledge of the changes in biomass accumulation in a fire-prone Mediterranean ecosystem.

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1. Introduction

In Mediterranean ecosystems, fire can influence plant population dynamics and change plant community structure (Bond and van Wilgen, 1996) by affecting the germination and establishment of non-sprouting woody species, called “seeder shrubs” (Lloret and Vilà, 1997; Wellington and Noble, 1985). Fire could produce direct and indirect positive effects on the seeder shrub germination. For example, this disturbance can act directly, stimulating seed germination by exposing seeds to high temperatures or other fire cues (Dayamba et al., 2008; Figueroa et al., 2009;

Keeley et al., 2005; Tieu et al., 2001; Tyler, 1995; Valbuena and Vera, 2002), or indirectly by increasing resources availability (Bond and van Wilgen, 1996; Whelan, 1995) or removing allelotoxins (Keech et al., 2005; Keeley et al., 1985). In particular, canopy removal caused by fire can produce changes in microclimatic conditions, for example by modifying light quantity and quality available for vegetation, and increasing temperature fluctuations, which could promote germination in some species (Bond and van Wilgen, 1996; Pons, 1992; Pugnaire and Lozano, 1997).

The northwestern Patagonia semiarid grasslands are fire prone systems, where the climate is Mediterranean, with accumulated rainfall in autumn–winter. In the northwestern Patagonia region, the fire regime over the past century has been affected by climate variation related to the ENSO phenomenon, and human land use (Veblen et al., 1999). In this area, El Niño events are associated with unusually high precipitations, while La Niña events are associated

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with droughts (Daniels and Veblen, 2000). Often, one event follows the other, and while El Niño promotes substantial biomass accumulation, La Niña events lead to substantial drying out of the vegetation, increasing its flammability.

Fabiana imbricata Ruiz et Pavón (Solanaceae) is the only seeder shrub of this region that forms conspicuous monospecific shrublands, which provide a degree of landscape heterogeneity within a grassland matrix. When a new shrubland colonizes the grassland, it strongly modifies local vegetation structure, reduces species richness (Dudinszky and Ghermandi, unpublished data) and increases fuel loads (1500 kg/ha of biomass in grasslands versus 16,000 kg/ha in shrublands; Bran et al., 2006; Defossé et al., 1999). *F. imbricata* is a key species in the ecosystem specifically related to fire regime. Studies of the postfire regeneration of this species would provide valuable information about the changes in biomass accumulation in a fire-prone Mediterranean ecosystem (Pausas and Lloret, 2007).

F. imbricata forms even-aged shrublands in which seedlings and juveniles are mostly absent. Studies of shrubland age using dendroecological techniques show that recruitment events coincide with landscape-scale disturbances, particularly fires (Oddi et al., 2010). In addition, high rates of seedling recruitment are detected near burned shrublands after severe fire, for example, in after the 1999 fire in the same region (Ghermandi et al., 2004, 2010). Furthermore, Ruete (2006) reported that the age of a shrubland coincided with the construction of a gas pipeline, which involved substantial soil disturbance. These results suggest that the recruitment of *F. imbricata* depends on disturbances such as fire and soil removal. However, it is unknown how these disturbances stimulate their recruitment. On one hand, it is possible that seeds, such as those of many other Mediterranean ecosystem shrubs, are stimulated directly or indirectly by fire. On the other hand, small seeds are known to be buried deeper in soil than larger seeds, and deeper burial reduces seedling emergence (Auld and Denham, 2006; Bond et al., 1999; Grundy et al., 2003). We expected that most of the seedbank would reside in the deeper layers and therefore that soil removal could be a plausible mechanism for bringing deeply buried seeds to the surface where they can germinate. Exposure of seeds on the surface through soil removal also occurs during postfire conditions due to wind erosion, and in windy regions such as Patagonia, soil removal could be an important indirect consequence of fire.

In Mediterranean environments, post-disturbance climatic conditions may also regulator this process. Seedling establishment in these environments occurs mostly in spring when rainfall is also low. Thus postfire spring rainfall may be crucial for establishment, similar to the woody plant *Eucalyptus incrassata* in Australia, which recruits only during favorable climatic condition following wild-fires (Wellington and Noble, 1985).

In this study we used an experimental approach to test the notion that recruitment of *F. imbricata* is promoted by fire followed by wet springs. Specifically, we hypothesized that: 1) soil erosion that exposes deeply buried seeds is required to illicit recruitment of *F. imbricata* seeds, 2) direct effects of heat on buried seeds could break their dormancy; 3) indirect effects of fire such as increased light and elimination of allelopathic substances could enhance recruitment, and 4) increased water availability would increase the emergence of *F. imbricata* in spring.

