

Effects of fire severity on early recovery of Patagonian steppes

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Abstract. Fire severity influences the recovery and biodiversity of plant communities. We compared the early post-fire recovery of plant functional groups in two sites (one burnt with high severity and one with low severity) in the north-western Patagonian steppe. We sampled the post-fire soil seed banks, as well as the composition and cover of aboveground plant species, and calculated richness, diversity and the percentage of exotic species. Low fire severity increased the diversity of aboveground vegetation and seed banks, whereas high fire severity reduced the cover of all functional groups, with the exception of fugitive species. Tiller production of perennial grasses decreased due to bud bank mortality. In the seed bank, high severity fire reduced fugitive species and increased exotic species. Fugitive species need fire to recruit, and the combination of fire cues and post-fire environmental conditions can explain the high abundance of these species after fire. In Patagonia, the use of fire is not considered a management option because fires are believed to be dangerous to humans, goods and services. However, north-western Patagonia is sparsely populated and the frequent wildfires pose no danger. It is necessary to increase the knowledge of the ecological processes of Patagonian ecosystems related to fire regime and land use, to achieve a reasonable balance between sustainable use and conservation in this region.

Additional keywords: fugitive species, functional groups, seed bank, semi-arid grasslands.

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Introduction

Semi-arid grasslands and steppes comprise 28% of the world's grasslands (World Resource Institute, see <http://www.wri.org>, accessed 1 July 2013). Although most previous research on steppes has focussed on enhancing forage production, the importance of these dry biomes as diverse ecosystems that act as reservoirs of diversity increasingly is being recognised (Tilman 2000).

The most important large-scale disturbances structuring semi-arid grasslands are fire and grazing (Noy-Meir 1995; Oesterheld *et al.* 1999; Pausas and Keeley 2009; Scheintaub *et al.* 2009; Ghermandi *et al.* 2010), but there are few studies on fire severity in grasslands (Trollope *et al.* 2002; Hunter and Omi 2006; Thaxton and Platt 2006; Fidelis *et al.* 2010). Fire severity is defined as the post-fire loss or change in organic matter aboveground and belowground (Keeley 2009) and is a major factor that determines post-fire responses of vegetation, and ecosystem recuperation (Pausas *et al.* 2003; Gimeno-García *et al.* 2004). Fire severity influences the time that plants are exposed to combustion, which in turn determines the effect of fire on vegetation (Bond and van Wilgen 1996). This factor can be assessed by tree canopy scorch, skeleton twig diameter, ash deposition and plant mortality. The latter is a common

measure applied in areas characterised by surface fire regimes such as the steppe (Keeley 2009). Remote sensing is another powerful tool used to assess fire severity (Keeley 2009), where indices such as the Normalised Burn Ratio (NBR) use spectral values to estimate fire severity (Cocke *et al.* 2005; Miller and Thode 2007; Miller *et al.* 2009).

The abundance and spatial arrangement of plants that survive fire is influenced by their mode of regeneration (resprouters v. seeders). Buds of resprouter species, and bulbs or tubers of geophytes buried deep in the soil, can tolerate high temperatures (Odion and Davis 2000; Gonzalez *et al.* 2010). Because seed susceptibility to heat varies, fire intensity can change community composition by influencing recruitment (Keeley and Fotheringham 2000). Because higher temperatures can stimulate germination in seeds from deeper soils, seedling recruitment, in general, is greater after high-intensity fires (Bond and van Wilgen 1996). Fugitive species are native species that appear soon after a fire and disappear 2 or 3 years later, but remain stored in the seed bank between fires (Gonzalez and Ghermandi 2008). Although this functional group makes a valuable contribution to grassland richness, little is known about its response to variations in fire severity. Many exotic species can also take advantage of large post-fire gaps (Keeley *et al.*

2003; Ghermandi et al. 2004). Exotic species are ruderal (*sensu* Grime 1979) and are usually post-fire fast colonisers (Ghermandi et al. 2004).

