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Aboveground Vegetation and Perennial Grass Seed Bank in Arid Rangelands Disturbed by Grazing[☆]

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ABSTRACT

Recruitment by seeds can be an important mechanism for recovery of plant communities following disturbance. Our objective was to assess the density and spatial patterning of perennial grass (highly preferred by herbivores) seeds in litter patches at locations with different aboveground vegetation structure in sites with different grazing history characteristic of the Patagonian Monte (Argentina). We asked whether structural differences in aboveground vegetation are reflected in the density and spatial patterning of perennial grass seeds in litter patches. We selected two study sites characteristic of the Patagonian Monte and within them three locations representing different vegetation states, resulting from different combinations of grazing and/or release from grazing history. At each location, we assessed the density of perennial grass seeds in litter patches at microsites beneath plant patches (canopy) and in interpatch areas without or with scattered vegetation (bare soil) at three dates during the reproductive and seed dispersal periods. The density of perennial grass seeds in litter patches was greater at canopy than at bare soil microsites, and the number of litter patches without seeds increased with decreasing total plant cover at both microsites. The density of perennial grass seeds in litter patches did not vary with differences in total plant cover or litter patch attributes at canopy microsites, while it was reduced with decreasing total plant cover at bare soil microsites. We concluded that differences in aboveground plant cover differentially affected the density of perennial grass seeds in litter patches at contrasting soil microsites. Thus potential microsites for perennial grass recruitment by seeds would increase from litter patches at bare soil microsites to litter patches at canopy microsites at locations with high and low aboveground plant cover, respectively. These issues should be considered for the sustainable management of these rangelands.

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Introduction

The regenerative process by seeds is essential to restore plant community dynamics and diversity in disturbed areas (Grime & Hillier, 2000; Wang et al., 2010). In arid ecosystems, the vegetation has a patchy structure consisting of shrub-grass patches with high plant cover distributed on a matrix of bare soil or low plant cover (Whitford, 2002; Tongway & Ludwig, 2005). Shrubby patches are mostly associated with large seed banks and induce favorable or ameliorated micro-environmental conditions (i.e., sheltering and high accumulation of litter, organic matter, and nutrients in soils) for plant

emergence and establishment (Aguilar & Sala, 1997; Bisigato & Bertiller, 2004; Arrieta & Suarez, 2005; Caballero et al., 2008; Pazos & Bertiller, 2008). In contrast, patches of bare soil or with scattered vegetation usually have small seed banks and unfavorable micro-environmental conditions (i.e., harsh microclimate, low accumulation of litter, organic matter, and nutrients in soil) limiting plant regeneration by seeds (Bertiller, 1996; Bertiller et al., 2002; Graae et al., 2011; Busso et al., 2012; Dybzinski & Tilman, 2012).

Grazing by domestic and native herbivores may affect the structure of the aboveground plant cover (reduced total, shrub, and perennial grass cover and fragmentation of shrub patches), the reproductive output of preferred plant species, as well as plant and soil processes over a wide range of arid and semiarid environments (Webb & Stielstra, 1979; Milchunas & Lauenroth, 1993; Bisigato & Bertiller, 1997; Bertiller et al., 2002; Cipriotti & Aguilar, 2005; Pazos et al., 2007; Bertiller & Ares, 2008; Carrera et al., 2008; Pazos et al., 2010; Bär Lamas et al., 2013). Perennial grasses are largely preferred and affected by native and domestic herbivores (Baldi et al., 2004; Bertiller & Ares, 2008) and are highly dependent on soil seed banks for the

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regeneration and conservation of their populations in a wide range of arid and semiarid ecosystems (Bertiller, 1996; Thompson, 2000; Pazos et al., 2007). This is particularly important in overgrazed rangelands with high perennial bunch grass mortality (Paruelo et al., 2008). Also, seedling emergence and establishment of perennial grasses depend on the favorable microenvironment induced by shrubby canopies (Montaña et al., 2001; Bisigato & Bertiller, 2004; Cipriotti & Aguiar, 2005; Pazos et al., 2010). Thus differences in the above-ground plant cover affecting the size and spatial distribution of soil seed banks of perennial grasses and the micro-environmental conditions of seedbeds may influence the regeneration and maintenance of perennial grass populations (O'Connor & Pickett, 1992; Bertiller, 1996; Busso & Bonvissuto, 2009; Bertiller & Ares, 2011; Tessema et al., 2012).

Litter accumulation on open patches of bare soil or with scattered vegetation may improve the soil microenvironment by reducing soil temperature and evaporation (Ruprecht et al., 2010) and increasing litter decomposition rates and soil nutrient levels (Carrera et al., 2005; 2008; Arriaga & Maya, 2007). Moreover, litter cover and other irregularities on the soil surface, such as biological crusts, could increase soil surface roughness and contribute to the entrapment of perennial grass seeds increasing the soil seed bank, as well as the availability of extra soil moisture (Aguiar & Sala, 1997; Bertiller & Ares, 2011; DeFalco et al., 2012; Farrell et al., 2012). Thus small spatial heterogeneities in the level of soil resources, in the microclimate of seedbeds, and in the size of seed reservoirs induced by litter accumulation in patches of bare soil or scattered vegetation could eventually enhance the opportunities for perennial grass recruitment in disturbed areas (Luzuriaga & Escudero, 2008; Pueyo et al., 2009; Ladd & Facelli, 2012). Accordingly, the assessment of the effects of differences in plant cover on density and spatial patterning of seeds of target species affected by grazing is a first step for evaluating the regenerative potential by seeds of these species. This is particularly important in those soil microsites suitable for plant recruitment.

