Effect of fire on recruitment of two dominant perennial grasses with different palatability from semi-arid grasslands of NW Patagonia (Argentina)

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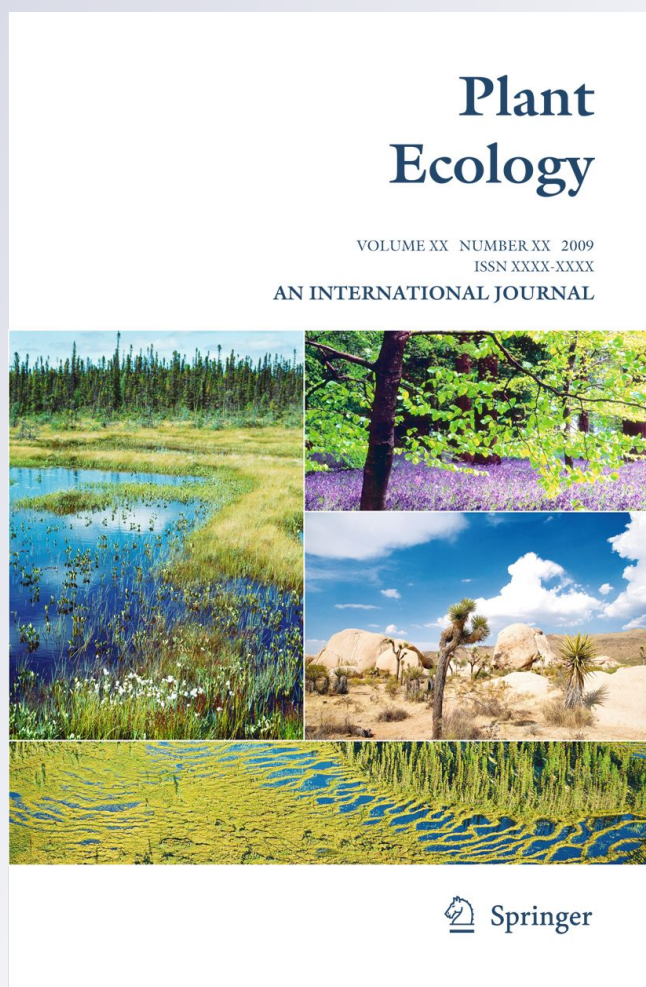
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Jorgelina Franzese · Luciana Ghermandi

Abstract Fire is a non-selective disturbance that impacts equally plant species that could be selected differentially by livestock. Post-fire recruitment dynamics is an important ecological process that has been barely studied in Patagonian grass species. This work analyzes the effect of fire on seed germination, seedling growth, and survival of *Pappostipa speciosa* (ex *Stipa speciosa*) and *Festuca pallescens*, two dominant perennial grasses from NW Patagonia that differ in palatability. We hypothesized that physical and chemical factors derived from fire differentially affect recruitment of these species. We performed experiments in the field and under laboratory and greenhouse conditions to study the integral effect of fire and of related abiotic factors (i.e., smoke, heat, charcoal, and ash) on different phases of recruitment of both species. Experimental burning promoted *P. speciosa* emergence over time, but they did not affect *F. pallescens* total emergence. Experimental burning decreased *P. speciosa* seedling growth (i.e., few leaves and small size), but they did not affect seedling survival. Smoke from laboratory experiments stimulated *P. speciosa* germination. Exposing *F. pallescens* seeds to 120°C decreased germination and seedling growth. Fire might act as a selective force on recruitment of both species, as well as changing competitive interactions during postfire regeneration. The effect of fire on the recruitment dynamics of the studied species depended strongly on both intrinsic species characteristics and meteorological conditions.

Keywords Germination · Seedling growth · Seedling survival · Disturbances · *Pappostipa speciosa* · *Festuca pallescens* · Grass palatability

Introduction

Grazing by domestic livestock and fire are two of the main disturbances affecting grasslands worldwide (Watkinson and Ormerod 2001). Both are large-scale disturbances that directly affect coverage, composition, and structure of vegetation (Gibson 2009). Unlike grazing, which mainly affects more palatable grass species (Bertiller and Bisigato 1998), fire is a non-selective disturbance that equally affects palatable and unpalatable species. However, the regeneration responses of different native grass species to fire will depend mainly on their intrinsic characteristics (Bond and van Wilgen 1996).

Fire has varied effects on the recruitment of native species of semi-arid environments (Fenner and Thompson 2005). Heat can reduce seed viability or promote seed germination (Baskin and Baskin 1998;

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Van Staden et al. 2000), while smoke, ash, and charcoal can produce chemical or physical changes in the seed environment that modify germination responses (Brown and Van Staden 1997; Pérez-Fernández and Rodríguez-Echeverría 2003). In turn, an increase in the temperature to which seeds are exposed can decrease seedling growth (Hanley and Fenner 1998). However, the increased availability of specific nutrients in the immediate post-fire may benefit the growth of those seedlings originating from seeds with limited reserves of these nutrients (Hanley and Fenner 1997).