2. Methods

2.1. Study area

Our study was carried out in semiarid grasslands at the San Ramón ranch, 30 km eastward of Bariloche, Northwestern Patagonia, Argentina (41°03' S, 71°01' W). The climate is temperate with

a Mediterranean precipitation regime (60% concentrated in May–August). Mean annual precipitation is 578 mm, and mean annual temperature is 8.7 °C (Meteorological Station, San Ramón ranch). Strong W-NW winds blow frequently throughout the year, accentuating water stress in the warm seasons. Soils of sandy-loam texture with superficial horizons containing organic matter are moderately developed (Haploxerolls, Gaitán et al., 2004). These grasslands are dominated by a tussock grasses matrix accompanied by sparse shrubs and shrublands, and also there are outcrops dominated by small patches of *Austrocedrus chilensis*. Dominant perennial tussock grasses are *Pappostipa speciosa* (Trin. and Rupr.) Romasch, ex *Stipa speciosa* and *Festuca pallescens* (St. Yves) Parodi, while dominant shrubs are *F. imbricata*, *Mulinum spinosum* (Cav.) Pers. and *Senecio bracteolatus* Hook et Arnott. The latter two species are middle-size shrubs which are sparsely distributed.

2.2. Study species

F. imbricata is a long-lived unpalatable shrub (ca. 150 yr; Oddi et al., 2010), 1.5–3 m high, that reaches sexual maturity at approximately 6 years, and produces abundant seeds. Seeds are very small (0.1 ± 0.01 mg; mean \pm SE, Ruete, 2006) and form persistent soil seed banks (Gonzalez and Ghermandi, 2008). Shrublands are distributed along the forest – steppe ecotone covering variable extensions (100 m² to several hectares) and are frequently located in the middle slope (Anchorena and Cingolani, 2002).

2.3. Experimental design

2.3.1. Seed collection

For each experiment seeds were collected from several randomly selected individuals in different shrublands. At the time of the experiments, seeds had been collected in the previous season. Seeds were stored in paper bags at room temperature until the experiments were performed. Only those seeds that felt full and firm when gently squeezed were used in the experiments (viability by pressure method, Zuluaga et al., 2004).

2.3.2. Canopy removal and soil disturbance

On October 2001 we delimited 16 plots (10 m diameter each) in two shrublands with the same aspect and slope. Distance among plots ranged from 5 to 10 m. In eight plots, we cut all shrubs to ground level (canopy removal treatment), while the remaining plots were left intact (control treatment). In the canopy removal treatment we also eliminated the herbaceous vegetation and mixed soil layers at a depth of 10 cm to expose buried seeds from half of each plot (canopy removal + soil disturbance treatment). We monitored the emergence of *F. imbricata* for eight years until January 2009.

2.3.3. Seed availability and distribution in the soil profile

On April 2004, we sampled the seed bank in each half of the plots corresponding to the canopy removal treatment without soil disturbance (see more details above) to test seed availability and distribution. We collected 10 cm diameter samples at 0–1 cm and 1–6 cm depth, which were stratified at 5 °C for two months (10 soil samples \times 2 depths \times 8 plots = 160 total samples). On September 2004, half of the samples (80) were placed in a greenhouse for 10 months. Pots were watered regularly and seedling emergence was registered weekly (seedling emergence method). Each of the 80 remaining soil samples was added to a saturated sodium chloride solution which separates the organic matter from the mineral soil fraction (Gonzalez and Ghermandi, 2012). Healthy seeds were

manually separated from the organic matter and counted under a binocular microscope (seed extraction method).

2.3.4. Effect of leaf leachate and light on seed germination

To assess the effect of leachate on seeds from two positions (surface soil with light, buried seeds in darkness), we performed a two-way ANOVA with leachate (leachate and non-leachate levels), and light (light and darkness levels) as factors. In March 2005, we sowed 20 seeds in 40 Petri dishes on double filter paper (10 replicates for each treatment). To perform the leachate treatment we made an infusion using *F. imbricata* leaves to simulate the natural extraction by rain of soluble substances that could be present in the litter. The infusion was obtained by immersing 25 g of leaves in 250 ml water at 36 °C for 30 min and sprayed on 20 Petri dishes (leachate treatment). The remaining dishes were sprayed with water (non-leachate treatment). Half of the Petri dishes assigned to leachate and non-leachate treatments were wrapped with aluminum foil (darkness treatment), and the remaining were unwrapped (light treatment). All dishes were placed in a germination chamber (24–31 °C, 13 h light) for two months, and rehydrated when they dried. Pots from the dark treatment were watered in semidarkness. We monitored seed germination weekly until the end of the experiment.