The objective of this study was to assess the density and spatial patterning of perennial grass (highly preferred by herbivores) seeds in litter patches at locations with different aboveground vegetation structure in sites with different grazing history, characteristic of the Patagonian Monte of Argentina. We asked whether structural differences in aboveground vegetation are reflected in the density and spatial patterning of perennial grass seeds in litter patches.

Methods and Materials

Study Area

Our study was carried out in the southern portion of the Monte Phytogeographical Province (Patagonian Monte) of about 48,000 km². Mean annual temperature is 13.7° C and mean annual precipitation is 235.9 mm (22-year average, CENPAT, 2009). Vegetation is characterized by the shrubland of *Larrea divaricata* Cav. and *Stipa* spp. (León et al., 1998). Shrubs and perennial grasses contribute more than 99% of the total biomass and are arranged in a patchy structure covering from 15% to 60% of the soil alternating with patches of bare soil or scattered vegetation (Bisigato & Bertiller, 1997; Bertiller & Ares, 2011). Perennial grasses are highly preferred by native and domestic herbivores while shrubs are scarcely selected (Baldi et al., 2004). Soils are a complex of Typic Petrocalcids- Typic Haplocalcids (del Valle, 1998). Sheep grazing was introduced at the beginning of the past century and has been usually arranged in large paddocks (c.a. 2 500 ha) sharing a single permanent watering point. Under these conditions, sheep grazing may lead to the creation of extended grazing gradients (piospheres), of more than 2 500 m around watering points (Bisigato & Bertiller, 1997; Pringle &

Landsberg, 2004; Brooks et al., 2006) or may create disturbed spot areas by selecting some preferred vegetation patches (Ares et al., 2003; Bertiller & Ares, 2008). The size of shrub patches, perennial grass cover, and total cover decreases with increasing grazing disturbance (Bertiller et al., 2002; Pazos et al., 2007; Bertiller & Ares, 2008; Bär Lamas et al., 2013). *Pappostipa speciosa* (Trin. & Rupr.) Romansch. (ex *Stipa speciosa*), *Nassella tenuis* (Phil.) Barkworth (ex *Stipa tenuis*), and *Poa ligularis* Ness ex Steud. (in order of importance) are the dominant perennial grass species in the area. *P. speciosa* is less preferred by domestic and native large herbivores than the other species. Other less abundant and highly preferred perennial grass species are *Elymus patagonicus* Speg. and *Jarava neaei* (Ness ex Steud.) Peñailillo (ex *Stipa neaei*) (Bisigato & Bertiller, 1997).

Within the study area, we selected two experimental sites (separated approximately 125 km from each other): La Elvira (EL): 43° 8' 52.0"S, 65° 42' 49.6"W; 157 m a.s.l. and La Esperanza (ES): 42° 12' 13.7"S, 64° 58' 55.6"W; 92 m a.s.l. Both sites are representative of the shrubland of *Larrea divaricata* Cav. and *Stipa* spp. (León et al., 1998) but have different grazing history. EL has been grazed by sheep from the beginning of the past century until present with a stocking rate of 0.11–0.14 sheep·ha⁻¹. ES was subjected to the same stocking rate until 2003, when a wildlife refuge was created. Since then, the stocking rate was gradually reduced (0.01 sheep·ha⁻¹·year⁻¹) until 2008 when all domestic herbivores were removed. After the removal of domestic herbivores, the population of the wild herbivore *Lama guanicoe* (guanaco) increased, reaching ca. 0.1 animal·ha⁻¹ at the date of this study (Escobar et al., 2004; FNP, 2013). At each experimental site, we selected three floristically homogeneous locations of at least 3 ha each (minimal area *sensu* Mueller-Dombois & Ellenberg, 1974; Bertiller & Ares, 2008; Bär Lamas et al., 2013) at different vegetation states (*sensu* Westoby et al., 1989; Briske et al., 2003; Beever & Pyke, 2005) with increasing signs of canopy disturbance induced by grazing history (D1, D2, D3, respectively). These locations were separated between 1 500 and 2 500 m from each other and were characterized by decreasing plant cover (total, shrub, and perennial grass cover) and shrub patch size (D1, D2, D3, respectively) (Bisigato & Bertiller, 1997; Bertiller et al., 2002; Pazos et al., 2007; Bertiller & Ares, 2008; Pazos et al., 2010; Bär Lamas et al., 2013).