The effects of grazing on the regrowth of palatable native grasses in semi-arid grasslands of Patagonia (Argentina) have been widely studied (e.g., Graff et al. 2007; Gittins et al. 2010; Busso et al. 2011). Although palatable species can tolerate defoliation better than unpalatable species (Gittins et al. 2011), high grazing pressure may nevertheless threaten their populations (León and Aguiar 1985; Gaitán et al. 2010). The effect of fire on the regrowth of native grasses that differ in palatability have been also examined (e.g., Robberecht and Defossé 1995; Peláez et al. 2003), but fewer studies have examined its effect on their seedling recruitment (Gonzalez and Ghermandi, in press).

Northwestern Patagonia is dominated by two perennial grass species: *Pappostipa speciosa* (ex *Stipa speciosa*) and *Festuca pallescens* (Correa 1998). These grasses have morphological and physiological traits that differentiate their vulnerability to disturbances, such as grazing and fire (Gonzalez et al. 2010). While *P. speciosa* is relatively less palatable, *F. pallescens* is highly palatable and is one of the most important forage species in the region (Velasco and Siffredi 2009). Although both grasses are adapted to fire, adult plants of *F. pallescens* have lower post-fire survival than those of *P. speciosa* (Gittins et al. 2011). Since species-specific responses determine differences in adult susceptibility to fire, it is also possible that they would determine differences in seedling post-fire recruitment patterns. However, little is known about the role of fire on seedling recruitment.

The aim of this work was to study the effect of fire on the responses of seed germination, seedling emergence, seedling growth, and survival of *P. speciosa* and *F. pallescens*. We hypothesized that physical and chemical factors associated with fire differentially affect the recruitment of these two species. We performed experiments in the field and under laboratory and greenhouse conditions to study the integral effect of fire and related abiotic factors (i.e., smoke, heat, charcoal, and ash) on different phases of seed recruitment of both species. We relate the results to a consideration of which mechanisms can be mediated by the species-specific responses, and the possible implications of these responses for grass recruitment dynamics.

Methods

Study area

The study was carried out in the northwestern Patagonian steppe, Argentina (41°03′19″ S–71°01′50″ W). Livestock grazing is the most important economic activity of the region, and it is based exclusively on natural vegetation (León and Aguiar 1985). Mean annual precipitation is 580 mm, of which 60% falls in autumn and winter, and mean annual temperature is 8.6°C (Meteorological Station, San Ramon ranch). Strong W–NW winds blow frequently throughout the year. The grassland is dominated by the perennial tussock grasses *Pappostipa speciosa* ((Trin. and Rupr.) Romasch, ex *Stipa speciosa*) and *Festuca pallescens* (St. Yves) Parodi. The dominant shrubs are *Fabiana imbricata* Ruiz et Pavón, *Mulinum spinosum* (Cav.) Pers., and *Senecio bracteolatus* Hook et Arnott. The vegetation cover is about 55%, of which 33% corresponds to *P. speciosa* and *F. pallescens*. Gaps (inter-tussock areas) are colonized by herbaceous species like the native forbs *Triptilion achilleae* Ruiz et. Pavón, *Plagyobothrys verrucosus* (Phil.) Johnst., and *Microsteris gracilis* (Hook.), and the exotic forbs *Erophila verna* (L.) Chevall., *Holosteum umbellatum* L., and *Rumex acetosella* L.

Study species

Pappostipa speciosa dominates at lower elevations than *F. pallescens* (<900 masl, and >1100 masl, respectively), and the species co-dominate in intermediate areas. The gradual shift from one community to another is set by an elevational change that determines a gradient of temperature and precipitation (Anchorena and Cingolani 2002).

Pappostipa speciosa and *F. pallescens* flower in late spring and produce seeds in early summer that are mostly dispersed by wind and animals at the end of

summer. Both species seem to have a high potential for recruitment since they have high seed production ($\sim$1,330 and $\sim$5,000 seeds/plant, respectively; Gittins 2001), a high proportion of viable seeds (98 and 88% viable seeds, respectively; Gonzalez pers. com.), and a high frequency of microsites suitable for their establishment (i.e., gap or inter-tussock areas; Defossé et al. 1997a). *Pappostipa speciosa* mean seed weight is 7.05 mg, and *F. pallescens* mean seed weight is 2.75 mg (Ghermandi 1992). Both grasses reproduce strictly from seed and form transient seed banks (Ghermandi 1997).

