Spatial patterns of the germinable soil seed bank of coexisting perennial-grass species in grazed shrublands of the Patagonian Monte

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Abstract We compared the size and spatial pattern of the germinable soil seed bank (GSB) of the three dominant perennial-grass species in the arid Patagonian Monte of Argentina. These species differ in plant functional traits, seed morphology, and in their preference by grazers. During three consecutive years, we sampled the soil seed bank at 1 m intervals and the intercepted diameter of perennial-grass species and shrub patches along 50-m linear transects at three sites with different grazing pressure. Soil samples were incubated at field capacity during 12 weeks and emerged seedlings counted. The largest-seeded and most xerophytic *Stipa speciosa* did not form a GSB. The other two grass species with more mesophytic traits and smaller seeds than *S. speciosa* formed different GSB. *Poa ligularis* formed a smaller and more heterogeneous GSB than *Stipa tenuis.* Grazing had not effect on GSB size of *P. ligularis* but increased the proportion of seeds under dense shrub canopies. In contrast, grazing reduced the size and also increased the proportion of the GSB of *S. tenuis* under shrub canopies. We conclude that the size and the spatial pattern of the GSB of the dominant perennial-grass species in the arid Patagonian Monte were related not only to seed and plant traits but also to the spatial distribution of grass plants and their exposure to grazers.

Introduction

Soil seed banks are important in relation to the conservation and regeneration potential of plant populations (Thompson 2000). Soil seed banks of arid and semiarid ecosystems are characterized by a high spatial heterogeneity due to the patchiness of the aboveground vegetation (Kemp 1989; Bertiller 1998), the short seed dispersal distances characterizing many desert plants (Ellner and Schmida 1981), and processes that govern the post dispersal redistribution of seeds in the soil (Chambers and MacMahon 1994). Desert soil seed banks also undergo large intra- and inter-annual fluctuations associated with variable seed inputs (seed production and dispersal) and seed losses by germination, predation, or death (Kemp 1989; Chambers and MacMahon 1994).

Perennial grasses are one of the dominant plant life forms in arid and semi-arid ecosystems of the world and sexual reproduction is an important way for the regeneration of most of their populations (O'connor and Everson 1998; Aguiar and Sala 1999; Bisigato et al. 2005). This plant life form usually has short seed dispersal distance (Cheplick 1998) and forms

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transient soil seed banks (Bertiller 1996; O'connor and Everson 1998; Marone et al. 2004), which results in a dynamics tightly dependent on the stochastic water inputs of arid ecosystems (Kemp 1989; Bertiller 1998). Also, important seed losses from the soil seed bank of perennial grasses may occur by seed predation (Mayor et al. 2003; Marone et al. 2004). Intrinsic seed characteristics such as the size, number, and morphology may strongly affect dispersal distances, seed redistribution, seed burial potential, and depletion of seeds from the soil seed bank of perennial grasses (Marone et al. 1998a; Chambers 2000; Willson and Traveset 2000).

Perennial grasses are one of the life forms most severely affected by grazing (O'connor and Everson 1998; Aguiar and Sala 1999; Bisigato et al. 2005). High herbivory rates on vegetative and reproductive soft tissues with high N concentration may affect plant performance, plant abundance, and reproductive output of perennial grasses (Augustine and McNaughton 1998; O'connor and Everson 1998; Pazos et al. 2007). Many studies reported a negative impact of herbivores on the size of the soil seed bank of perennial grasses (O'connor and Pickett 1992; Bertiller 1996; Mayor et al. 2003) but few of them analyzed the effect of grazing on spatial patterns of soil seed bank of coexisting perennial-grass species with contrasting plant functional traits and seed morphology. This could be important in relation to the probability of seedling emergence and recruitment of different perennial-grass species in ecosystems degraded by grazing.