Patagonian steppes occupy 786 000 km² between 37 and 55°S, and are covered by different vegetation types (45% shrub desert, 30% shrub-grass semi-desert, 20% grass steppe, 5% meadows) (Soriano et al. 1983). The most productive grasslands of the region are found in northern sub-Andean Patagonia where annual precipitation is 500–600 mm and vegetation cover 60–70% (Ghermandi et al. 2004). Although the pre-settlement Patagonian steppe ecosystems were grazed by native herbivores (i.e. *Lama guanicoe*, guanaco), domestic grazing by introduced sheep and cattle is relatively recent (<100 years). Sheep ranching influenced guanaco densities in the arid lands of Patagonia and played an important role in the guanaco population decline during the last century (Baldi et al. 2001).

The long fire history in Patagonia began during the late Miocene (c. 1×10^7 years ago) when the Andes became a barrier for the humid western winds, cooling and drying extra-Andean Patagonia. This trend facilitated the advance of new vegetation types that were adapted to more arid conditions (Barreda et al. 2007). During the subsequent Pliocene and Pleistocene (between 5×10^6 and 10 000 years ago), climatic change, volcanism and naturally occurring wildfires (caused by lightning) shaped Patagonian vegetation into grass and grass-shrub steppes (Barreda et al. 2007), progressively becoming more fire prone. Human presence in the area during the Holocene (from ~11 000 years ago) probably increased fires, as there are several charcoal records in grass steppes of extra-Andean Patagonia of the early Holocene (Bianchi 2000).

The work reported here compares the short-term recovery of two burnt grasslands after natural fires of different severity in north-western Patagonia. We compared vegetation and seed bank attributes (richness, diversity and evenness), percentage of exotic species in vegetation and seed bank, total cover and cover of functional groups, and total seed bank and seed bank of functional groups, between two similar burnt areas (i.e. both had similar slope, exposure, soil, vegetation characteristics, land use and meteorological conditions). In addition, we measured vegetation cover during the spring of 1999 and 2005 in two unburnt grasslands, located in the same areas, and compared the vegetation cover in both grasslands before and after the fires to determine the degree of severity of fires. We hypothesised that short-term post-fire regeneration of different plant functional groups may be related to fire severity. We expected that high fire severity would: (1) reduce the cover of resprouter species, (2) increase seedling recruitment of fugitive species, (3) reduce the seed bank of the total community, (4) increase the seed bank of fugitive species and (5) increase the percentage of exotic species in the vegetation and in the seed bank.

Methods

Study area

The climate of north-western Patagonia is temperate with a Mediterranean precipitation regime (60% in May–August). Mean annual temperature is 7.4°C and mean annual precipitation is 580 mm. Mean maximum temperature of the warmest month (January) is 21.7°C and mean minimum temperature of the coldest month (July) is –3.4°C (San Ramón ranch

Meteorological Station, unpubl. data). Strong west to north-west winds blow frequently throughout the year.

Topography is hilly with numerous rocky outcrops; dominant soils are Haploxerolls with sandy loam texture (Gaitán et al. 2004). The study area is located in the Subandean district of the Patagonian phytogeographic province, which is characterised by perennial grasses (Cabrera 1971). The dominant grasses are *Pappostipa speciosa* (ex *Stipa speciosa*) and *Festuca pallescens*. The area also includes native shrublands dominated by *Fabiana imbricata* and *Discaria articulata*, whereas less common species include *Acaena splendens*, *Senecio bracteolatus* and *Mulinum spinosum* (Anchorena and Cingolani 2002). The main economic activity of the region is livestock production (cattle and sheep) based on grazing of natural grasslands (León and Aguiar 1985).

We studied the vegetation and the seed bank in two burnt areas. The high-severity (HS) fire occurred on the San Ramón ranch, 30 km east of Bariloche, Argentina (41°03'19"S). On 25 January 1999, lightning ignited a fire (Ayessa and Barrios 1999). The ignition and spread of fire were favoured by unusual summer conditions (rainfall in 1998–1999 was 60% lower than the historical average). The low-severity (LS) fire occurred on the La Fragua ranch, 40 km east of Bariloche, (41°05'19"S). On 5 February 2005, a fire was ignited by train sparks along the railroad that crosses the property. The burnt areas were 10.2 km apart (Fig. 1).

Pre-fire and post-fire precipitation

We compared annual precipitation in the 4 years before the San Ramón (1994–1997) and La Fragua (2000–2003) fires. The years immediately before the fires were not included in the comparison because 1998 was a very dry year (363 v. 580 mm historical mean value). We also compared precipitation of the fire years (1999 and 2005).