Effects of fire on seedling recruitment

Field experiments

We delimited 0.5-m-diameter plots ($n = 20$) in gaps (inter-tussock areas) inside a 1-ha cattle exclosure. In March 2008 (after seed dispersion), we removed the top 5 cm of soil in each plot. Soil was sterilized (2 days at 100°C) to kill the soil seed bank and then returned to the plot. For each species, we sowed 50 seeds in each of ten plots. We estimated the viability by the pressure method (Zuluaga et al. 2004) to select *F. pallescens* seeds and the flotation method to separate *P. speciosa* seeds. We created a 30-cm-wide buffer zone around each plot by cutting all vegetation to ground level. In May 2008, five plots per species were burned (burned treatment, B) with a portable propane gas burner, while the remaining plots were not burned (unburned treatment, U). Plant biomass from the grassland, spread evenly over the soil surface, was used as fuel. K-type thermocouples connected to dataloggers were placed on the soil surface and buried in the soil at the same depth as seeds (1 cm) to monitor temperatures during fires. We ceased burning when the surface thermocouple registered $\sim$600°C, which is within the temperature range expected for semiarid grasslands with similar fine fuel availability (preliminary tests of this study; Wright and Bailey 1982). After burning, we put translucent plastic cylinders (10 cm tall) around the plots to avoid secondary seed dispersion and granivory by crawling insects. Seedling emergence was monitored in late fall 2008 (June) and in the following spring (monthly from September to December). Seedling growth (height and leaf number) and survival were recorded monthly for two growing

seasons: December 2008 to April 2009, and September 2009 to April 2010.

Laboratory and greenhouse experiments

In February 2008, we collected seeds from randomly chosen *P. speciosa* and *F. pallescens* tussocks. Seeds were stored in paper bags at room temperature until October 2008, when we exposed the seeds to heat, smoke, charcoal, ash (hereafter "laboratory fire treatments"), and control treatments. We used five replicates of ten seeds by fire treatment and control (5 replicates × 10 seeds × 7 treatments = 350 seeds per species). For the heat treatments, seeds were placed in an oven for 5 min at 60, 90, or 120°C. The temperatures selected were within the temperature range that seeds buried in the superficial soil layers experience during grassland fires (Wright and Bailey 1982). We exposed the seeds to dry heat, because fires occur during summer when the superficial soil is dry (Franzese et al. 2009). For the smoke treatment, seeds were exposed to smoke for 10 min (Pérez-Fernández and Rodríguez-Echeverría 2003). The smoke came from combustion of biomass belonging to the dominant grassland species. The plant material was burned inside a 200 l drum, which was connected to a 100-cm³ box through a galvanized tube. Samples were placed on shelves inside the box (Dixon et al. 1995). Charcoal and ash were obtained from the combustion of biomass from the dominant grassland species. For the charcoal and ash treatments, we applied 4 ml of 10 g/l of pulverized charcoal solution or ash solution, respectively, to each sample (Buhk and Hensen 2006). Samples in the control group were not treated with heat, smoke, charcoal, or ash. After treatment, seeds were placed in Petri dishes on simple filter paper and treated with pulverized fungicide (Carbendazim®), watered with 4 ml distilled water (except for samples from the charcoal and ash treatments), and wrapped with transparent film to reduce evaporation. Filter papers that dried out during the experiment were re-hydrated. The Petri dishes of all treatments (including control) were placed in a germination chamber for 2 months, simulating an autumn photoperiod: March: day: 7–20 h, 18.1°C/night: 4.7°C; April: day: 8–19 h, 13.5°C/night: 2.0°C. Diurnal temperatures for March and April corresponded to the mean maximum monthly temperatures in the study site, while night temperatures were mean

minimal temperatures for each month (Baskin and Baskin 1998). We monitored seed germination (i.e., radicle protrusion) weekly during the first month and biweekly during the second month. To evaluate post-germination responses, ten seedlings per species and treatment were transplanted after radicle appearance into individual trays (8 × 5 cm) filled with grassland soil and allowed to grow for 65 days in a greenhouse. Before transplanting them, we measured their root length and height. At the end of the experiment we measured root length and height, counted the leaves, and weighed the dry biomass (60°C for 24 h) of all seedlings.

Data analysis

To assess how the field experimental burning affects *P. speciosa* seedling emergence over time, we used repeated-measures ANOVA. We did not analyze seedling emergence over time in *F. pallescens* because this species showed a massive emergence pulse with no new seedlings subsequently. We assessed the effects of field experimental burnings on *F. pallescens* total emergence with *t* tests. Log-rank tests were used to compare seedling survival between burned and unburned treatments by species. Also, these tests were used to compare *P. speciosa* seedling survival between the two studied growing seasons within Burned and Unburned treatments, respectively. We did not compare *F. pallescens* survival between growing seasons because all seedlings died before the end of the first growing season. To assess how field experimental burning affects *P. speciosa* seedling growth (i.e., leaf number and height, cm) over time (in each growing season), we used repeated-measures ANOVAs. For these analyses, we excluded those data from plants that died before the end of each growing season. Leaf number data were log-transformed prior to repeated-measures ANOVA analysis. The values of accumulated precipitation and mean temperature in the spring–summer 2008/2009 and 2009/2010 were compared with mean historical precipitation and mean historical temperature (1984/2010) in the same periods, using a *t* test for single means.

Total germination rates between laboratory fire treatments and control were compared with, a one-way ANOVA (Dunnet post-hoc test) for *P. speciosa* and a Kruskal–Wallis test (comparisons of mean ranks for all groups post-hoc test) for *F. pallescens*.