Several species of perennial grasses varying in the degree of xerophytism, seed size and morphology, and preference by herbivores coexist in the shrublands of the Patagonian Monte. A recent study (Pazos et al. 2007) showed that plant density and size of the three dominant perennial-grass species was differently affected by the intensity of livestock grazing. Plants of the three species also showed contrasting spatial patterns in relation to shrub patches in areas excluded from grazing. However, increasing grazing pressure led to the confinement of grass plants under shrub patches, which would act as biotic refuges against herbivores (Milchunas and Noy-Meir 2002). These differences among species were related to their functional traits and preference by herbivores, but it was also hypothesized that differences in seed dispersal ability and seedling recruitment would

substantially contribute to the generation of the observed patterns. In this sense, the knowledge of the size and spatial distribution of the soil seed bank of these species under different intensities of grazing is a first step to address these issues as shown in other arid ecosystems (Guo et al. 1998; O'connor and Everson 1998; Aguiar and Sala 1999). Furthermore, this information is relevant in relation to the potential of regeneration and recovery of perennial-grass cover in arid grazing lands.

Previous studies in sites excluded from grazing in the Patagonian Monte showed that perennial grasses have transient soil seed banks and that the highest total seed density is found in microsites neighboring established grass plants (Bertiller 1998; Bisigato and Bertiller 2004a). In this work, we asked whether differences in plant functional traits, seed morphology, and spatial patterning of mature plants of coexisting perennial-grass species are associated with the size and spatial patterning of the soil seed bank with respect to shrub patches under different intensities of livestock grazing.

Materials and methods

Study area

This study was carried out in the Patagonian Monte, Argentina (42°–44°S and 64°–68°W) (León et al. 1998). Mean annual precipitation is 235.9 mm, with high mean inter-annual variation, and mean annual temperature is 13.4°C (series 1982–2001) (CENPAT 2003). Soils are a complex of Typical Petrocalcids and Typical Haplocalcids (Soil Survey Staff 1998). Vegetation is a shrubland dominated by *Larrea divaricata* Cav. and *Stipa* spp. (León et al. 1998) covering from 40 to 60% of the soil. The dominant plant life forms are shrubs and perennial grasses arranged in a two-phase mosaic consisting of a high-cover phase formed by patches of shrubs and perennial grasses dispersed on a low-cover phase of scattered plants of perennial grasses and bare soil (Bisigato and Bertiller 1997). The dominant tall-medium shrubs are *L. divaricata*, *Schinus johnstonii* Barkley, *Chuquiraga hystrix* Don., *Atriplex lampa* Gill. ex Moq., and *Lycium chilense* Miers ex Bert. Dwarf shrubs are represented by *Nassauvia fuegiana* (Speg.) Cabrera, *Junellia seriphioides* (Gillies and

Hook) Mold., and *Acantholippia seriphioides* (A. Gray) Mold. The dominant perennial grasses are *Stipa tenuis* Phil., *S. speciosa* Trin. and Rupr., and *Poa ligularis* Nees ex Steud (Bisigato and Bertiller 1997). Nomenclature follows Correa (1971–1999). We point out that the current valid names for *Stipa tenuis* and *S. speciosa* are *Nassella tenuis* (Phil.) Barkworth and *Jarava speciosa* (Trin. and Rupr.) Peñailillo, respectively. However, we followed the Correa's nomenclature in relation to our previous published works in the Patagonian Monte.

Sheep grazing in the area, introduced at the beginning of the past century, is usually organized in ranches of about four paddocks of ca. 2500 ha each sharing a single permanent watering point. Grazing disturbance reduced perennial-grass cover and consequently the relative cover of shrubs increased (Bisigato and Bertiller 1997).