Fire severity assessment

We compared post-fire mortality data (collected in 1999) of the 1999 fire in San Ramón (Gittins 2001) with post-fire data from four 50-m transects that were surveyed in April 2005 in La Fragua. A plant was considered dead if it had not resprouted. Moreover, we compared the vegetation cover between burnt and unburnt areas in the spring following fires in 1999 and 2005.

We also used NBR values to assess the potential differences between fire severities in the burnt areas. NBR is defined as $(\text{NIR} - \text{SWIR}) \div (\text{NIR} + \text{SWIR})$, where NIR is the near infrared reflectance and SWIR is the shortwave infrared reflectance (Key and Benson 1999). A more negative NBR value indicates higher fire severity (Verbyla et al. 2008). We used two Landsat Thematic Mapper (TM) post-fire images (one for each fire) in a uni-temporal approach using images obtained on 10 February 1999, and 26 February 2005. These images were selected because they were the closest to the fire that were available. The image digital levels were converted to reflectance taking into account the calibration coefficients of TM images and sensor observation conditions. Each image was then processed with the NBR index to establish the boundaries of both fires. We used the 4-NIR and 7-SWIR spectral bands of the Landsat images and worked with 30-m pixels. Both areas were flat and thus we ignored the NBR variations due to the slope.

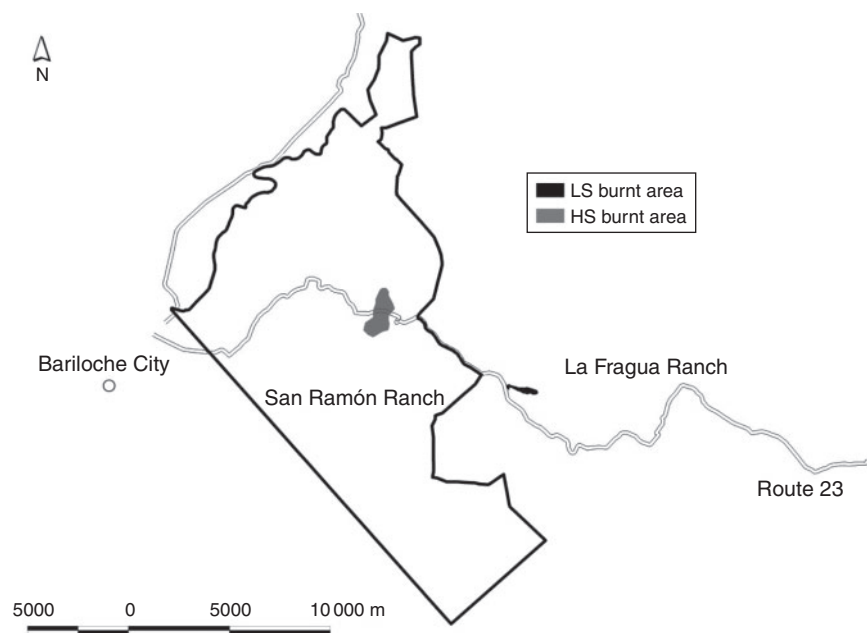


Fig. 1. Map indicating the location of the burnt areas.

We randomly sampled 50 pixels inside each fire to calculate average NBR.

We evaluated grassland biomass by calculating the normalised difference vegetation index (NDVI) in unburnt areas near the fires in San Ramón and La Fragua. NDVI is defined as $(\text{NIR} - \text{RED}) \div (\text{NIR} + \text{RED})$, where NIR is the near infrared reflectance and RED is the red reflectance (Rouse *et al.* 1973). NDVI values were calculated for 2005 in La Fragua and for 1999 and 2005 in San Ramón using the same images as above. We calculated 2005 NDVI values in San Ramón to compare the biomass of both grasslands in a year not affected by a drought. We randomly sampled 50 unburnt pixels from each image to calculate NDVI.