We calculated mean germination time (MGT) for each species and treatment as:

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

where t_i is the number of days starting from the date of sowing and n_i is the number of seeds that germinated each day (Dayamba et al. 2008). We compared MGT between laboratory fire treatments and control for each species using the same analysis that we used to compare total germination. For the MGT analysis, replicates with no germination were excluded. We compared *F. pallescens* growth variables between laboratory fire treatments and control before seedlings were transplanted with one-way ANOVA (height, cm) and Kruskal–Wallis (root length, cm) tests. We excluded the 120°C treatment from the statistical analysis of growth variables because we did not obtain recently germinated seeds with the appropriate radicle development for transplantation. To compare the variables measured in *F. pallescens* seedlings at the end of the greenhouse experiment among treatments, we used a one-way ANOVA (height, cm, and root length, cm) and a Kruskal–Wallis test (leaf number, and biomass, mg). Post-hoc tests—Dunnet and comparisons of mean ranks for all groups—were used to compare each laboratory fire treatment with the control after ANOVA and Kruskal–Wallis, respectively. We did not analyze the effects of laboratory fire treatments on *P. speciosa* seedling growth because most of the seedlings from the control and 120°C treatments could not be transplanted due to their weak development. Significance level was 0.05, but marginal significances were noted when *P* values were between 0.05 and 0.1. Standard errors (SE) were used to calculate variation. In the figures, we present untransformed data.

Results

Effects of fire on seedling recruitment

Field experiments

Both species germinated in spring, differing little in germination date but strongly in germination dynamics: while most *P. speciosa* seeds germinated gradually, over more than 2 weeks, *F. pallescens* seeds
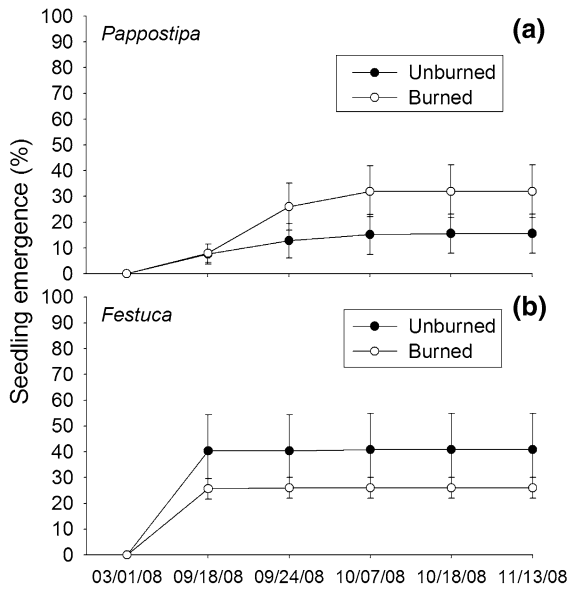
Fig. 1 Cumulative germination percentage (mean ± SE) in unburned and burned treatments. **a** *Pappostipa speciosa* and **b** *Festuca pallescens.* San Ramón ranch, NW Patagonia steppe (Argentina)

Fig. 2 Daily minimum temperatures (per hour) of those days with below zero temperatures during the 11 days prior to the first monitoring. Meteorological station INTA, San Carlos de Bariloche, NW Patagonia steppe (Argentina)

germinated in a massive pulse (Fig. 1). Most *F. pallescens* seedlings died ($B = 77\%$ and $U = 83\%$) shortly after emergence (only the radicle had emerged), just before the first monitoring (09/18/08). Between the beginning of September and the day of the first monitoring there were 12 days with frosts (Meteorological Station, INTA Bariloche). Daily minimum temperatures (per hour) of those days with below zero temperatures during the 11 days prior to the first monitoring are shown in Fig. 2. Frost-heaving likely caused *F. pallescens* seedling death, because radicles were completely exposed on the frozen soil.

Maximum mean surface temperatures during the experimental burnings were 603°C for *P. speciosa* and 548°C for *F. pallescens* plots, and maximum mean temperatures at 1-cm soil depth were 85 and 70°C in *P. speciosa* and *F. pallescens* plots, respectively. Field experimental burnings significantly affected *P. speciosa* seedling emergence over time as shown by the greater emergence in Burned plots over the period of the experiment (Treatment × Time: $F_{4,32} = 2.75$, $P < 0.05$; Fig. 1). Total emergence of *F. pallescens* did not differ significantly between treatments ($t_8 = -1.01$, $P = 0.33$).