Sampling

We recorded the total, shrub, and perennial grass cover across four randomly located 25-m linear transects by the line intercept method (Mueller-Dombois & Ellenberg, 1974) at each site and location in August 2010. Moreover, for seed/soil sampling at litter patches, we randomly selected 15 sampling points at each site and location in September 2009, December 2009, and March 2010. This time period encompasses the reproductive and seed dispersal periods of perennial grass species with different phenology and flowering responses to precipitation (Bertiller et al., 1991; Campanella & Bertiller, 2008). Perennial grasses in the Patagonian Monte, as well as in other Patagonian ecosystems, form transient seed banks because their seeds usually germinate immediately after dispersal. Accordingly, they are dependent on the yearly replenishment of the seed bank (Bertiller, 1992; Bertiller, 1996; Bertiller, 1998; Pazos & Bertiller, 2008). At each sampling point, we identified the largest litter patch at two microsites: 1) underlying the nearest shrub-grass patch canopy greater than 1 m in diameter (canopy) and 2) at the contiguous open patch of bare soil or scattered vegetation greater than 1 m in diameter (bare soil). We measured the largest and smallest orthogonal diameter of each litter patch, to assess litter patch (size) area (Mueller-Dombois & Ellenberg, 1974). We estimated litter cover within a sampling area (8.5 cm diameter) at the

point of maximal litter accumulation within the litter patch before extracting one cylindrical soil core (2 cm depth). Litter-soil samples were placed in incubation boxes and maintained at optimal conditions (field capacity; lighting period: 12 h, 18° C; dark period: 12 h, 10° C) in a growth chamber during 6 months and stirred at monthly intervals as reported in a previous study with Patagonian grasses (Bertiller & Ares, 2011). We counted the emerged seedlings of perennial grasses at weekly intervals during 6 months. We used total seed counts to assess 1) the mean density of germinable seeds (seed number · m⁻²) of perennial grasses in litter patches at the two microsites at each location and site, 2) the frequency distribution of litter patches with different amounts of seeds at each microsite at each location, and 3) to relate the density of seeds with litter patch attributes (cover and size) and with total, shrub, and perennial grass cover.

Statistical Analyses

We used ANOVA to test for significant differences in total, shrub, and perennial grass cover among sites and locations. Variables were logarithmically transformed in those cases when assumptions of ANOVA were not met. Tukey's test was used for multiple comparisons (Sokal & Rohlf, 1997). The relationships between litter patch size or cover and plant (total, grass, shrub) cover at canopy (underlying shrub-grass patch canopies) and bare soil (patches of bare soil or with scattered vegetation) microsites at the six study locations was evaluated by regression analyses. We used a Mann Whitney test to compare the size and cover of litter patches, as well as the density of germinable seeds of perennial grasses between microsites (canopy, bare soil). Samples from September, December, and March were combined for the analyses. We compared the frequency distribution of litter patches with different amounts of seeds at each microsite between sites, locations, and microsites by chi-square test. We performed regression analyses to relate the density of seeds of perennial grasses with litter patch attributes (cover and size) and with total, perennial grass and shrub cover by microsite. Also, step-wise regression was performed to explore multiple regression models between perennial grass seed density and plant cover-litter patch attributes. Significance was set at $P \leq 0.05$ throughout the study. All statistical analyses were performed with the package SPSS 7.5 for Windows (Norusis, 1997).

Results

Site Characteristics

The mean total plant cover was greater at ES ($21.37 \pm 0.30\%$) than at EL ($10.37 \pm 0.18\%$). The greatest total plant cover was found at ES-D1 ($27.62 \pm 2.51\%$) and the lowest at EL-D2 ($8.1 \pm 1.4\%$) and EL-D3 ($8.4 \pm 1.3\%$) (Fig. 1A). Shrubs had greater contribution to total plant cover than perennial grasses at both sites (ES, EL) and locations (D1, D2, D3). The greatest shrub cover was found at ES-D1 ($23.4 \pm 2.3\%$) and the lowest at EL-D2 ($7.7 \pm 1.3\%$) and EL-D3 ($8.3 \pm 1.2\%$). The greatest cover of perennial grasses was found at ES-D1 ($4.2 \pm 0.21\%$) followed by that at EL-D1 ($2.2 \pm 0.9\%$). The cover of shrubs did not significantly ($P > 0.05$) correlate to that of perennial grasses across all sites and locations, although a trend of increasing grass cover with increasing shrub cover was observed at each site (Fig. 1B).

Litter Patch Characteristics

The size of the litter patches did not vary with plant cover at bare soil microsites (range of variation from $0.038 \pm 0.009 \text{ m}^2$ to $0.086 \pm 0.026 \text{ m}^2$; Fig. 2A, Table 1A), while it significantly increased with

