



Seed rain alteration related to fire and grazing history in a semiarid shrubland



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ABSTRACT

In arid environments, vegetation is distributed in patches. Herbivory and fires promote changes and seed rain plays a key role in the soil seed bank and the colonization of new spaces. This study focuses on the effect of different land use histories on the spatial and temporal seed rain distribution in Patagonia. We placed traps to capture seed rain of perennial grasses, shrubs and annual forage dicots at five sites with different grazing and fire histories. With grazing and fire seed rain diversity is higher than in absence of disturbances. Functional groups seed rain in vegetation patches did not show differences between sites, but at the interpatch level, grazing increased shrub seed and decreased perennial grass seed in the seed rain. Fire decreased the effects of grazing on shrub seed rain, but did not change its effects on perennial grasses. Shrub species showed a minimum abundance in the seed rain in the undisturbed site. Our results suggest that changes described for vegetative attributes are reflected in the seed rain, and this could reinforce the patch-interpatch pattern; fire did not reduce the grazing effects because it decreased the seed rain of the preferred grasses and increased the less preferred ones.

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1. Introduction

In arid environments, the vegetation is distributed in patches immersed in a bare soil matrix (“interpatches”) (Aguilar and Sala, 1999). These patches are conformed of phytogenic mounds dominated by shrubs, with grasses, subshrubs, herbs and biological crusts growing under their canopy (Bisigato and Bertiller, 1999; Cecchi et al., 2001). Several mechanisms have been proposed to explain the maintenance of these structures, including a complex balance between competition and facilitation (Caballero et al., 2008). Recently, it has been highlighted that the formation of vegetation patches is a product of grazing in the semiarid regions of the world (Allington and Valone, 2013).

Disturbances, such as herbivory, fire and drought, forge the structure and functioning of grassland ecosystems (Oesterheld et al., 1999). Under grazing conditions, key resources, such as water and nitrogen, are more available in the shrub patches (Allington and Valone, 2013). Also, the importance of the shrub patches as a

seed source and trap forms a spatial pattern of the soil seed bank that reinforces this heterogeneous distribution (Caballero et al., 2008). Concentration of defoliation and trampling in the interpatches reduces the cover of the grasses and biological crusts that protect the soil, leading to edaphic changes that decrease nutrient concentration and infiltration, and increase the loss of vegetation cover in these spaces (Allington and Valone, 2013; Fuls, 1992). These losses of vegetation and soil cover may, eventually, result in a partial reduction of the soil seed bank (Caballero et al., 2008). In addition, cattle may indirectly affect pollination levels through modifications in the plant community and between plants and their pollinators (Tadey, 2008; Vázquez and Simberloff, 2004). Once that situation is reached under grazing conditions, the interpatches are seldom revegetated and they become the centers from which the desertification process advances in these systems (Fuls, 1992; Chartier and Rostagno, 2006; Chartier et al., 2011).

In the Patagonia, excessive grazing is one of the main causes of desertification (Bertiller and Bisigato, 1998; León and Aguiar, 1985). Several authors explained how traditional management has caused several changes in the vegetation (e.g., Bär Lamas et al., 2013; Bisigato et al., 2005; Bisigato and Bertiller, 1997; León and Aguiar, 1985; Peter et al., 2012, 2013). Soil erosion is one of the principal processes of degradation in the Monte region (e.g., Chartier et al.,

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2011; Chartier and Rostagno, 2006; Parizek et al., 2002), and its continuous and accelerated advance may cause irreversible changes (Gaitán et al., 2007) limiting perennial grasses establishment (Bisigato and Bertiller, 2004; Chartier and Rostagno, 2006), although in some cases grazing exclusion has allowed the vegetation to recover (Funk et al., 2012).

Fire is a management tool commonly used to foment changes in vegetation that leads to a reduction in the shrub layer and an improvement in the desirable grasses. Several studies have pointed out these changes (Bran et al., 2007; Peláez et al., 2010), but others did not find any evidence to support this practice (Peter et al., 2013). Once fire has occurred, the wind redistributes the nutrients and propagules accumulated under the shrub canopy (Bóo et al., 1996; Ravi & D'Odorico, 2009), homogenizing the distribution of the vegetation (Rostagno et al., 2006).