After two growing seasons, *P. speciosa* seedling survival was similar ($\sim 50\%$) in burned and unburned
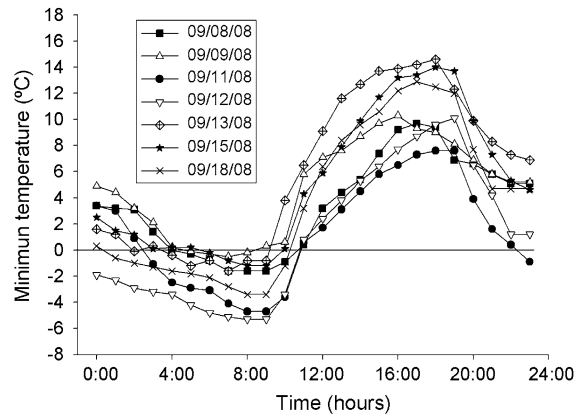
treatments ($\chi^2 = 0.10$, df $= 1$, $P = 0.75$; Fig. 3a). We observed lower seedling survival at the end of the first growing season than at the end of the second season for each treatment ($B = 56$ vs. 79%, $\chi^2 = 6.59$, df $= 1$, $P < 0.05$; $U = 44.3$ vs. 100%, $\chi^2 = 12.21$, df $= 1$, $P < 0.001$). The seedlings recorded as dead were completely dry, and the greatest mortality was recorded during the first spring–summer after germination (2008/2009). This period was stressful, with below-normal precipitation (historical mean (1984/2010): 207 vs. 146 mm, $t_{25} = 3.57$, $P < 0.01$) and above-normal temperature (historical mean (1984/2010): 11.0 vs. 11.6°C, $t_{25} = -4.1$, $P < 0.001$). By contrast, the following spring–summer (2009/2010) was unusually wet (historical mean (1984/2010): 207 vs. 333 mm, $t_{25} = -7.29$, $P < 0.001$) and cool (historical mean (1984/2010): 11.0 vs. 9.7°C, $t_{25} = 7.99$, $P < 0.001$). Survival of *F. pallescens* seedlings did not differ between burned and unburned plots ($\chi^2 = 0.009$, df $= 1$, $P = 0.92$), and all seedlings died before the end of the first summer after germination (Fig. 3b).

Pappostipa speciosa seedlings from Burned plots had fewer leaves during the first growing season than those from the Unburned plots (Treatment: $F_{1,59} = 17.7$, $P < 0.001$), independently of time (Treatment × Time: $F_{4,236} = 0.85$, $P = 0.49$; Fig. 4). However, these differences were not statistically significant during the second growing season (Treatment: $F_{1,49} = 2.40$, $P = 0.12$; Treatment × Time: $F_{7,343} = 1.47$, $P = 0.17$; Fig. 4). In the first growing season
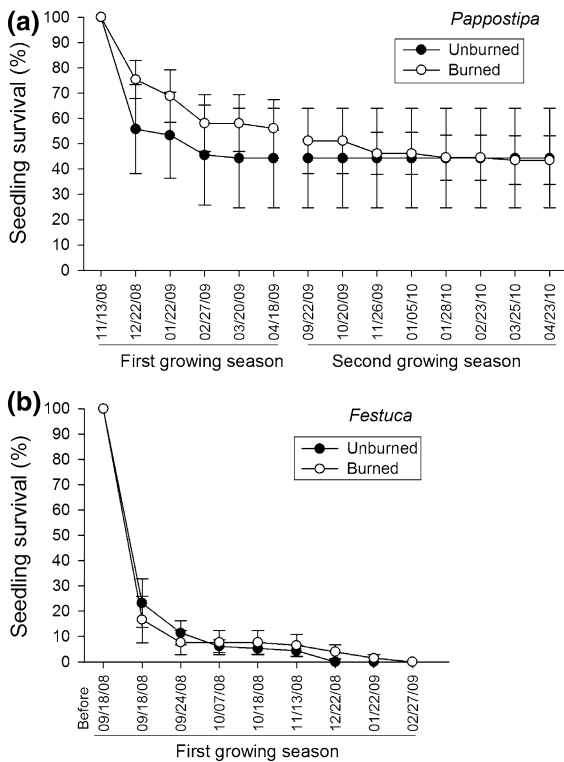
Fig. 3 Seedling survival in burned and unburned treatments. **a** *Pappostipa speciosa,* and **b** *Festuca pallescens.* San Ramón ranch, NW Patagonia steppe (Argentina)
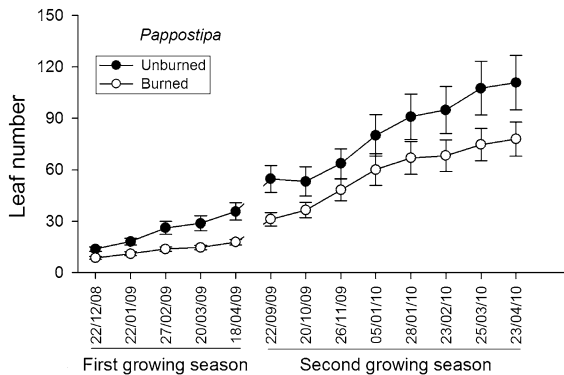