Sampling technique

The composition and cover of plant species were measured in spring (November), in 18 randomly distributed 1×2 -m plots in the HS burnt area (1999) and in 20 plots in the LS burnt area (2005). The distance between plots was ≥ 10 m. The soil seed bank was sampled in early autumn (April) in 1999 (HS) and in 2005 (LS). We randomly gathered 120 soil samples in the HS and 100 in the LS burnt areas. Soil cores were 10 cm in diameter and 3 cm in depth in each area. Previous seed bank studies carried out in the same region showed that 90% of the seeds are present within 3 cm of the soil surface (Ghermandi 1992, 1997). Cores were stratified at 5°C for 1 month and then were stored in the dark during June and July. In August, the soil samples were sieved to remove stones and debris, spread over a layer of sterile sand in individual plastic trays in a greenhouse and watered daily (Ghermandi 1997). Emerging seedlings were identified, counted and removed every week from September to March. When the first germination pulse ended, we mixed the soil to allow germination of buried seeds (Ghermandi 1995; Gonzalez and Ghermandi 2008).

Data analysis

Pre-fire and post-fire annual accumulated precipitation was compared using a *t*-test.

We determined mean NBR values and variability for each date and tested for differences using *t*-tests. The species were classified into four functional groups: typical gap annuals and biannuals (TGA), fugitives (F), perennial herbs (PH) and perennial grasses and shrubs (PGS). TGA species are herbs or grasses that recruit and colonise the inter-tussock gaps. They reproduce only from seeds and form persistent or transient seed banks. This group includes exotic and native species. Fugitive species are also annual or biannual species that colonise the inter-tussock gaps, but they need disturbances (like fire) to germinate and establish. They appear immediately after a fire from persistent seed banks but their cover disappears or diminishes dramatically 1 or 2 years later (Ghermandi *et al.* 2004). In our system, all F species are native. Perennial herbs are species that survive fires with subterranean organs like bulbs, tubers and rhizomes. They also colonise the inter-tussock gaps. Perennial grasses and shrubs are species that constitute the matrix vegetation. They have bud banks and transient seed banks, and resprout after a fire. We compared functional group vegetation mean cover and seed bank density using an ANOVA with post-hoc Tukey test for multiple comparisons. The seed density variable violated the normality assumption, and we could not normalise the data using the logarithmic, square root or arcsine transformations. We therefore analysed data using non-parametric Mann–Whitney and Kruskal–Wallis tests. We calculated species diversity for each burnt area using Shannon–Wiener Index: $H = -S p_i \ln p_i$, where S is the total number of species in the census and seed bank and p_i is the proportion of the cover or individuals in the seed bank of each species i that contribute to the total in the sample. We also estimated evenness, using the index: $J = H \div \log(S)$.

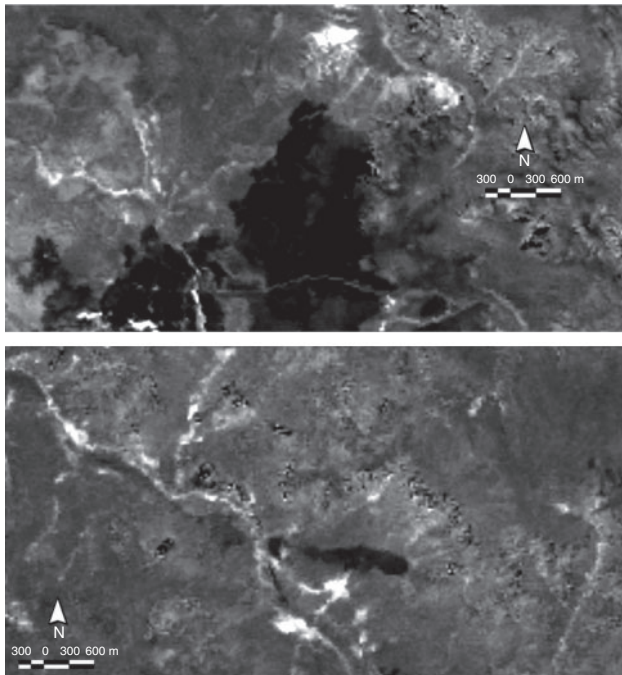


Fig. 2. NBR images showing how the digital processing allowed the identification of both fires. 10 February 1999 (top) (High-severity fire) and 26 February 2005 (bottom) (Low-severity fire).