In grasslands, these disturbances determine the longevity of the soil seed bank (Fenner and Thompson, 2005). In degraded areas of Patagonian Monte, the limiting factors for perennial grass recruitment are the spatial distribution of the soil seed bank and water availability (Bisigato et al., 2009). Seed rain composition and abundance play a key role because they have direct effects on the soil seed bank (Fenner and Thompson, 2005), which is the only source of potential recruiters after a severe fire (Galíndez et al., 2012). So, seed rain and remaining soil seed bank are involved in the colonization of new spaces (Thompson, 2000). Therefore, management practices that tend to sustain and/or increase perennial grass soil seed bank will contribute to their re-establishment (Bertiller and Aloia, 1997). Various studies on seed rain (Bonvissuto and Busso, 2007) and soil seed banks (Bertiller, 1998; Bertiller and Aloia, 1997; Busso and Bonvissuto, 2009; Pazos and Bertiller, 2007) in the Patagonian Monte have already been undertaken.

The findings of Peter et al. (2013) indicated that this semiarid rangeland is resilient to fire, but not to continuous grazing. The objective was to study the effect of different land use histories (involving grazing and fire) on the composition of the seed rain, and its spatial and temporal distribution in northeastern Patagonia. We hypothesized that seed rain responds in the same way as vegetative attributes such as frequency and cover. Therefore, our predictions were that: (1) seed rain diversity will be higher under intermediate disturbance (such as moderate grazing), (2) the abundance of perennial grasses in the seed rain will decrease under grazing conditions, whereas the abundance of shrubs and annual forage dicots in the seed rain will increase, (3) the differences promoted by grazing will decrease in burnt sites, so the heavily-grazed areas that were burnt will be similar to the moderate-grazed unburnt areas.

2. Materials and methods

2.1. Study area

The study area was in Adolfo Alsina (40° 40' S, 64° 10' W) department, Río Negro province, Argentina and it is representative of the Patagonian Monte. The climate is dry subtemperate, with warm summers (mean temperature 24 °C) and mild winters (mean temperature 7 °C). Soils are Aridisols; mean annual precipitation is around 255 mm, with high within and between year variability. Moderate northwesterly wind occurs throughout the year (Godagnone and Bran, 2009). Vegetation in the area is characterized by shrubland steppe, corresponding to the Monte Phytogeographical Province, South District, North Patagonia Sub-district (Roig et al., 2009); with a herbaceous layer of predominantly winter-growing grasses. This community is dominated by *Larrea divaricata* Cav., *Chquiraga erinacea* D. Don and *Condalia microphylla* Cav. in the shrub layer, and *Nassella tenuis* (Phil.) Barkworth in the herbaceous

layer. Other shrubs, e.g. *Prosopis flexuosa* var. *depressa* F.A. Roig, *Senna aphylla* (Cav.) H.S. Irwin & Barneby, *Lycium chilense* Miers ex Bertero, *Monttea aphylla* (Miers) Benth. & Hook., *Schinus johnstonii* F.A. Barkley and *Ephedra ochreatea* Miers can be found in the area. *Poa ligularis* Nees ex Steud., *Piptochaetium napostaense* (Speg.) Hack., *Jarava plumosa* (Spreng.) S.W.L. Jacobs & J. Everett, *Pappostipa speciosa* (Trin. & Rupr.) Romasch., *Nassella longiglumis* (Phil.) Barkworth (= *Nassella clarazii*), and the annual species *Schismus barbatus* (L.) Thell., *Erodium cicutarium* and *Daucus pusillus* Michx (Cabrera, 1971) are also commonly found in the herbaceous layer. The study area has almost 100 years of grazing history, with an average stocking rate of ≈ 0.18 sheep ha⁻¹ (Peter et al., 2013).

2.2. Sampling design

The area of the study was 30 × 10 km of a vegetation unit which comprised several ranches with different land uses. Five areas with different land-use histories related to grazing and fire were selected using the judgment employed by Peter et al. (2013):

- Heavily-grazed area (HG): site grazed by sheep at an average stocking rate, but situated ≤ 600 m from the water point.
- Moderate-grazed area (MG): site grazed by sheep at an average stocking rate, but situated ≥ 2500 m from the water point.
- Ungrazed area (UG): site located near a railway from which domestic livestock had been excluded for over 50 years.
- Burnt ungrazed area (BU): site burnt in 2002 (eight years before sampling) excluded to livestock after the fire.
- Burnt grazed area (BG): site burnt in 2002 (eight years before sampling) which remained grazed by sheep at the average stocking rate, and situated ≤ 600 m from the water point.