Fig. 4 *Pappostipa speciosa* leaf number (mean ± SE) in burned and unburned treatments. San Ramón ranch, NW Patagonia steppe (Argentina)

seedlings from Burned plots were shorter than those from Unburned plots (Treatment: $F_{1,59} = 2.78$, $P = 0.1$), independently of time (Treatment × Time: $F_{4,236} = 0.58$, $P = 0.67$; Fig. 5). Differences in seedling height between treatments were accentuated
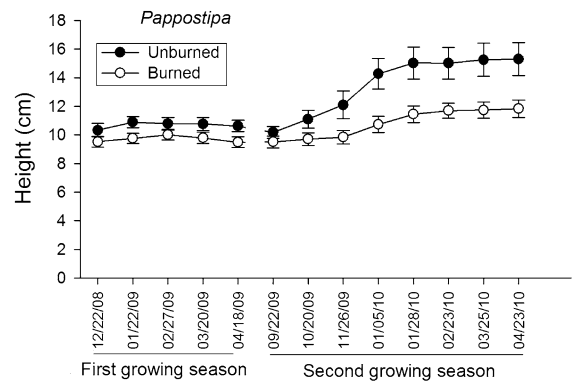

Fig. 5 *Pappostipa speciosa* height (cm, mean ± SE) in burned and unburned treatments. San Ramón ranch, NW Patagonia steppe (Argentina)

over the second growing season (Treatment: $F_{1,49} = 7.06$, $P < 0.05$; Treatment × Time: $F_{7,343} = 5.26$, $P < 0.001$; Fig. 5).

Laboratory and greenhouse experiments

Smoke increased germination of *P. speciosa* ($F_{6,28} = 2.04$, $P = 0.09$). Seeds treated with smoke for 10 min had twofold higher germination rates than untreated seeds (Fig. 6a). Seeds in 120°C, charcoal and ash treatments had significantly greater MGT than untreated seeds ($F_{6,26} = 6.57$, $P < 0.001$, $P < 0.07$, $P < 0.06$ respectively; Fig. 7a). In most treatments, *P. speciosa* germination showed a gradual increase without pronounced peaks.

Exposure to the highest temperature for 5 min caused a statistically significant drop in *F. pallescens* germination rate ($H = 19.36$, $P < 0.05$), which was fivefold lower than that obtained in the untreated seeds (Fig. 6b). In addition, seeds exposed to 120°C had the longest MGT ($H = 21.11$, $P = 0.32$; Fig. 7b) with no marked germination peaks. Germination in the remaining treatments peaked between 0 and 11 days.

Recently emerged *F. pallescens* seedlings showed no differences in height or root length among treatments (pre-transplant measures: $F_{5,54} = 1.77$, $P = 0.13$; $H = 10.24$, $P = 1.00$, respectively; Table 1). After 65 days, we observed that seedlings from laboratory fire-treated seeds generally grew less than those from control seeds (Table 1). However, ash had no negative effect on seedling growth. The remaining fire factors affected growth variables differently. Leaf number was decreased by exposure to 60°C
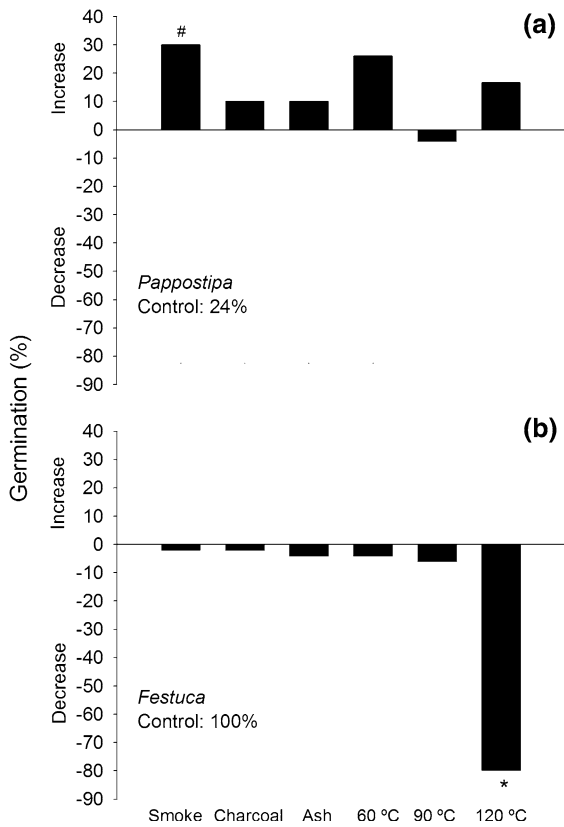
Fig. 6 Differences in germination (%) between laboratory fire treatments and control. An increase in germination indicated that more seeds germinated after a laboratory fire treatment than the control, while a decrease indicated that fewer seeds germinated. A value of zero indicates that there were not differences. **a** *Pappostipa speciosa*, **b** *Festuca pallescens*. Symbols show significant differences between each laboratory fire treatment and the control. $^{\#}P < 0.1$; $^{*}P < 0.05$

Fig. 7 Differences in mean germination time (MGT, days) between laboratory fire treatments and control. An increase in MGT indicated that seeds in a laboratory fire treatment germinated more slowly than the control, while a decrease in MGT indicates that that seeds in a laboratory fire treatment germinated more quickly than control. A value of zero indicates that there were not differences. **a** *Pappostipa speciosa*, **b** *Festuca pallescens*. Symbols show significant differences between the fire treatment and the control. $^{\#}P < 0.1$; $^{***}P < 0.001$

($H = 21.65$, $P < 0.01$) and smoke ($H = 21.65$, $P = 0.06$). Aerial biomass was negatively affected by 60°C and by smoke ($H = 19.94$, $P < 0.01$), and root biomass was decreased by 90°C, by smoke, and by charcoal ($H = 22.40$, $P < 0.05$). Charcoal also increased seedling height ($F_{5,51} = 4.73$, $P < 0.05$). Root length did not differ among treatments ($F_{5,51} = 1.63$, $P = 0.16$).