We calculated the similarity between vegetation and seed bank composition using the Sørensen Index: $2a \div (2a + b + c)$, where a is the number of species common to both sites and b and c are the number of species exclusive to one site or the other (Mueller-Dombois and Ellenberg 1974).

Results

Pre-fire and post-fire precipitation

The mean annual accumulated precipitation of the 4 years before the fires was similar in the two burnt areas: 525 mm (1994–1997, HS) and 619 mm (2000–2003, LS) ($t_6 = -0.98$, $P = -0.37$). The annual accumulated precipitation of the year in which fires occurred was also similar in the two burnt areas: 631 mm (1999, HS) and 623.2 mm (2005, LS) ($t_6 = -0.19$, $P = 0.84$).

Fire severity assessment

Post-fire mortality of tussock grasses differed between the two burnt areas: 31.8% in HS and 1.7% in LS (Mann–Whitney $U = 10$, $P = 0.029$). Vegetation cover decreased by 58% (22.3% burnt *v.* 52.4% unburnt) in the HS burnt area and 32% (50.2% burnt *v.* 73.6% unburnt) in the LS burnt area. NBR distinguished burnt and unburnt areas for both fires, allowing delineation of the areas affected by fire. The fires had different NBR values ($t_{98} = -21.16$, $P < 0.001$) (Fig. 2): the mean NBR in the HS burnt area was 33% more negative than in LS burnt area (-0.6 ± 0.03 *v.* -0.46 ± 0.04).

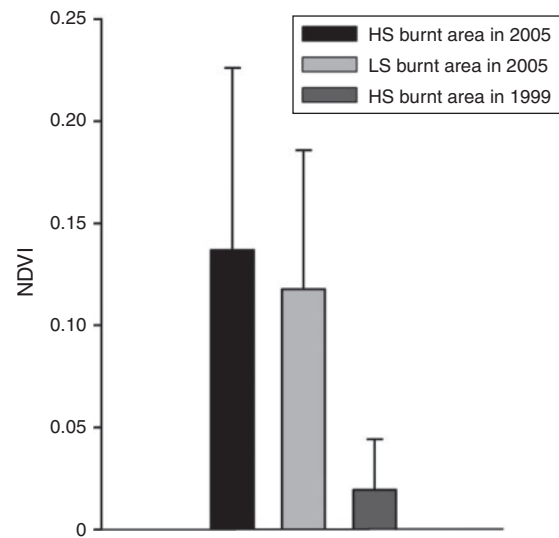


Fig. 3. NDVI values in high fire severity area (HS burnt area) in 2005 and 1999, and in low fire severity area (LS burnt area) in 2005.

NDVI values from the burnt areas differed between 1999 and 2005 ($t_{98} = 9.58$, $P < 0.001$, HS = 0.02 ± 0.02 , LS = -0.12 ± 0.07), but were similar when compared in the same year (i.e. 2005) ($t_{98} = 1.21$, $P = 0.22$, HS = 0.14 ± 0.09 , LS = 0.12 ± 0.07) (Fig. 3).

Vegetation and seed bank attributes

Aboveground species richness was similar in the burnt areas (HS, 22; LS, 23), but seed bank species richness in the LS burnt area was higher than in the HS burnt area (17 *v.* 9 species, Table 1). The diversity of aboveground species and of the seed bank in the LS burnt area was higher than in the HS burnt area (Table 1). In both burnt areas, the percentage of exotic species in the seed bank was higher than that in the aboveground vegetation. The proportion of exotic species in the seed bank of HS burnt area (55%) was higher than in that of LS burnt area (47%, Table 1) (Mann–Whitney $U = 98.9$, $P = 0.01$).

Aboveground vegetation functional groups

Total cover in the HS burnt area was twice that in the LS burnt area (Mann–Whitney: $U = 179.5$, $P < 0.001$). Mean TGA and PGS cover was significantly higher in the LS burnt area than in the HS burnt area (Mann–Whitney $U = 280$, $P = 0.04$; $U = 212$, $P < 0.001$). In contrast, mean cover of fugitives was four times higher in the HS burnt area than in the LS burnt area (Mann–Whitney: $U = 486$, $P < 0.001$) (Fig. 4a). In the HS burnt area, fugitives contributed 46% to the total vegetation cover, whereas TGA cover was significantly lower than the cover of the other functional groups ($H = 34.24$, $P < 0.001$) (Fig. 4a). In the LS burnt area, perennial herbs were the main contributors to the vegetation cover (45%). The cover of fugitives was not significantly different from that of the TGA functional group ($P > 0.05$) but it was lower than the PH and PGS groups ($P < 0.05$) (Fig. 4a).