Three years after the fire occurrence, a five year drought event took place, and mean annual rain ranged from 35% to 75% of the average value (Funk et al., 2012). HG and MG were included in the same paddock, but were 2000 m apart from each other. So grazing intensities of these areas were selected using piospheres (Bisigato y Bertiller, 1997), which are radial grazing gradients created in arid lands from the water point. UG was situated at <100 m from MG, and surrounded by a wire fence to exclude it from livestock grazing. The burnt sites (BG and BU) were separated by fence.

At each paddock, five shrubby islands with a diameter greater than one meter were chosen randomly. On each vegetation patch, one seed trap was placed under shrub cover ($n = 5$) and another at the adjacent interpatch space ($n = 5$), with a minimum distance of 1 m from the island edge. Seed traps were built with synthetic fabric (wadding), cut in 30 × 30 cm square units and 1.5 cm thick, and attached to the ground with a metal frame and nails. This type of seed trap was considered appropriate due to the density of the wadding material and the anchorage mechanism of the seeds produced by most of the species included in this study (pers. obs.).

The sampling period was one year long, from September 2010 to August 2011. Seed traps were replaced every two month over this period.

2.3. Sample processing

Seed traps were placed in labeled paper bags and subjected to -18 °C for three days to avoid seed predation by insects trapped in the wadding. After this process, samples were kept in a dark dry place. As all propagules found were fruits with one seed we will refer to them as seeds from here on. During the processing of the traps, seeds were manually removed from the wadding, identified to species level (when possible) and counted. A database was created to facilitate species identification, by collecting seeds

directly from the mother plants during each field visit. The seeds of *Larrea* and *Poa* could not be determined to species level. They presented two species with overlapping distributions and similar seed morphology in the study area. The *Larrea* spp. included *L. divaricata* and *L. cuneifolia*, and the *Poa* spp., *P. ligularis* and *P. lanuginosa*. Only potentially viable seeds were included in the analysis. The viability of the seeds was estimated visually, considering entirely filled seeds as those with potential viability (Gómez-Aparicio, 2008).

Three main functional groups were considered for this study: perennial grasses, shrubs and annual forage dicots (AFD). Annual grasses were not included in this study because their small seeds could not anchor in the seed trap.

Abundance was pointed out as the number of seeds per m², and it was estimated with the quantity of seeds per trap (0.09 m²) and extrapolated to square meter. Total percentage refers to the percentage of each species in relation with the total number of seeds, and the functional group percentage to the number of seeds in relation with the total number of seeds in each functional group.

2.4. Statistical analyses

We made comparisons of the number of seeds of functional groups and their main species (grasses with more than 5000 seeds/m² and shrubs with more than 1000 seeds/m²). To analyzed differences between treatments and seasons we used one way ANOVA (F); and for differences between patches and interpatches we applied Student t test (t). Data were previously transformed to meet normality and homoscedasticity requirements (Table 1). These requirements were tested using Shapiro–Wilks test for normality and Levene test for homocedasticity. The data which did not comply with the ANOVA requirements (whether transformed or untransformed) were analyzed using Kruskal–Wallis nonparametric test (H). Tukey's HSD test was applied to ANOVA and Kruskal–Wallis analyses.

We compared the seed rain diversity between treatments using the Shannon diversity index.

All the statistical analyses were carried out using InfoStat software (Di Rienzo et al., 2011).

3. Results

3.1. Seed rain general description

In the year of this study, propagules corresponding to 19 taxa of

the functional groups considered were found in the seed rain (Table 2). Seed rain was dominated by the perennial grass *Poa* spp. and the annual dicot *E. cicutarium*, comprising 51.97% and 21.26% of the total seeds counted, respectively (Table 2).

3.2. Effects of the land use history on the seed rain seasonal abundance

Contribution of perennial grasses to the seed rain was greater in spring and summer (H = 71.78, p < 0.0001). In the undisturbed site (UG) perennial grasses showed greater abundance in seed rain in the spring (F = 135.45, p < 0.0001), especially due to the input of *Poa* spp., which was the most abundant species in that season in UG (H = 11.91, p = 0.0008). In the moderate grazed and burnt sites (MG, BG and BU), the most abundant seed rain period was extended from spring until summer (H = 14.23, p < 0.01; H = 14.93, p = 0.0017; H = 14.50, p = 0.0017). This could be explained by the input of *Nassella tenuis* in MG (F = 5.55, p = 0.0036), *Pappostipa speciosa* in BG and BU (F = 5.45, p = 0.0039; F = 6.48, p = 0.0016). Finally, under heavy grazing pressure (HG), grass abundance in seed rain was maximum during summer (F = 24.26, p < 0.0001) due to the contribution of *N. tenuis* (F = 13.83, p < 0.0001).