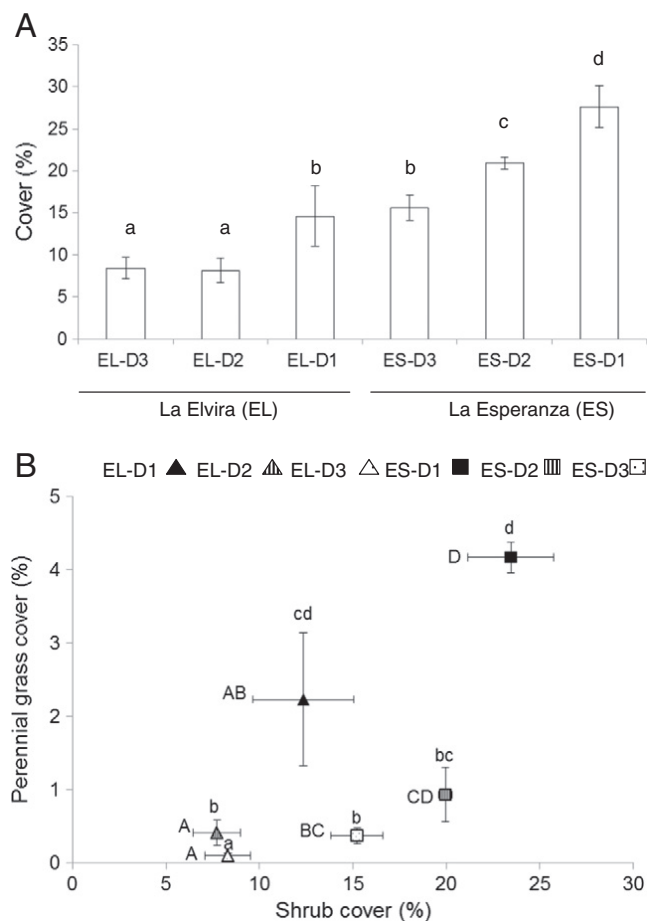


Fig. 1. A, Total plant cover. B, Perennial grass and shrub cover at the six study locations differing in grazing history. Different lowercase letters indicate significant differences in A, total plant and B, perennial grass cover, and different uppercase letters indicate significant differences in shrub cover among locations (ANOVA and Tukey test). Vertical and horizontal lines indicate one standard error. EL indicates La Elvira experimental site; ES, La Esperanza experimental site. Grazing disturbance levels: D1 (low), D2 (medium), D3 (high).

increasing shrub and total cover at canopy microsites (range of variation from $1.2 \pm 0.1 \text{ m}^2$ to $3.5 \pm 0.5 \text{ m}^2$; Fig. 2B, Table 1B). The cover of litter patches was not significantly related to plant cover at bare soil microsites (range of variation from $13.4 \pm 1.8\%$ to $49.4 \pm 6.5\%$; Fig. 2A, Table 1A), although it was significantly higher at ES than at EL (42.7 ± 3.7 and $18.91 \pm 1.6\%$, $F_{1,270} = 21.5$, $P < 0.01$). At canopy microsites, the cover of litter patches significantly decreased with increasing shrub cover and marginally decreased with increasing total plant cover (range of variation from $71.0 \pm 5.4\%$ to $99.7 \pm 0.2\%$; Fig. 2B, Table 1B). Litter patches were smaller and had lower cover at bare soil (size: $0.06 \pm 0.006 \text{ m}^2$, cover: $32.0 \pm 2.1\%$) than at canopy microsites (size: $2.0 \pm 0.1 \text{ m}^2$, cover: $84.7 \pm 1.7\%$) across sites and locations (Size: $U = 780$, $P < 0.001$; and Cover: $U = 12110$, $P < 0.001$).

Density of Perennial Grass Seeds in Litter Patches

The mean density of perennial grass seeds in litter patches across all sites and locations was smaller at bare soil than at canopy microsites ($13.3 \pm 2.3 \text{ seeds} \cdot \text{m}^{-2}$ and $38.5 \pm 6.6 \text{ seeds} \cdot \text{m}^{-2}$, respectively; $U = 32729$, $P = 0.001$). Seeds of *Nassella tenuis* and *Poa ligularis* were the most abundant, and those of *Elymus patagonicus*, *Pappostipa speciosa*, and *Jarava neaei* were the least frequent and mostly found at canopy microsites. The variable best correlated to perennial grass seed density at bare soil microsites was the total plant