Table 1. List of species present in aboveground vegetation (Veg) and soil seed bank (Sb) in areas burnt with fires of high and low severity (HS and LS)

Note, the Family and origin (OR), either native (N) and exotic (E), are also indicated. Asterisks indicate the presence of the species at the site. Equations of diversity of Shannon–Wiener Index (H) and evenness (J), where S is the total number of species in the census and seed bank and p_i is the proportion of the cover or individuals in the seed bank of each species i that contribute to the total in the sample

Species	OR	Veg-HS	Sb-HS	Veg-LS	Sb-LS
Typical gap annuals and biannuals					
<i>Apera interrupta</i> (Poaceae)	E	*	*	*	*
<i>Epilobium paniculatum</i> (Oenotheraceae)	E	*		*	*
<i>Erodium cicutarium</i> (Geraniaceae)	E			*	
<i>Erophila verna</i> (Brassicaceae)	E	*	*	*	*
<i>Holosteum umbellatum</i> (Caryophyllaceae)	E	*	*	*	*
<i>Microsteris gracilis</i> (Polemoniaceae)	N			*	*
<i>Plagiobothrys verrucosus</i> (Boraginaceae)	N	*			
<i>Triptilion achilleae</i> (Asteraceae)	N	*		*	
<i>Verbascum thapsus</i> (Scrophulariaceae)	E	*	*		*
<i>Vulpia australis</i> (Poaceae)	N		*		
<i>Veronica</i> sp. (Scrophulariaceae)	E				*
Fugitives					
<i>Boopis gracilis</i> (Calyceraceae)	N	*		*	
<i>Camissonia dentata</i> (Oenotheraceae)	N			*	*
<i>Descurraia pimpinellifolia</i> (Brassicaceae)	N				*
<i>Heliotropium paronychioides</i> (Boraginaceae)	N	*	*	*	*
<i>Montiopsis capitata</i> (Portulacaceae)	N				*
<i>Montiopsis polycarpoides</i> (Portulacaceae)	N	*			
<i>Nicotiana linearis</i> (Solanaceae)	N	*			
Perennial herbs					
<i>Acaena pinnatifida</i> (Rosaceae)	N			*	
<i>Calceolaria polyrrhiza</i> (Scrophulariaceae)	N	*		*	*
<i>Carex andina</i> (Cyperaceae)	N				*
<i>Carex</i> sp. (Cyperaceae)	N				*
<i>Cerastium arvense</i> (Caryophyllaceae)	E				*
<i>Hypochaeris radicata</i> (Asteraceae)	E	*			
<i>Juncus</i> sp. (Juncaceae)	N			*	
<i>Olsynium junceum</i> (Iridaceae)	N	*	*		
<i>Rodophiala mendocina</i> (Amaryllidaceae)	N	*		*	
<i>Rumex acetosella</i> (Polygonaceae)	E	*	*	*	*
<i>Taraxacum officinale</i> (Asteraceae)	E			*	
Perennial grasses and shrubs					
<i>Festuca argentina</i> (Poaceae)	N	*		*	
<i>Festuca pallescens</i> (Poaceae)	N	*		*	
<i>Hordeum comosum</i> (Poaceae)	N	*		*	*
<i>Mulinum spinosum</i> (Umbelliferae)	N	*			
<i>Pappostipa humilis</i> (Poaceae)	N			*	
<i>Pappostipa speciosa</i> (Poaceae)	N	*	*	*	
<i>Poa</i> sp. (Poaceae)	N	*		*	
<i>Senecio bracteolatus</i> (Asteraceae)	N			*	
Richness		22	9	23	17
Diversity ($H = -S \cdot p_i \cdot \ln p_i$)		1.83	0.94	2.01	1.51
Evenness ($J = H \div \log S$)		1.36	0.98	1.48	1.23
Exotic (%)		32	55	30	47