Shrub seed rain occurred mainly during summer and autumn (H = 40.01, p < 0.0001). In HG, shrub seed rain was maximum in the summer (F = 24.33, p < 0.0001), it was extended to autumn in MG (F = 21.04, p < 0.0001), and it took place mostly in the autumn in BU and UG, both ungrazed sites (F = 7.24; p = 0.0028; H = 10.62, p = 0.0084). These seasonal patterns were explained by the seed input of *Larrea* spp. in HG (H = 12.65, p = 0.0005), an increase in *C. erinacea* in addition to *Larrea* spp. for MG (H = 17.05, p = 0.0009), and the contribution of *C. erinacea* alone for UG (H = 8.59, p = 0.0192). During the autumn, seed rain in BU did not show the contribution of any particular shrub species (H = 4.33, p = 0.1029). BG showed no differences in the shrub seed rain between seasons (F = 1.47, p = 0.2604).

Seasonal dynamics of AFD showed a maximum seed rain in the spring, decreasing to the summer, and being minimum in the autumn and winter (H = 47.96, p < 0.0001). No differences were found between sites among seasons (spring: H = 2.31, p = 0.1676; summer: H = 3.97, p = 0.3450; autumn and winter data could not be analyzed due to the absence of AFD seeds in the rain during these seasons).

3.3. Seed rain diversity

The Shannon diversity index was calculated using all species found

Table 1
Transformation of seed rain abundance data. a) For comparison among seasons for each functional groups and sites. b) For comparison among total seed rain, species and functional groups between patches and interpatches at sites. Abbreviations: ln = natural log; nt = not transformed data.

a)		General	UG	MG	HG	BU	BG		
Seasonal description (comparisons between seasons)	Perennial grasses	ln	ln	ln	ln	nt	nt		
	grass species		nt	rank	rank	ln	ln		
	Shrubs	nt	ln	ln	ln	ln	rank		
	shrub species		nt	nt	nt	nt	ln		
	AFD	nt	nt	nt	nt	nt	nt		
b)		General	Patches	Inter patches	Patches vs interpatches				
					UG	MG	HG	BU	BG
Effects on total seed rain		ln	ln	ln					
Effects on functional groups and their main species	Perennial grasses		ln	ln	nt	nt	nt	nt	nt
	<i>N. tenuis</i>		ln	ln	nt	ln	ln	ln	ln
	<i>P. speciosa</i>		nt	ln	nt	nt	rank	ln	ln
	<i>Poa</i> spp.		nt	ln	ln	nt	ln	ln	ln
	Shrubs		ln	ln	ln	ln	nt	nt	ln
	<i>C. erinacea</i>		ln	nt	rank	nt	nt	rank	nt
	<i>Larrea</i> spp.		ln	ln	rank	ln	nt	ln	nt
	Annual forage dicots		ln	ln	ln	nt	nt	nt	nt
<i>E. cicutarium</i>		nt	nt	ln	nt	nt	ln	ln	

Table 2

Species found in the seed rain. Table shows the total seed abundance for the sampling period and the percentages of each species related to its functional group and to the total seeds.

Species	Abundance (seeds/m ²)	Percentage	
		Functional group	Total
Shrubs		11.17	
<i>Brachyclados lycioides</i>	188.89	1.60	0.18
<i>Bredemeyera microphylla</i>	66.67	0.56	0.06
<i>Chuquiraga erinacea</i>	3144.44	26.62	2.97
<i>Condalia microphylla</i>	866.67	7.34	0.82
<i>Cyclolepis genistoides</i>	400.00	3.39	0.38
<i>Larrea</i> spp.	6288.89	53.25	5.95
<i>Schinus johnstonii</i>	855.56	7.24	0.81
Annual forage dicots		21.36	
<i>Erodium cicutarium</i>	22,477.78	99.51	21.26
<i>Medicago minima</i>	111.11	0.49	0.11
Perennial grasses		67.47	
<i>Jarava plumosa</i>	577.78	0.81	0.55
<i>Melica bonariensis</i>	33.33	0.05	0.03
<i>Nassella longiglumis</i>	1511.11	2.12	1.43
<i>Nassella tenuis</i>	8688.89	12.18	8.22
<i>Pappostipa speciosa</i>	5488.89	7.69	5.19
<i>Piptochaetium napostaense</i>	88.89	0.12	0.08
<i>Poa</i> spp.	54,944.44	77.02	51.97

in the seed rain and showed significant differences between sites (Fig. 1). Diversity was highest in the site with two simultaneous disturbances (fire and grazing), medium in sites with only one disturbance (fire or grazing) and lowest in the undisturbed site (Fig. 1).