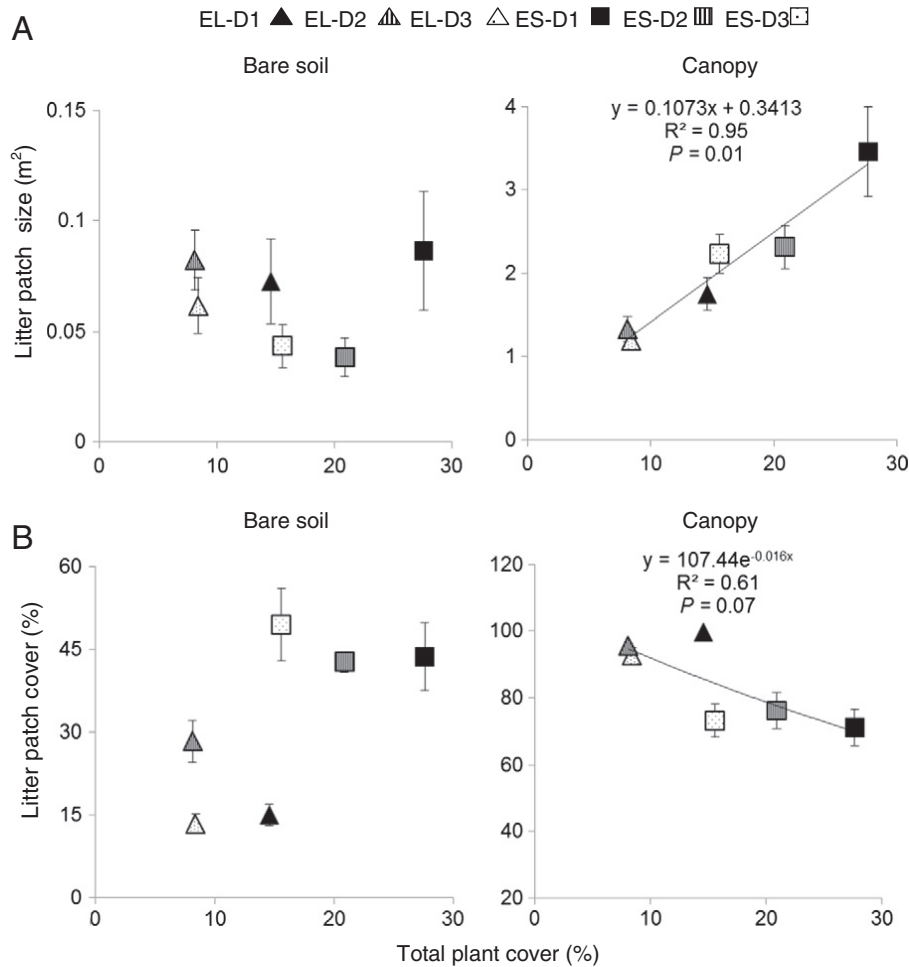


Fig. 2. Relationship between **A**, litter patch size and **B**, litter patch cover and total plant cover at canopy and bare soil microsites at the six locations differing in grazing history. Significant equations fitted by simple regression analysis at the top of each panel. Vertical lines indicate one standard error. EL indicates La Elvira experimental site; ES, La Esperanza experimental site. Grazing disturbance levels: D1 (low), D2 (medium), D3 (high).

cover (Fig. 3A, Table 2A). However, the seed density of perennial grasses at canopy microsites was not related to total plant, shrub, and perennial grass cover or attributes of litter patches (Fig. 3A, Table 2B). Except for ES-D2, the largest perennial grass seed density at canopy microsites occurred at the locations with the largest total plant cover (ES-D1: 105.3 ± 20.4 seeds·m⁻², ES-D3: 136.5 ± 49.5 seeds·m⁻², EL-D1: 109.2 ± 37.9 seeds·m⁻²; Fig. 3A). Multiple

regression models were not significant for the variance in the density of perennial grass seeds at either bare soil or canopy microsites (data not shown).

We found lower number of perennial grass seeds·litter patch⁻¹ at bare soil microsites (1.8 ± 0.6 seeds·patch⁻¹) than at canopy microsites (131.9 ± 28.0 seeds·patch⁻¹) across all sites and locations ($U = 32087$, $P < 0.001$). The variable best correlated to the number of perennial grass seeds·litter patch⁻¹ at both microsites was the total plant cover (Fig. 3B). At bare soil microsites, we found an exponential relationship indicating that the largest increase in seeds occurred along with the highest plant total cover, while at canopy microsites, the number of seeds increased evenly with total cover, but this relationship was not significant ($R^2 = 0.51$, $P = 0.11$). Multiple regression models were not significant for the variance in the number of perennial grass seeds·patch⁻¹ at either bare soil or canopy microsites (data not shown).

Table 1
Binary Pearson correlation among perennial grass, shrub, and total plant cover and litter patch attributes at (A) bare soil and (B) canopy microsites across sites and locations.

	A. Bare soil microsite		B. Canopy microsite	
	Litter patch size	Litter patch cover	Litter patch size	Litter patch cover
Perennial grass cover	$r = 0.56$ $P = 0.25$ $n = 6$	$r = 0.19$ $P = 0.72$ $n = 6$	$r = 0.80$ $P = 0.058$ $n = 6$	$r = -0.31$ $P = 0.63$ $n = 6$
Shrub cover	$r = -0.13$ $P = 0.81$ $n = 6$	$r = 0.71$ $P = 0.11$ $n = 6$	$r = 0.96^*$ $P = 0.003$ $n = 6$	$r = -0.83^*$ $P = 0.04$ $n = 6$
Total plant cover	$r = 0.01$ $P = 0.99$ $n = 6$	$r = 0.65$ $P = 0.17$ $n = 6$	$r = 0.97^*$ $P = 0.001$ $n = 6$	$r = -0.77$ $P = 0.075$ $n = 6$

* Statistical significant correlations are identified with an asterisk.