Seed bank functional groups

Total seed bank density was significantly higher in the LS burnt area than in the HS burnt area (Mann–Whitney: $U = 12\,095$, $P < 0.03$). Seed bank density of fugitives was 20 times higher in the LS burnt area than in the HS burnt area (Mann–Whitney

$U = 15\,240$, $P < 0.001$). No significant differences were found between the other functional groups (Mann–Whitney TGA: $U = 8908$, $P = 0.31$; PH: $U = 11\,707$, $P = 0.16$) (Fig. 4b). In the HS burnt area, TGA seed bank density was significantly higher than the seed bank of the other functional groups, accounting for

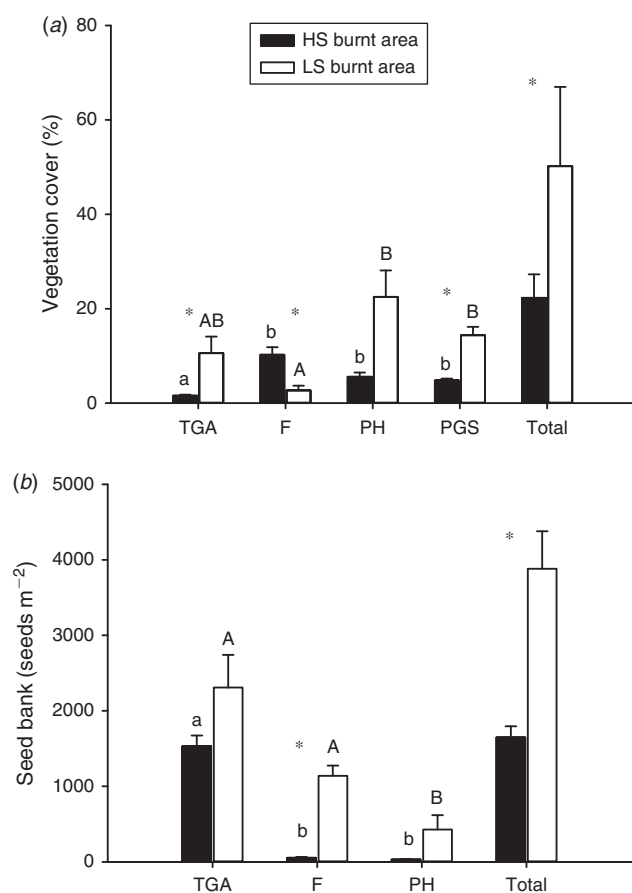


Fig. 4. Mean (\pm s.e.) of typical gap annual and biannual herbs (TGA), fugitives (F), perennial herbs (PH), perennial grasses and shrubs (PGS) and total species in high fire severity area (HS burnt area) and low fire severity area (LS burnt area). (a) Vegetation cover (%) and (b) seed bank (seeds m^{-2}). Asterisks (*) indicate significant differences in mean cover and seed density between burnt areas. Different lower-case letters indicate significant differences in mean cover and seed density among functional groups in HS burnt area. Different upper-case letters indicate significant differences among functional groups in LS burnt area.

92% of the total seeds ($H = 328.2$, $P < 0.001$) (Fig. 4b). In the LS burnt area, the main contributor to the seed bank was also the TGA group (59%) followed by the F group (29%) ($H = 163.8$, $P < 0.001$). No significant differences were found between these two functional groups ($P > 0.05$). The contribution of the PH and PGS groups to the seed bank was very low (Fig. 4b).

Similarity between aboveground vegetation and seed bank

The similarity (as measured by the Sørensen index) between the aboveground vegetation and the seed bank in the HS burnt area was 48%, whereas in the LS burnt area similarity was 50%. Similarity of the burnt areas was 64% for aboveground vegetation and 46% for the seed bank.

Discussion

The difference in severity between the two fires examined here was measured in two ways: (1) by comparing the post-fire reduction of vegetation cover and (2) by calculating the NBR index. Both methods showed that the San Ramón fire was more

severe than the La Fragua fire. Although the grasslands are located on different ranches, they are similar enough to be comparable. In fact, the 2005 NDVI index value indicates that if both grasslands were subject to the same climate (temperature and precipitation), biomass production would be very similar. However, the severe drought of 1998 reduced biomass production in San Ramón (low NDVI in 1999) and provided the setting for the high-severity fire caused by two lightning events in January 1999.