Study species

We selected the three dominant perennial-grass species of the Patagonian Monte (*Poa ligularis, Stipa tenuis*, and *S. speciosa*), which represent more than 90% of the total perennial-grass cover in both grazed and ungrazed areas. These species have contrasting morpho-functional traits as mature plants, vary in the degree of xerophytism (Pazos et al. 2007), and have different seed size and morphology (Correa 1978). In this work, the term 'seed' refers to 'sexual dispersal units' composed by the caryopsis and external coats (Cheplick 1998). *Stipa speciosa* (monoecious) is the species with the most xerophytic traits: it has the lowest N concentration in green leaves, the highest leaf mass per area, and the deepest root system (Bertiller et al. 1991; Pazos et al. 2007). The anthecium and caryopsis lengths are similar ranging from 10 to 12 mm. Seeds possess a hygroscopic awn longer than 35 mm and a stark spikelet stalk (sensu Gutterman (1993)). The other two species show mesophytic traits and do not differ between them in most leaf traits except for the presence of pubescence in leaves of the monoecious *S. tenuis* (Pazos et al. 2007). The anthecium and caryopsis lengths of *S. tenuis* are similar ranging from 4 to 8 mm. Seeds have also stark spikelet stalks and a hygroscopic awn longer than 70 mm. The anthecium and caryopsis lengths of the dioecious *P. ligularis* vary between 1.5

and 2.8 mm and posses long sticky hairs at the base (Correa 1978). *Poa ligularis* is the most preferred and *S. speciosa* the least preferred species by wild and domestic herbivores (Pazos et al. 2007).

Sampling sites

We selected three sampling sites of 2 ha each encompassing three different grazing pressures at Estancia San Luis (42°39′S, 65°23′W; 10.000 ha). One of them (EX) was a site excluded from domestic grazing for the last 12 years. The other two sites were located at a paddock grazed by sheep at 1 km and at 4 km from the permanent watering point. Based on previous studies in the area (Bisigato and Bertiller 1997; Bertiller et al. 2002), these locations correspond to sites with heavy (H) and light (L) past and present grazing pressure, respectively. All sites were freely grazed by wild herbivore mammals (*Lama guanicoe, Dolichotis patagonum*, and *Lepus europaeus*).

Precipitation records

We recorded precipitation events with an automatic data logger (21X Micrologger, Campbell Scientific, Logan, USA) at the study area (EX site) during the period January 2002-December 2005. We calculated the annual precipitation (January-December) for each year and we compared these values with the long-term mean annual precipitation for the series 1994–2005 of the study area.

Sampling and measurement of the germinable soil seed bank, plant density of perennial grasses, and cover of shrub patches

We sampled the soil seed bank of the three perennial-grass species (the 'grass soil seed bank assemblage' in the sense of Csontos (2007)) at the three sites (EX, L, and H) in April 2003, 2004, and 2005. The dates of sampling approximately corresponded to the end of the seed rain period of the perennial grasses (Bertiller 1998). At each sampling date and site, we delimited a 50 m linear transect in the direction of predominant winds (SW–NE) (CENPAT 2003). We collected 50 circular soil-cores (12 cm diameter, 3 cm depth),

including litter, at the center of contiguous 1-m segments along each transect making a total sampled soil-volume of 16,965 cm^3 at each site and date. We did not sample the seeds at deeper soil layers in accordance with the sampling considerations discussed by Csontos (2007) and some characteristics of the sampled soil seed banks. Previous works in other arid ecosystems of the world showed that the largest portion of the soil seed bank is located in the first 2–3 cm of the soil (Kemp 1989; Gutterman 1993; Guo et al. 1998; Marone et al. 1998a; O'connor and Everson 1998). Moreover, the plant group of perennial grasses has a transient soil seed bank in the study area (Bertiller 1998) and, in consequence, seeds have little chance to be buried, reach deep soil layers, and remain alive (O'connor and Everson 1998).

We also recorded the position and intercepted diameter of the plants of each perennial-grass species (*P. ligularis*, *S. tenuis*, and *S. speciosa*) and shrub patches along each transect. We calculated the plant density (number of plants per 50 m transect) and percentage cover of each grass species at each transect, and plant density at 1-m segments along transects per site and year. We also calculated the density (number of shrub patches per 50 m transect) and percentage of cover of shrub patches per transect and shrub cover at 1-m segments along transects per site and year.