3.4. Effects of land use history on seed rain

3.4.1. Effects on total seed rain

In this study, the most abundant seed rain was in UG, while the lowest abundant was in BG ($H = 14.74$, $p = 0.0053$). We found different seed abundance between sites in patches and interpatches. The patches showed the highest seed rain abundance in UG and the lowest in BU ($F = 4.19$, $p = 0.0127$). The interpatches also had the highest seed rain abundance in UG, but the lowest values in the heavily grazed sites (HG and UG) ($F = 7.81$, $p = 0.0006$). Comparing patches and interpatches at every particular site, the only site that showed differences was BU ($t = 3.84$, $p = 0.0049$), where the interpatches had more seeds.

3.4.2. Effects on functional groups and their main species

Perennial grasses did not show any statistically significant

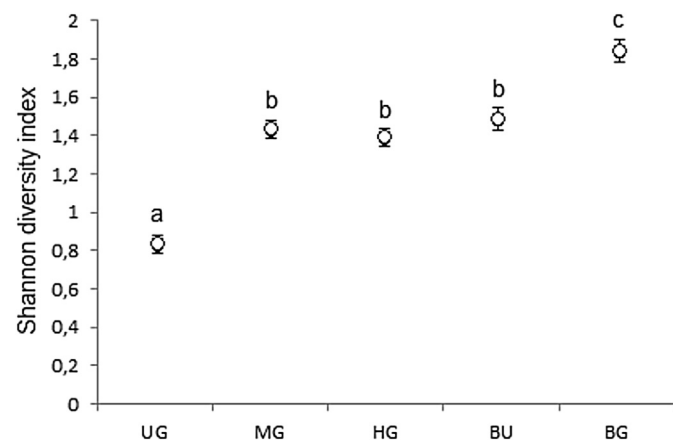


Fig. 1. Shannon diversity index calculated using all species in the seed rain at each site, with 95% confidence intervals. Different letters indicate statistically significant differences ($p < 0.05$) between sites. References: UG: ungrazed site, MG: moderate grazed site, HG: heavily grazed site, BU: burnt ungrazed site, BG: burnt grazed site.

differences between patches and interpatches ($t = 0.86$, $p = 0.3949$), or between patches among sites ($F = 1.80$, $p = 0.1684$). This functional group showed significant differences between the interpatches of the different sites, having a higher abundance of seed rain in UG and lower in HG and BG ($F = 5.98$, $p = 0.0025$) (Fig. 2). The main species of this group showed a similar pattern when patches and interpatches were analyzed separately, Fig. 2 shows the results for interpatches only. The only species which did not followed this pattern was *Pappostipa speciosa*, a non-palatable grass, which showed the highest abundance in BU and the lowest in HG in the interpatches (Fig. 2); and the highest in BG in the patches ($H = 11.07$, $p = 0.0283$).

Shrubs had the same seed rain abundance between patches and interpatches ($t = 1.15$, $p = 0.2578$). Although no differences were found between patches at different sites ($F = 1.37$, $p = 0.2796$), in the interpatches shrub seed rain showed the highest values in HG and MG, and the lowest in UG and BG (Fig. 3). *Larrea* spp. showed maximum seed rain in grazed sites (HG and MG); followed by *C. erinacea*, with the highest values in MG (Fig. 3).

AFD did not show any significant differences between patches and interpatches ($t = -1.90$, $p = 0.0629$), or between the patches ($F = 2.33$, $p = 0.9140$), or the interpatches ($F = 1.14$, $p = 0.3643$) at the different sites. *E. cicutarium*, the main species in this functional group, did not showed any differences between the patches ($H = 1.32$, $p = 0.8554$), or the interpatches ($F = 1.15$, $p = 0.3619$) either.

When we compared the specific seed abundance between patches and interpatches in each site, only *N. tenuis* showed differences in seed rain abundance, with more seeds in the interpatches in BG ($F = 6.28$, $p = 0.0366$).