Fire severity affects post-fire grassland dynamics. The response of the TGA and F species differed between grasslands that burnt with different severity (Fig. 4). The HS fire probably stimulated the germination of fugitive species more than did the low-severity fire. These fugitive species colonised gaps where they competed with TGA species. In the LS burnt area, fugitives were scarcely stimulated by fire cues and the cover of TGA species was higher. Fugitive species need fire to recruit and increase their populations (Ghermandi et al. 2004; Keeley et al. 2006). The combination of fire cues (e.g. smoke, heat-shock) and post-fire environmental conditions can explain the high abundance of fugitive species after fire (Gonzalez and Ghermandi 2012a). In particular, in sites with high fire severity, buried seeds experience higher temperatures, which can stimulate the germination of seeds from a greater range of soil depths (Bond and van Wilgen 1996). The apparent absence of fugitive seeds in the seed bank is likely due to the difficulty of detecting them by germination: seeds of fugitive species have dormancy that makes their detection in seed bank by the seedling emergence method difficult (Gonzalez and Ghermandi 2012b). As a matter of fact, in another study carried out in grassland on the San Ramón ranch, the seed extraction method revealed a high abundance of fugitive species in the post-fire seed bank (Gonzalez 2002). For this reason, the contribution of fugitive species to the seed bank (sampled in the first post-fire autumn) was probably poor even if fugitive recruitment in the first post-fire spring showed the presence of seeds of this functional group in the soil.

High fire severity reduced the PH and PGS cover due to the mortality of entire or partial bud banks of these resprouter species. Bud mortality is reflected by low production of tillers (PG) and resprouts (shrubs). In other studies carried out in the same ecosystem, mortality and post-fire growth of dominant grass species, *P. speciosa* and *F. palleseus* and shrub species *M. spinosum* and *S. bracteolatus*, differed between species (Gittins et al. 2011) and between heat treatments (Gonzalez 2011). Also, Robberecht and Defossé (1995) observed that tiller production of *F. idahoensis* was reduced in plants exposed to high heat experimental treatment.

Grouping species into functional groups contributes to the study of the structure and the dynamics of steppe vegetation related to two principal disturbances – fire and grazing – that structure the ecosystems. The functional groups composed of only native species were the fugitives and the perennial grasses and shrubs (see Table 1). Fugitive species appear early and disappear quickly in the years that follow a fire, and their seeds remain stored in the soil seed bank between fires (Ghermandi et al. 2004; Keeley et al. 2006). They constitute 40% of total gap native species and represent a significant part of species richness in steppe. The basic structure of the steppe is a matrix of native perennial grasses and shrubs that resprout after a fire with the

space between matrix species being occupied by more dynamic species (PH and F). All native perennial herbs either possess subterranean organs, i.e. rhizomes, or are geophytes (e.g. *Rodophiala mendocina* and *Olsynium junceum*) that can escape high temperatures during fires, whereas fugitives form persistent seed banks (storage effect *sensu* Chesson 2000) (Ghermandi and Gonzalez 2009).

Grazers introduced exotic herbs into the grassland that shared with native herbs the gaps between tussocks and shrubs (Franzese and Ghermandi 2012). Exotic invasion probably interfered with abundance and richness of native gap species (Byers *et al.* 2002; Franzese and Ghermandi 2011). Fire severity did not affect the proportion of exotic species in aboveground vegetation, but high fire severity increased their proportion in the seed bank.

Wildfires occur frequently in north-western Patagonia, but the use of fire is not considered as a management option because wildfires are suppressed to avoid harm to humans and the destruction of goods and services. Fire can increase grassland productivity, but the conversion of grazing lands into other economically viable activities (e.g. ecotourism, forestry, agriculture) is an increasing challenge. We recommend that the area of protected steppes be expanded, because only 8% is currently conserved by the Argentine National Park Administration (Mermoz and Martin 2005). It is necessary to better understand the principal ecological processes that affect vegetation dynamics of Patagonian grasslands to achieve a reasonable balance between sustainable use and conservation. Our results should enhance the knowledge of how an important aspect of fire regime (i.e. fire severity) modifies species richness and the general functioning of semi-arid grasslands.

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