Spatial Distribution of Perennial Grass Seeds in Litter Patches

We found that the frequency of litter patches with perennial grass seeds increased with increasing total plant cover both at bare soil and canopy microsites, except for ES-D2 with high aboveground cover and high number of microsites without seeds (Fig. 4). The frequency

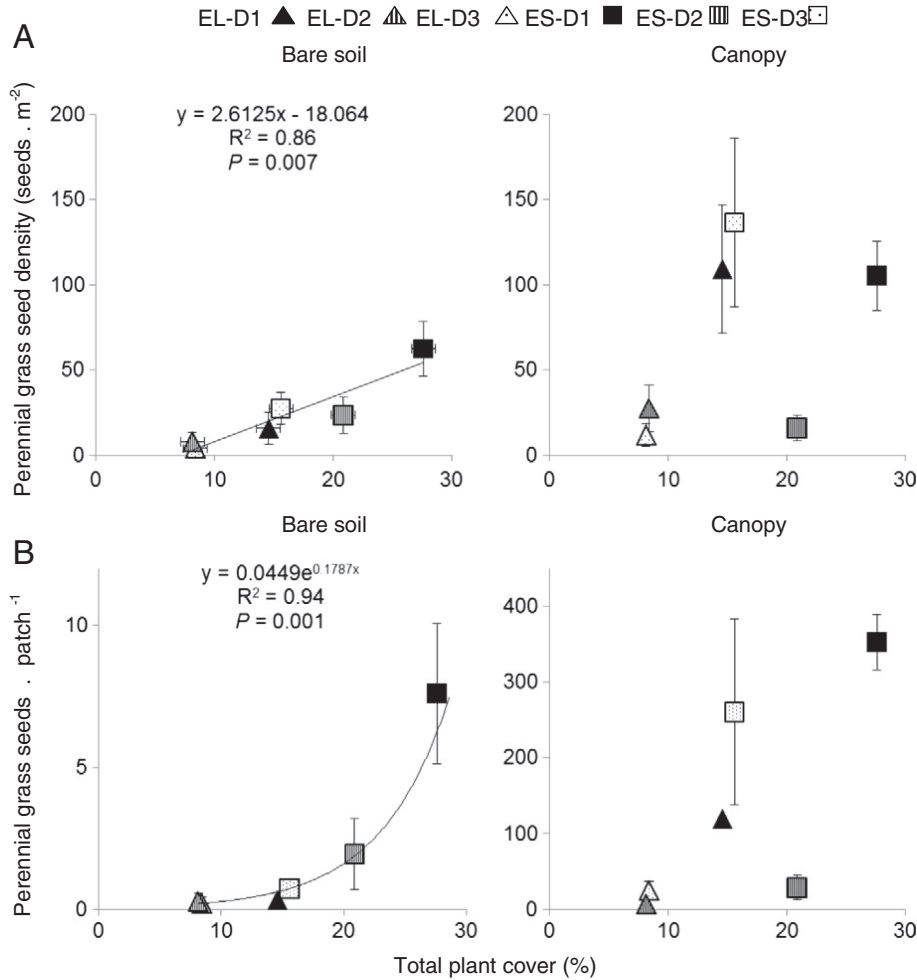


Fig. 3. A, Seed density (number of seeds · m⁻²) and B, number of seeds · litter patch⁻¹ of perennial grasses in relation to total plant cover in litter patches at bare soil and canopy microsites at the six locations differing in grazing history. Significant equations fitted by simple regression analysis at the top of each panel. Vertical lines indicate one standard error. EL indicates La Elvira experimental site; ES, La Esperanza experimental site. Grazing disturbance levels: D1 (low), D2 (medium), D3 (high).

of litter patches bearing seeds was greater for canopy than bare soil microsites ($\chi^2 = 15.8, P = 0.015$).

Table 2

Binary Pearson correlation between the density of perennial grass seeds at (A) bare soil and (B) canopy microsites and plant cover (perennial grass, shrub, and total) and patch litter attributes (size and cover).

	Perennial grass seed bank	
	A. Bare soil microsite	B. Canopy microsite
Perennial grass cover	$r = 0.84^*$ $P = 0.038$ $n = 6$	$r = 0.46$ $P = 0.36$ $n = 6$
Shrub cover	$r = 0.89^*$ $P = 0.016$ $n = 6$	$r = 0.37$ $P = 0.47$ $n = 6$
Total plant cover	$r = 0.93^*$ $P = 0.007$ $n = 6$	$r = 0.41$ $P = 0.42$ $n = 6$
Litter patch size	$r = 0.23$ $P = 0.66$ $n = 6$	$r = 0.50$ $P = 0.32$ $n = 6$
Litter patch cover	$r = 0.66$ $P = 0.16$ $n = 6$	$r = -0.33$ $P = 0.52$ $n = 6$

* Statistical significant correlations are identified with an asterisk.

Discussion

The six locations selected for this study may be arranged across a gradient of total plant cover resulting from different combinations of grazing by domestic and native large herbivores (sheep and guanaco, respectively), release from domestic grazing, and eventually differences in vegetation and soils between both sites separated approximately 125 km from each other. The highest total cover corresponded to the locations at “La Esperanza” (ES) site (released from domestic grazing) and the lowest total cover to locations at “La Elvira” (EL) site (under domestic grazing). Moreover, the lowest total cover value of ES was equivalent to the highest total cover of EL. This gradient is consistent with gradients of grazing disturbance reported for the shrubland of *Larrea divaricata* Cav. and *Stipa* spp. characterized by decreasing total, perennial grass and in some cases shrub cover, as well as reduced shrub patch size with increasing grazing disturbance (Bisigato & Bertiller, 1997; Bertiller et al., 2002; Pazos et al., 2007; Bertiller & Ares, 2008; Pazos et al., 2010; Bär Lamas et al., 2013). However, it is not possible to separate eventual site differences from possible grazing history effects as these two aspects are confounded in this study.