We incubated the soil samples at 80–100% soil field capacity (ca. 15% soil moisture on dry weight basis; −0.01 MPa) in plastic trays (17 × 13 cm) during 12 weeks at 18–20°C with a light period of 12 h. Emerged seedlings were weekly identified, counted, and removed. Each soil sample was monthly stirred and reincubated. A previous study indicated that most of seeds of the three species germinate under these incubation conditions (Bertiller 1998). We expressed the size of the germinable soil seed bank (GSB) of each species as the number of germinated seeds per dm^2 soil. Further, we calculated the proportion of perennial-grass seeds and plants (pooled 1-m segment data of the 3 years per species and site, $n = 150$) by categories of shrub cover (0–25, 26–50, 51–75, 76–100%).

Data analysis

We assessed the significance of the differences in density, intercepted diameter, and total percent cover of shrub patches among sites by one-way ANOVA (Norusis 1997). We assessed the significance of the differences in the logarithmic-transformed plant density, intercepted diameter, and arcsin transformed grass cover values among species and sites, and among species and years by two-way ANOVA using Tukey test for multiple comparisons (Norusis 1997). We assessed the significance of the differences in the GSB among species, sites, and years by Kruskal–Wallis tests (Norusis 1997). We compared the distribution of proportion of seeds and grass plants by categories of shrub cover among species and sites using the *G*-test (Norusis 1997).

Results

Precipitation

The annual precipitation in 2002, 2003, and 2005 was 261, 220, and 205 mm, respectively, and fell within the 95% confidence interval of the mean annual precipitation in the area for the period 1994–2005 (245 ± 49 mm). In contrast, the annual precipitation in 2004 (185 mm) was lower than the long-term mean.

Size and abundance of shrub patches and perennial grasses

The density, intercepted diameter, and total cover of shrub patches did not significantly differ among sites ($F_{2,6} = 0.77$, $p = 0.504$; $F_{2,203} = 0.16$, $p = 0.85$; and $F_{2,6} = 0.36$, $p = 0.712$, respectively, Table 1). *Stipa tenuis* was the only species whose density was

Table 1 Mean (±1 SE) density, intercepted diameter, and total cover of shrub patches at sites excluded from grazing (EX) and with light (L) and heavy (H) grazing pressure

	EX	L	H
Shrubs per 50 m transect	21.3 ± 4.8 a	27.0 ± 2.9 a	20.7 ± 3.9 a
Intercepted diameter (cm)	82.1 ± 9.3 a	74.4 ± 7.5 a	91.6 ± 13.3 a
Shrub cover (%)	35.0 ± 6.8 a	40.2 ± 3.0 a	37.3 ± 0.6 a

Different lowercase letters indicate significant differences among sites at $p < 0.05$

Table 2 Mean (± 1 SE) grass density, intercepted diameter, and grass cover of the three perennial grass species at the study sites
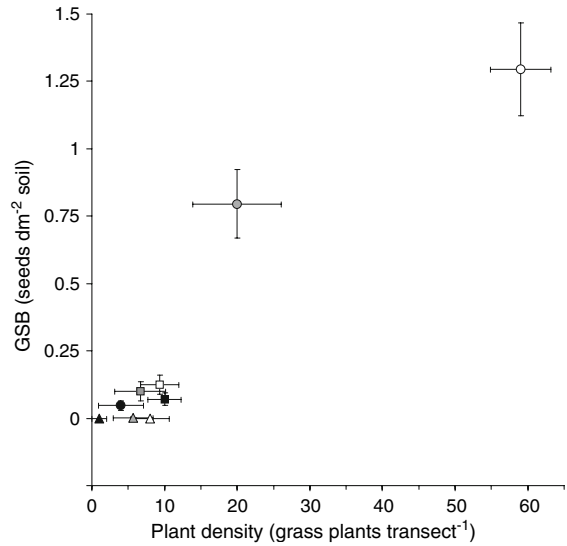
Site	Poa ligularis	Stipa tenuis	Stipa speciosa
	Grass plants per 50 m transect		
EX	9.33 ± 2.60 Aa	59.00 ± 4.16 Bb	8.00 ± 2.65 Aa
L	6.67 ± 3.48 Aa	20.00 ± 6.11 Aa	5.67 ± 2.73 Aa
H	10.00 ± 2.31 Aa	4.00 ± 3.06 Aa	1.00 ± 1.00 Aa
	Intercepted diameter of grass plants (cm)		
EX	3.57 ± 0.42 Aa	4.55 ± 0.20 Ab	7.21 ± 0.85 Bb
L	2.05 ± 0.20 Aa	2.48 ± 0.16 Aa	4.12 ± 0.57 Aa
H	2.50 ± 0.27 Aa	3.00 ± 0.39 Aab	4.33 ± 0.88 Aa
	Grass cover (%)		
EX	0.67 ± 0.18 Aa	5.37 ± 1.21 Bb	1.15 ± 0.37 Aa
L	0.27 ± 0.16 Aa	0.99 ± 0.36 Aa	0.47 ± 0.30 Aa
H	0.44 ± 0.14 Aa	0.24 ± 0.21 Aa	0.11 ± 0.11 Aa