2.3.5. Effect of heat on seedling emergence

In November 2008, we tested the effect of dry heat (using an oven) on seedling emergence by exposing seeds to high temperatures for a 5 min interval. There were three heat treatments: 80 °C, 120 °C and unheated control. The selected temperatures were within the temperature range that the buried seeds experience in surface soils during grassland fires (Wright and Bailey, 1982). After treatment, seeds were sowed in pots containing sterilized soil (2 days at 100 °C) and placed in a greenhouse. We used 10 replicates of 10 seeds per treatment. Pots were watered daily and seedling emergence was monitored weekly for three months.

2.3.6. Effect of different simulated spring rainfalls on seedling emergence

In October 2010, we sowed 10 seeds in each of the 112 pots (10 × 13 cm²) that contained sterilized grassland soil (2 days at 100 °C). Pots were assigned to four different watering treatments ($n = 28$ by treatment): dry, normal, wet, and very wet; simulating the quantity of rainfall in the spring season. The water amount was calculated based on the mean value of monthly average precipitation from October to December (1928–2009 Meteorological Station, San Ramón Ranch) and set proportionally to the pot area (mm per month): dry spring: 12.5 ml (mean – 1 Standard Deviation, SD), normal spring: 25 ml (mean), wet spring: 37.5 ml (mean value + 1 SD), and very wet spring: 50 ml (mean + 2 SD). Water amount was distributed regularly throughout the experiment (three times per week). Seedling emergence was checked once a week during three months.

2.3.7. Data analysis

Canopy removal and soil disturbance treatment data were not analyzed due to extremely low seedling germination results. We used Wilcoxon Matched Pairs test to compare the number of seeds in the seed bank between the two depths. A factorial ANOVA was used to evaluate the effect of leaf leachate and light on germination (log-transformed data). ANOVA contrasts were carried out to test significant interactions between the main effects in the factorial design. We compared seedling emergence data from heat treatments with a *t*-test since we did not obtain emergence from the 120 °C treatment. To compare seedling emergence among different spring rainfall treatments, we used a Kruskal–Wallis test.

Differences *a posteriori* were tested with the comparisons of mean ranks for all group tests. For all tests significance level was 0.05 and standard error (SE) was used to calculated variation.

3. Results

We recorded seedling emergence in only the canopy removal + soil disturbance treatment, and it was very low. Only nine seedlings emerged in one 78.5 m² plot, which equates to 0.1 seedling m⁻². This seedling density represented less than 0.001% of the superficial seed bank estimated by the manual seed separation method (Table 1). Only one seedling survived until the end of the experiment. We recorded huge differences in the size of the seed banks using two different methods, with seed abundance two orders of magnitude greater using the extraction than the emergence method. Data from the manual seed separation method showed that the deeper soil layer (1–6 cm) contained more seeds than the surface layer (0–1 cm) (Table 1; $Z = 2.5$; $P = 0.008$). We also found that germination in laboratory conditions depended on both light and leaf leachate treatments (light × leachate: $F_{1,36} = 13.79$, $P < 0.001$). Leachate addition and darkness decreased germination ($P < 0.001$) (Fig. 1). Heat had a detrimental effect on seed germination; emergence was lower after exposure at 80 °C ($32\% \pm 4.4$; mean \pm SE) compared with the controls ($48\% \pm 5.4$; $t_{18} = 2.30$, $P = 0.033$). In the greenhouse experiments we found zero or near zero seedling emergence under simulated dry and normal spring rainfall conditions (Fig. 2). Seedling emergence in wet and very wet spring rainfall treatments was extremely variable ($15\% \pm 21$ and $8.5\% \pm 15$ respectively), and we only found significant differences among very wet and the two lower precipitation levels ($H = 28.22$, $P < 0.001$, Fig. 2). There were no differences between wet and very wet spring treatments ($P = 0.17$).

4. Discussion

F. imbricata does not recruit in mature shrublands, though massive recruitment episodes of this species have been observed after fire and soil disturbance. After the occurrence of a severe wildfire in January 1999, new shrubs were detected (Ghermandi et al., 2010; Oddi et al., 2010; Oddi, 2013). Similarly, three recruitment pulses after fires in 1964, 1976 and 1989 were also identified by dendroecological techniques (Oddi, 2013). Apparently, *F. imbricata* recruitment depends of disturbances (principally fire), but it is unknown through which mechanism.

We examined the soil seed bank and found a large number of seeds, which indicates that seed availability would not be limiting recruitment of *F. imbricata*. Nevertheless, the low germination rates recorded from soil seed bank samples under greenhouse conditions suggest that there could be other factors besides water that inhibit seed germination. Effectively, the laboratory experiments showed that germination was inhibited by leaf leachate. The presence of potentially phytotoxic secondary metabolites, such as

Table 1

Seed number (mean \pm SE) obtained by seedling emergence and seed extraction method. Percentage of seeds that germinated (estimated from the seed extraction method) is shown between parentheses. Different lower-case letters indicate significant differences between soil depths within each method. Statistical comparisons by Mann–Whitney test (seedling emergence) and Wilcoxon Matched Pairs test (seed extraction). $P < 0.05$.