Discussion

Post-fire recruitment dynamics is an important ecological process that has been barely studied in Patagonian grass species. Fire differentially affected the recruitment patterns of *P. speciosa* and *F.*
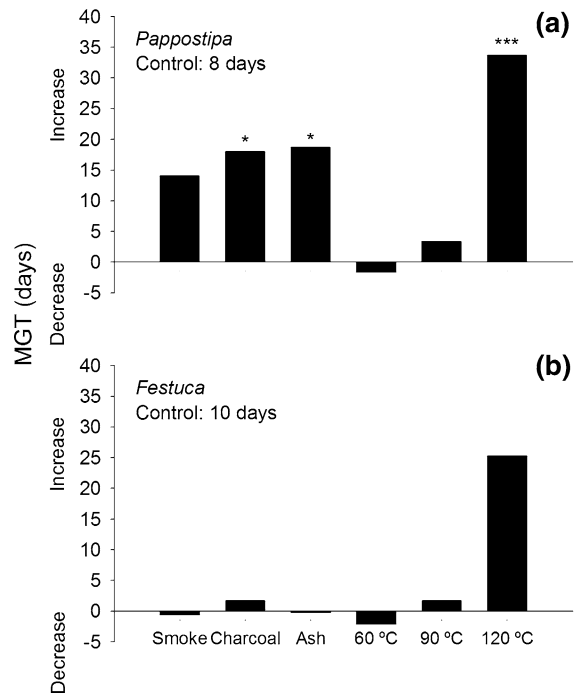
pallescens, two dominant grasses from Patagonian steppes with marked differences in palatability. Experimental burning positively affected *P. speciosa* emergence and tended to affect *F. pallescens* emergence negatively. Laboratory experiments confirmed field results and allowed us to determine which specific factor was responsible for the differences. A short exposure of seeds to high temperatures negatively affected germination percentages of *F. pallescens*, while a short exposure to smoke increased *P. speciosa* germination percentages. The high temperature treatment was almost lethal for *F. pallescens* seeds, while *P. speciosa* seeds tolerated it. Differences in seed structure and size could explain these responses. In *F. pallescens*, the lemma covers half of the caryopsis, and the other half is covered by the palea, which is thin (almost translucent) and dissociated from the lemma (Correa 1978). In *P. speciosa*, the lemma is thick and wraps around the

Table 1 The effect of abiotic fire-related factors on growth variables of *F. pallescens* seedlings before transplanting them and 65 days after transplanted

' Minutes of treatment. Symbols show significant differences between the fire treatment and the control. [#] $P < 0.1$; * $P < 0.05$, ** $P < 0.01$. We did not show data for 120°C treatment because seedlings were too poorly developed to be transplanted (see text for details)

Festuca	Root length (cm)	Height (cm)	Leaf number	Aerial biomass (mg)	Root biomass (mg)
Pre-transplant					
Control	4.0 ± 0.78	5.4 ± 0.46			
60°C × 5'	4.6 ± 0.82	4.7 ± 0.40			
90°C × 5'	4.5 ± 0.71	5.5 ± 0.33			
Smoke × 10'	2.8 ± 0.54	5.4 ± 0.42			
Charcoal (1 g/l)	3.1 ± 0.52	5.5 ± 0.35			
Ash (1 g/l)	2.0 ± 0.31	6.3 ± 0.39			
65 days after transplant					
Control	17.4 ± 1.5	9.1 ± 0.4	13.8 ± 0.8	39.0 ± 3.5	80.5 ± 7.9
60°C × 5'	15.3 ± 1.1	7.7 ± 0.5	6.7 ± 0.4**	15.8 ± 1.4**	36.5 ± 3.6
90°C × 5'	14.8 ± 1.3	7.7 ± 0.5	10.6 ± 1.7	22.4 ± 4.5	34.1 ± 6.3*
Smoke × 10'	11.0 ± 1.6	8.4 ± 0.8	7.6 ± 0.8[#]	16.1 ± 3.9**	34.4 ± 14.2*
Charcoal (1 g/l)	15.7 ± 1.8	12.1 ± 1.2*	7.9 ± 1.2	20.1 ± 3.0	31.0 ± 7.0*
Ash (1 g/l)	14.4 ± 1.9	10.1 ± 0.9	14.3 ± 1.8	34.8 ± 7.6	89.2 ± 17.4

caryopsis completely. Furthermore, the lemma is longitudinally wound around the caryopsis, forming a tight pipe (Correa 1978). The structures that cover *F. pallescens* seeds seem to provide little protection from heat. Seed size may also be important: previous research has noted the importance of the seed surface/volume ratio on seed sensitivity to high temperatures (Reyes and Casal 1995; Escudero et al. 2000). González-Rabanal and Casal (1995) proposed that this relationship could be true in seeds that have a similar structure, a characteristic that can be shared at the family level. Because *F. pallescens* seeds are smaller, they could have been more negatively affected by high temperature than *P. speciosa* seeds. In contrast to *P. speciosa* (Ghermandi 1995), the lack of self-burial mechanisms in *F. pallescens* would constitute an additional disadvantage in facing fire.