4. Discussion

Disturbances delayed the contributions of perennial grasses and shrubs to the seed rain, which is not explained by phenological changes in these species, but a replacement of species with different seed release seasons in each functional group. Fire and grazing combined enhanced seed rain diversity, instead of only a moderated disturbance, as moderated grazing. Then, our first prediction was not supported by these results. The grazing effect on seed abundance was particularly marked in the interpatches,

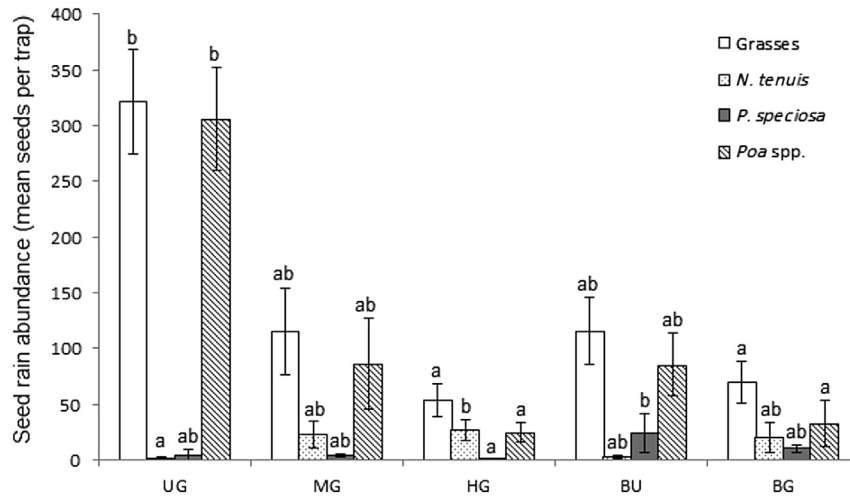


Fig. 2. Abundance of perennial grasses and the main species in interpatches at different sites (mean seed abundance per trap ± SE). Different letters indicate statistically significant differences between sites ($p < 0.05$). References: UG: ungrazed site, MG: moderate grazed site, HG: heavily grazed site, BU: burnt ungrazed site, BG: burnt grazed site.

where grazing increased shrub seeds in detriment of perennial grasses, as was in part expressed in our second prediction. Our third prediction, about the effects of fire on seed rain, was partially supported by the results. Fire and grazing had similar effects on diversity, although fire did not increase the perennial grass abundance, it decreased the shrub seed rain while grazing increased it, in agreement with our prediction. Probably, the reduction was caused by depletion of the cover of the established vegetation, but this conclusion exceeds the objectives of this work.

4.1. Land use effects on seed rain diversity

The site that was burnt and heavily grazed had the maximum Shannon-Wiener index value. Villagra et al. (2009) pointed out the positive effects of disturbances over the diversity, promoting an heterogeneous environment that allows species variability. Our results showed that different grazing pressures (heavy and

moderate) have the same effect over the diversity value. Besides, grazing have similar effect than the fire followed by cattle exclusion. Although grazing and fire enhanced diversity values (compared with the undisturbed condition), the maximum diversity value was obtained when this disturbances occurred together. Possibly, the abundance of species that are promoted by grazing decreased because of fire effect, and vice versa. So, the effects of these disturbances over species abundance could be compensated.

4.2. Land use effects on seed rain abundance

4.2.1. Total seed rain

The lower total seed rain abundance observed in situations with several changes, such as BG (fire and grazing), may indicate that the species replacement observed by Peter et al. (2013) during the recovery process at this site is not followed by seed production,