Soil depth	Seedling emergence (seeds m ⁻²)	Seed extraction (seeds m ⁻²)
0–1 cm	10 \pm 6 (0.19%) a	5092 \pm 1800 a
1–6 cm	24 \pm 11 (0.17%) a	14053 \pm 4968 b

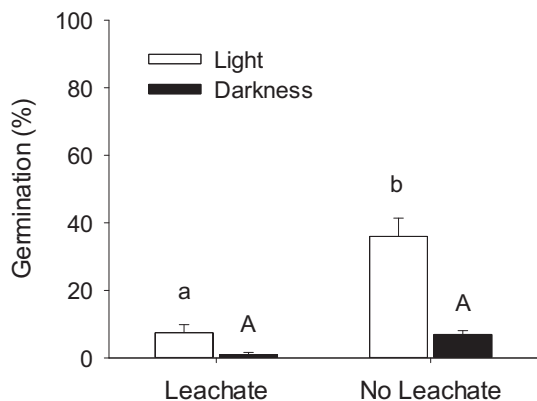


Fig. 1. Germination percentage (mean \pm SE) in light and darkness conditions with and without leachate presence, respectively. Capital letters show differences between leachate levels within the darkness condition, while smaller letters show differences between leachate levels within the light conditions. $N = 10$. $P < 0.05$.

sesquiterpenes and anthraquinones, has been demonstrated in *F. imbricata* (Brown, 1994a, 1994b; Knapp et al., 1972; Schmeda-Hirschmann and Papastergiou, 1994) although the allelochemic effects of these substances have not yet been proven.

Heat did not stimulate seed germination (very low at 80 °C and nil at 120 °C). We do not exclude the possibility that other fire cues not tested in this study (smoke, ash, charcoal) could trigger seed germination, as in other Mediterranean species (Keeley et al., 2005). The 1999 postfire extensive establishment (Oddi, 2013) was probably due to a combination of soil buffering during fire and soil erosion after fire. Soil acts as a heat buffer at very shallow depths. In experimental burns carried out in the study area, soil surface mean temperature ranged between 548 and 603 °C, while average temperature at a depth of 1 cm was 85% lower (Franzese and Ghermandi, 2012). In the 1999 postfire, the surficial soil layer erosion (Ghermandi, pers. obs.), caused by winds, probably exposed unheated seeds that had been buried in deeper soil layers.

The effects of fire on shrub recruitment can be indirect, as when fire destroys vegetation and/or substances present in soil that inhibit seed germination (Keeley et al., 1985; Whelan, 1995), or direct, as when heat stimulate germination (Keeley, 1986). Fire opens the canopy and makes resources, particularly light, available for germination of most species (Baskin and Baskin, 1989; Bond and van Wilgen, 1996). However, in our study, canopy opening through

the experimental removal of shrubs did not stimulate seed germination.

Although *F. imbricata* is well adapted to the semiarid environment through foliar reduction and the presence of a thick leaf cuticle, it is sensitive to water stress during the establishment period. This sensitivity may not be a problem for this long-lived species because the probability of having at least one recruitment opportunity during the lifespan of an adult plant is high. Seeds of this species need the occurrence of a disturbance and sufficient water to germinate. If these conditions do not occur one after the other, then plants will probably not establish.

In summary, therefore, the results of this study indicate that the fire-driven mechanisms responsible for recruitment of *F. imbricata* include: 1) exposing the seeds at the surface, 2) the elimination of allelopathic compounds, and 3) the occurrence of abundant spring rains. Increases in the density of these shrubs are likely to lead to the development of monospecific shrublands, with marked effects on ecosystem structure and functioning (e.g. Eldridge et al., 2011; Sala et al., 1989; Van Auken, 2000).

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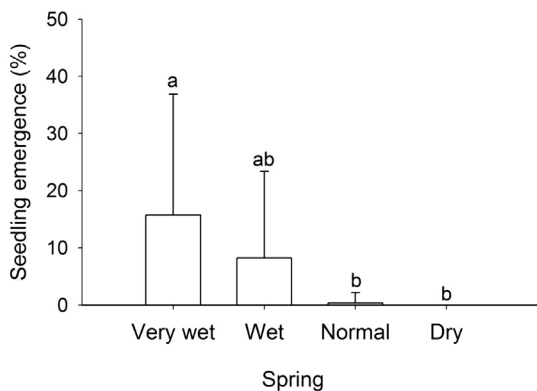


Fig. 2. Seedling emergence percentage (mean \pm SE) in four spring rainfall treatments: Very wet, wet, normal, and dry. Letters show differences between treatments. $N = 28$. $P < 0.05$.

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