Seed densities of perennial grasses found in our study ranged from 11.7 to 136.5 seeds · m⁻² in canopy and from 3.9 to 62.4 seeds · m⁻² in bare soil microsites. The maximum values in both microsites are within the range reported for arid-semiarid

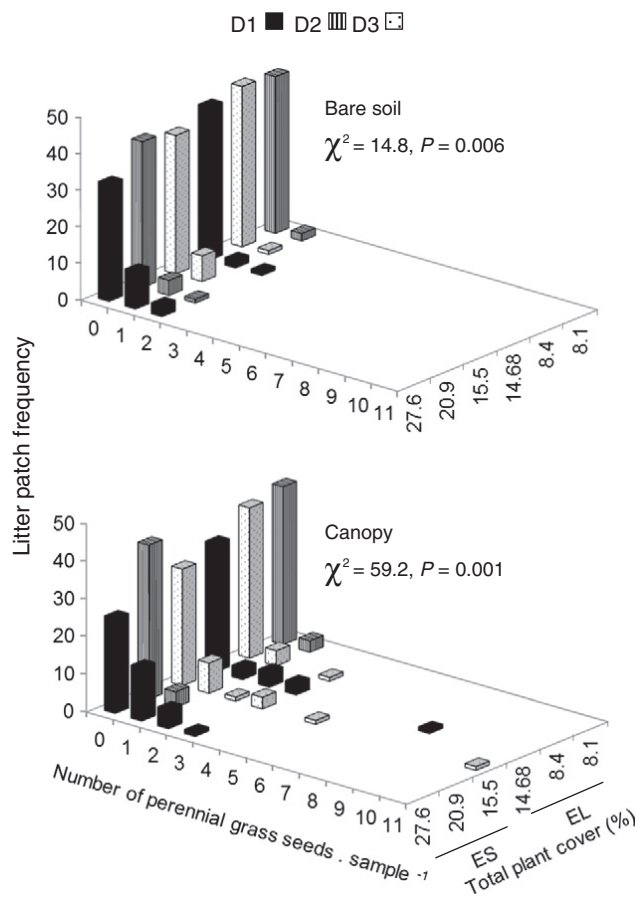


Fig. 4. Frequency distribution of patches with different number of perennial grass seeds at bare soil and canopy microsites at the six locations differing in grazing history. EL indicates La Elvira experimental site; ES, La Esperanza experimental site. Grazing disturbance levels: D1 (low), D2 (medium), D3 (high). Chi square values at the top of each panel refer to comparisons among locations at each microsite. Bare soil vs. canopy. Chi square value between microsites (bare soil vs. canopy perennial grass seed bank: $\chi^2 = 15.8$, $P = 0.015$).

ecosystems (Peters, 2002; Wang et al., 2005; Caballero et al., 2008) while the minimum values are similar to perennial grass seed densities in soil reported by DeFalco et al. (2009) in degraded shrublands of the Mojave desert. Overall, the mean density of perennial grass seeds was larger at canopy (38.5 ± 6.6 seeds \cdot m $^{-2}$) than at bare soil microsites (13.3 ± 2.3 seeds \cdot m $^{-2}$). This contrast highlights the importance of plant canopies on the dynamics of perennial grass seed banks and litter patches, probably through canopy impacts on litter and seed inputs (i.e., litterfall, seed rain, entrapment of seeds and litter) and/or on litter and seed losses or redistribution (i.e., seed transport by water and wind, seed predation) (Aguar & Sala, 1997; Bertiller, 1998; Caballero et al., 2008; Pazos & Bertiller, 2008; Campanella & Bertiller, 2010; Pekas & Schupp, 2013). The mean density of perennial grass seeds in litter patches was higher than overall means of perennial grass seeds at canopy and bare soil microsites reported for the Monte rangelands (Bertiller, 1998; Pazos & Bertiller, 2008; Busso & Bonvissuto, 2009). Seeds of *Nassella tenuis* and *Poa ligularis* were the most abundant, and those of *Elymus patagonicus*, *Pappostipa speciosa*, and *Jarava neaei* were the least frequent and mostly found at canopy microsites. However, we did not find a significant relationship between perennial grass seed attributes and differences in aboveground cover or attributes of litter patches at canopy microsites. The lack of canopy and litter effects on perennial grass seeds in litter patches could be related to different balances between seed inputs and seed losses induced by plant cover.

Large seed losses may occur beneath dense plant canopies with large perennial grass seed input and accumulation, due to the large abundance of predators, predation rates, and selective pressure on perennial grass seeds (Kemp, 1989; Ostoja et al., 2013). On the other hand, seed and litter redistribution by effect of wind or water could occur underneath plant canopies with reduced cover, enhancing seed and litter patchiness (De Soyza et al., 1997). In this sense, we observed decreasing numbers of litter patches with seeds of perennial grasses and increasing litter concentration in small patches with decreasing aboveground plant cover at canopy microsites. Alternatively, the lack of correlation between perennial grass seeds and aboveground cover could be due to the intrinsic perennial grass seed bank patchiness and/or differences among species in seed persistence in soil (Schneider & Allen, 2012).