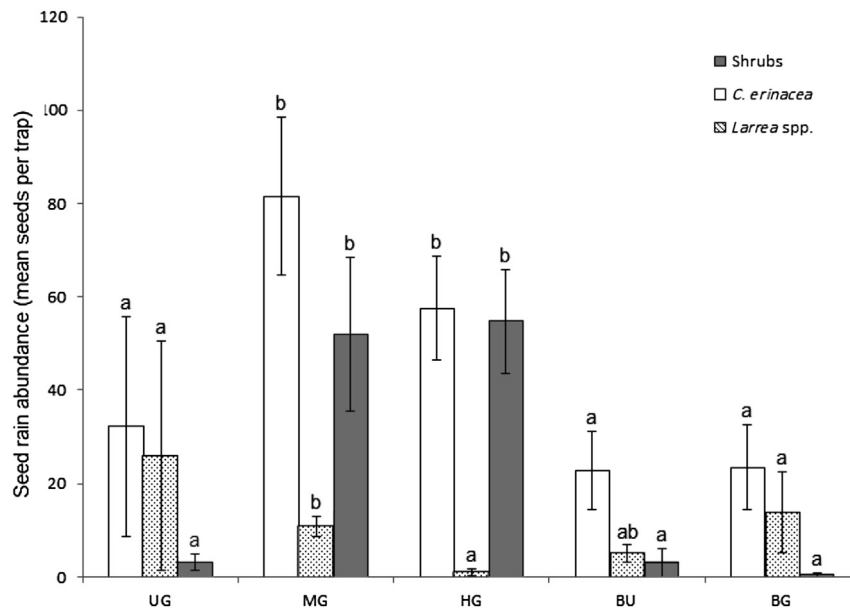


Fig. 3. Abundance of shrubs and the main species in interpatches of different sites (mean seed abundance per trap ± SE). Different letters indicate statistically significant differences between sites ($p < 0.05$). References: UG: ungrazed site, MG: moderate grazed site, HG: heavily grazed site, BU: burnt ungrazed site, BG: burnt grazed site.

perhaps because the focus is on compensatory growth at this stage (Peláez et al., 2003). Additionally, cattle could have negative effects on the pollination process, probably for the diminution in the flowers density (Tadey, 2008; Vázquez and Simberloff, 2004), promoting the previously described situation. This might also explain why the maximum seed rain abundance occurred in an unburnt and ungrazed site (UG).

4.2.2. Perennial grasses

The lack of differences in the seed rain between patches and interpatches at all sites (except for *Nassella tenuis* in BG) was coincident with the findings of Mayor et al. (2003) in the soil seed bank of *Piptochaetium napostaense* and *N. tenuis*. Homogeneous seed rain could explain the lack of effects of shrub cover on perennial grass soil seed bank formation. However, considering cattle effects at the interpatch level, further soil seed bank analysis in the study area is necessary to draw firmer conclusions.

The absence of differences in grasses seed rain between patches of different sites may indicate that shrubs maintain similar conditions under their canopy independently of external pressures. Our data do not provide any evidence of the secondary capture capacity by shrub patches, because the traps used in this study assured the anchorage of primarily dispersed seeds only avoiding the anchorage of seeds of secondary dispersal (mostly due to lateral movement of seeds promoted by wind). Therefore, is important to clarify that all seeds found in the traps arrived directly from the mother plants.

As the effects of land use on seed rain were observed at the interpatch level, the following section discusses the effects on these spaces. *Pappostipa speciosa* seed rain, the only non palatable species included in the analysis, showed the same pattern observed by Peter et al. (2013) in plant cover and by Franzese and Ghermandi (2012) in seedling emergence, increasing after fire occurrence in ungrazed situations. *Poa* spp. seed rain was dominant in the ungrazed site (UG), while *Nassella tenuis* increased and *Poa* spp. severely decreased under heavy grazing conditions. A negative effect on the cover, density and frequency of *Poa ligularis* was described in various systems (Funk et al., 2012; Morici et al., 2006; Peter et al., 2013), whereas the frequency of *P. lanuginosa* increased under grazing conditions (Peter et al., 2013). Thus, *Poa* spp. seed rain dramatically decreased under grazing, this could be because this disturbance has negative effects on the previously mentioned population attributes. This negative effect was notable in species with a low number of very dense panicles and seeds with a low dispersal capacity (O'Connor and Pickett, 1992; Pazos and Bertiller, 2007), as might be the case for these taxa (Funk et al., 2014). Our results showed that lower abundance of this taxon in the soil seed bank under grazing, as described by Morici et al. (2006), might be due to its scarcity in the seed rain, in addition to the negative effects of cattle on the seed bank formation. On the other hand, the increase of *N. tenuis* in the seed rain under grazing conditions was in agreement with the increase in frequency observed by Peter et al. (2013) and the increase in biomass and growth described by Kröpfl et al. (2007) for the study area. This can be explained by its compensatory growth (Kröpfl et al., 2007) and its higher tolerance to grazing (Fernández et al., 2009). Also, some authors had related the presence of awns on the seeds, such as those of *N. tenuis*, to a high dispersal capacity (Chambers, 2000; O'Connor et al., 1992). These advantages in the dispersal capacity are not reflected in an abundant soil seed bank for similar grazed systems (Mayor et al., 2003; Pazos and Bertiller, 2007). The high abundance of *N. tenuis* in the seed rain and the scarce abundance of this species in the soil seed bank might be evidence of some interference by grazing in the soil seed bank formation.