Smoke can produce physico-chemical alterations in external and internal seed covers that influence germination (Egerton-Warburton 1998; Keeley and Fotheringham 1998). This abiotic fire-related factor can act on enzymatic systems and biochemical processes in ways that mimic after-ripening (Brown and Van Staden 1997). Gasque and García-Fayos (2003) suggested that glumes of *Stipa tenacissima* seeds impose dormancy through a chemical mechanism, because removing glumes produced an increase in germination similar to that produced by after-ripening. Similarly, we hypothesize that smoke causes a chemical transformation of *P. speciosa* glumes that

promotes seed germination. However, this and other hypotheses (such as mechanical constrains to germination) must be tested.

Heat shock of seeds can affect not only germination but also seedling growth (Hanley and Fenner 1997; Escudero et al. 2000). Differences in seedling size due to heat pre-germination treatments can change competitive interactions among neighboring plants and therefore influence patterns of post-fire plant community recovery (Escudero et al. 2000; Hanley et al. 2001). *Pappostipa speciosa* seedlings from the burned plots and *F. pallescens* seedlings from laboratory fire-treated seeds developed less than those observed in untreated plots or seeds. Although the decreased growth did not change survival in field experiments, it is possible that, under natural circumstances (where inter-specific competition in gaps is expected), seedlings from fire-affected seeds could have a lower competitive ability. We do not know why *P. speciosa* seedlings from the control and 120°C (laboratory) treatments did not reach an appropriate development level to be transplanted. However, poor growth in those seedlings from seeds exposed to high temperature may reflect deleterious effects on the embryos (Hanley and Fenner 1998).

Weather during spring and summer greatly influenced seedling survival. The hot, dry conditions during the first spring–summer after seed sowing accentuated the characteristic water stress of this period, leading to high seedling mortality. Though

water deficit was negative for seedlings of both grass species, it had a more detrimental effect on *F. pallescens*, with all their seedlings dying desiccated, indicating that summer drought was the main cause of seedling mortality. *Pappostipa speciosa* is better adapted than *F. pallescens* to low plant water potentials (Fernández et al. 2002, 2006). The dominance of *P. speciosa* at lower altitudes reflects this adaptation. Our data support the conclusions of Bertiller et al. (1996) that *F. pallescens* can successfully establish only during exceptionally wet summers. However, seedlings must first escape from frost to establish.

Festuca pallescens and *P. speciosa* germination dynamics strongly influenced their establishment. The massive mortality of *F. pallescens* seedlings was related to their synchronous germination, with few seedlings, likely those whose radicles remained buried, surviving frost. Likewise, Defossé et al. (1997b) found that the peak of *F. pallescens* emergence coincided with the month of most frost-heaving occurrence, when seedling mortality was high. Because the probability of simultaneous occurrence of frost and germination is very high (mean frequency of days with frost in September: 17.4; Bustos and Rocchi 1993), frost can be considered a major limiting factor for *F. pallescens* establishment. By contrast, *P. speciosa* had delayed and gradual germination that allowed it to escape from frost. Asynchronous germination ensures that only a portion of seeds will be ready to germinate under suitable conditions at a particular moment (Gasque and García-Fayos 2003).

Concluding remarks

The effects of fire and grazing on grasses with different palatability depend on many factors, such as intrinsic species characteristics, plant development stage, and environmental conditions (Silvertown et al. 1994; Bond and van Wilgen 1996; Cingolani et al. 2003). In our study, the responses of species with diverse palatability were mediated by intrinsic species characteristics and meteorological conditions.

The independent effects of fire and grazing on vegetation are relevant but those derived from their interaction can have greater ecological importance (Archibald et al. 2005; Allred et al. 2011). However, due to its complexity, it is difficult to generalize about the recruitment response that diverse types of plants produce toward fire-grazing interactions. Most of this complexity is caused by the strong influence of species-specific and context-specific factors over the shaping of plant recruitment responses to this interaction. For example, in North America, the seedling survival response of a high palatable native grass (*Schizachyrium scoparium*) after clipped and burned, depended primarily on seedling age (Limb et al. 2011). On the other hand, in central Argentina, the recruitment response of a poor edible native grass (*Paspalum quadrifarium*) after the application of fire-grazing treatments, depended mainly on the availability of suitable microsites (Laterra et al. 1994). We also highlighted the importance of focusing on particular types of resident plant responses because this knowledge could have important implications on local management. Furthermore, the contribution that our research makes to the understanding of the ecological mechanisms behind particular plant responses, may help to clarify those responses observed in other semi-arid environments.

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