At bare soil microsites, we found a clear positive relationship between the aboveground plant cover and perennial grass seed attributes (seed density and number of litter patches with seeds), without significant differences in the size and cover of litter patches. This could result from decreasing seed inputs, augmented distances from seed sources, increased seed redistribution by wind or water, and increased trampling at bare soil microsites with decreasing plant cover (Kemp, 1989; Marone et al., 1998; Aguiar & Sala, 1999; Bertiller et al., 2002; Pazos & Bertiller, 2008; DeFalco et al., 2009; Rusterholz et al., 2011). Litter patches at canopy microsites may act as the primary seed sources for neighboring litter patches in bare soil areas, mostly enhancing perennial grass seed density at bare soil at locations with high aboveground vegetation. In addition, more efficient seed entrapment could occur in less disturbed litter patches under conditions of high total plant cover (Aguar & Sala, 1999; DeFalco et al., 2009; Ruprecht & Szabó, 2012).

The combination of seed accumulation and enhanced levels of soil resources and microclimate in litter patches (O'Connor & Pickett, 1992; Bertiller, 1996; Mazzarino et al., 1998; DeFalco et al., 2009; Ruprecht et al., 2010; Busso et al., 2012) may increase the potential for regeneration of perennial grasses from the soil seed bank (Luzuriaga & Escudero, 2008; Pueyo et al., 2009; Ladd & Facelli, 2012). However, litter patches could also preclude grass seeds from germinating due to physical and chemical constraints, as reported for other ecosystems (Young & Evans, 1975; Fowler, 1988; Rotundo & Aguiar, 2005), and high aboveground cover could increase plant competition (Grime & Hillier, 2000; Luzuriaga & Escudero, 2008; DeFalco et al., 2009; Wang et al., 2010). Accordingly, bare soil microsites at locations with high aboveground vegetation could be opportunistic microsites for perennial grass recruitment due to larger perennial grass seed banks than other noncanopy microsites, intermediate litter cover (43–50%), favorable micro-environmental conditions induced by litter, and low intraspecific and interspecific competition. In contrast, perennial grass recruitment by seeds at canopy microsites of locations with high aboveground vegetation and litter (92–100%) cover could be affected by litter restrictions (Young & Evans, 1975; Fowler, 1988; Rotundo & Aguiar, 2005), grass–grass root competition (Defossé et al., 1997), or competition with shrubs having dimorphic roots systems able to capture soil resources from the same soil layers as perennial grasses (Rodriguez et al., 2007). Moreover, litter patches at canopy microsites with low aboveground vegetation cover could also be an alternative for perennial grass recruitment by seeds due to reduced litter cover (71–76%), large perennial grass seed bank, ameliorated micro-environmental conditions created by plant canopies, and reduced intraspecific and interspecific competition (Aguar & Sala, 1997; Mazzarino et al., 1998; Bisigato & Bertiller, 2004; Arrieta & Suarez, 2005; Caballero et al., 2008; Busso et al., 2012). Lastly, bare soil microsites at locations with disturbed aboveground plant cover might be the least favorable microsites for perennial grass recruitment by seeds being limited by

small seed banks, very low litter cover (13–28%), and adverse micro-environmental conditions (Fowler, 1988; Bisigato & Bertiller, 2004).

The potential opportunities for perennial grass recruitment from seeds inferred from the soil seed bank patterning observed in our study are consistent with the spatial patterns of perennial grass populations assessed at different vegetation states in the Patagonian Monte (Bertiller et al., 2002; Pazos et al., 2007, 2010). These studies reported a concentration of perennial grass bunches around canopies of shrubby plant patches at locations with disturbed aboveground vegetation and a wide perennial grass distribution with grass bunches occupying both interpatch and canopy areas at conserved vegetation states with high aboveground cover.

In conclusion, our findings indicate the preponderant role of aboveground vegetation cover on perennial grass seed accumulation in litter patches and on the potential for recovery of perennial grasses cover. However, differences in the aboveground plant cover had larger influence on the seed bank of perennial grasses at bare soil than at canopy microsites. The spatial patterns observed suggest that the potential microsites for perennial grass recruitment by seeds might shift from litter patches at bare soil microsites to litter patches at canopy microsites, at locations with high and low canopy cover.

Management Implications

Our findings showed that lower aboveground plant cover negatively affected the density of perennial grass seeds in litter patches and influenced the spatial patterning of those seeds. These differences may influence the potential for regeneration of perennial grasses and the conservation of the populations of these plant species in arid rangelands of the Patagonian Monte. Accordingly, management actions should be focused on the increase and maintenance of perennial grass seed banks in litter patches mostly at bare soil microsites through artificial seed addition or by seasonal reductions in sheep stocking rates in order to increase perennial grass seed production and dispersal. This, in turn, may enhance the potential for regeneration and restoration of perennial grass cover in litter patches at bare soil microsites with favorable seedbed microenvironments and lower plant competition compared with litter patches in canopy microsites.

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