Fire decreased the perennial grass seed rain abundance, in

agreement with the scarce seed bank of this functional group observed by O'Connor and Pickett (1992) in other burnt grazed systems. The positive effects of fire on grass cover and growth observed in similar systems (Bran et al., 2007; Peláez et al., 2003) depends on the rainfall events following fire (Rostagno et al., 2006). In the study area, a strong drought after fires (Funk et al., 2012) could explain its negative effects on *N. tenuis* frequency described by Peter et al. (2013) and its repercussion on the seed rain.

The effects of grazing on the *Poa* spp. and *N. tenuis* seed rain pattern (decreasing the first species and increasing the second) is not weakened by fire actions, coinciding with the findings of Peter et al. (2013) in terms of cover. However, these results indicated that fire followed by drought caused a decrease in the seed rain of these species and in the functional group as a whole. Our findings suggest that, after eight years of post-fire recovery, the low seed availability of grasses might strongly limit seedling recruitment and, thus, limit the future stability of this system, especially under grazing conditions.

4.2.3. Annual forage dicots

The lack of differences observed for the group, and for *E. cicutarium* between sites, agreed with the results of Mayor et al. (1999) in the soil seed bank in the Caldenal region. *E. cicutarium* also showed high seed production and dispersal in that region (Fresnillo-Fedorenko, 1990; Peláez et al., 1995). Our results might suggest that climatic differences between the Monte and the Caldenal regions (specially in terms of rainfall), and fire occurrence, have no effects on its species dispersal capacity. Therefore, *E. cicutarium* seed production was not affected by the disturbances under study. *Medicago minima*, the other species included in this functional group, showed low values in the seed rain and did not be included in the statistical analysis.

4.2.4. Shrubs

The lack of differences in the shrubs seed rain abundance between patches and interpatches disagreed with previous studies of soil seed bank in the same (Funk et al., 2010) and similar (Bertiller, 1998) areas. Our results suggested that shrubs have a high dispersal capacity but the livestock trampling and erosive processes (hidric and eolic) at the interpatch level, promote the scarce seed availability in these spaces (Funk et al., 2010; Bertiller, 1998). This reinforces the patch-interpatch pattern.

Fire reduced shrub seed rain, in agreement with the decrease in *Larrea* spp. frequency observed by Peter et al. (2013), but differs from their findings regarding *C. erinacea*, for which the increase in this species coverage found by these authors did not imply a significant increase in its seed rain at burnt sites.

In relation to grazing, the *C. erinacea* seed rain abundance pattern, being at a maximum under moderate grazing (MG) and minimum under heavy grazing (HG), coincided with the findings of Peter et al. (2013) regarding frequency and cover under the same land use conditions. These results, and the increasing of *Larrea* spp. and *N. tenuis* combined in grazed sites, correspond with changes in the shrub structure associated with herbivory (Bisigato et al., 2005; Fernández et al., 2009; Peter et al., 2013). Under heavy grazing conditions, shrubs with dense canopy (e.g. *C. erinacea*) are replaced by those with an open canopy (e.g. *Larrea* spp.) that allow cattle movement through the vegetation patches (Bisigato et al., 2005; Fernández et al., 2009). This also explains the replacement of *Poa* spp. by *N. tenuis* under grazing. Also, *Larrea* spp. seedlings are easily established on bare soil under grazing, and its growth promotes soil nitrogen accumulation, stimulating *N. tenuis* germination (Bisigato and Bertiller, 1999). Therefore, under grazing conditions, seed rain follows this same pattern and reinforces it.

5. Conclusion

Replacement of *Poa* spp. for *N. tenuis* is evident, restricting the first species to the ungrazed sites and the second species to grazed ones. Our results indicate that changes in vegetative attributes observed in other grazed systems are reflected in seed rain, reinforcing this tendency. The lack of differences between patches and interpatches for grasses, shrubs and annual forage dicot seed rain gives evidence of homogeneous seed dispersal for these functional groups.

On the other hand, the use of fire as a management tool to reduce shrub cover does not seem to reduce the grazing effects on the seed rain. On the contrary, fire might tend to decrease the seed rain abundance of the preferred grasses (*Poa* spp. and *N. tenuis*), and increase the seed rain of the less preferred species (*P. speciosa*). Due to these undesirable changes, the use of fire as a management tool should be prescribed considering the climatic conditions that follow.

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