Acronyms for sites as in Table 1. Different uppercase letters indicate significant ($p < 0.05$) differences among species at each site. Different lowercase letters indicate significant ($p < 0.05$) differences among sites for each species

Fig. 1 Mean (± 1 SE) germinable soil seed bank (GSB, seeds dm^{-2} soil) and plant density (grass plants per 50 m transect) of *Poa ligularis* (squares), *Stipa tenuis* (circles) and *S. speciosa* (triangles) at sites excluded from grazing (open symbols), and with light (grey filled symbols) and heavy (black filled symbols) grazing pressure

reduced with increasing grazing pressure (significant species × site interaction, $F_{4,18} = 3.57$, $p = 0.026$) (Table 2). At the EX site, the density of this species was significantly higher than those of *Poa ligularis* and *S. speciosa*, but plant density did not significantly differ among species at L and H sites (Table 2). The plant intercepted diameter of the three species decreased with increasing grazing pressure ($F_{2,362} = 19.58$, $p < 0.001$), but this effect was significant only for both *Stipa* species (Table 2). In addition, the intercepted diameter of *S. speciosa* plants was significantly higher than those of the other two species ($F_{2,362} = 10.15$, $p < 0.001$) only at the EX site (Table 2). Despite the differences in plant size, the grass-species cover varied in a similar way as plant density (significant species × site interaction, $F_{4,18} = 5.80$, $p = 0.004$) (Table 2). There were no significant differences in grass density of any species among years ($F_{2,18} = 0.93$, $p = 0.412$).

Size of the germinable soil seed bank (GSB)

Stipa tenuis was the only species whose GSB varied among sites ($\chi^2 = 81.44$, $p < 0.001$). This species displayed the largest GSB at both EX and L sites in comparison with the other species ($\chi^2 = 142.01$,

$p < 0.001$, and $\chi^2 = 75.73$, $p < 0.001$, respectively) while at the H site, the GSB of *S. tenuis* was reduced and did not differ from that of *P. ligularis* (Fig. 1). *Stipa speciosa* did not show a GSB (Fig. 1). We only found one germinable seed of this species in the L site. *Stipa tenuis* was the only species showing significant differences in the size of the GSB among years ($\chi^2 = 32.45$, $p < 0.001$), with the highest value in 2003.

Spatial pattern of grass plants with respect to the cover of shrub patches

The distribution of *P. ligularis* plants with respect to the cover of shrub patches at EX sites significantly differed from those at L ($G = 34.76$, $p < 0.001$) and H sites ($G = 43.13$, $p < 0.001$), but it did not differ between the latter sites ($G = 8.52$, $p = 0.055$). The proportion of plants of *P. ligularis* increased with increasing cover of shrub patches at EX sites while it was larger at both the lowest and the highest shrub cover categories than at the intermediate ones at L and H sites (Fig. 2). The proportion of plants of *S. tenuis* decreased with increasing cover of shrub patches at all sites. We did not find differences in the

Fig. 2 Proportion of seeds (black bars) and plants (white bars) of *Poa ligularis* and *Stipa tenuis* by shrub-cover categories at sites excluded from grazing (**a**), and with light (**b**) and heavy (**c**) grazing pressure (three-year pooled data, $n = 150$). The significance of the differences between the distributions of seeds and plants is indicated by the respective *G*-test
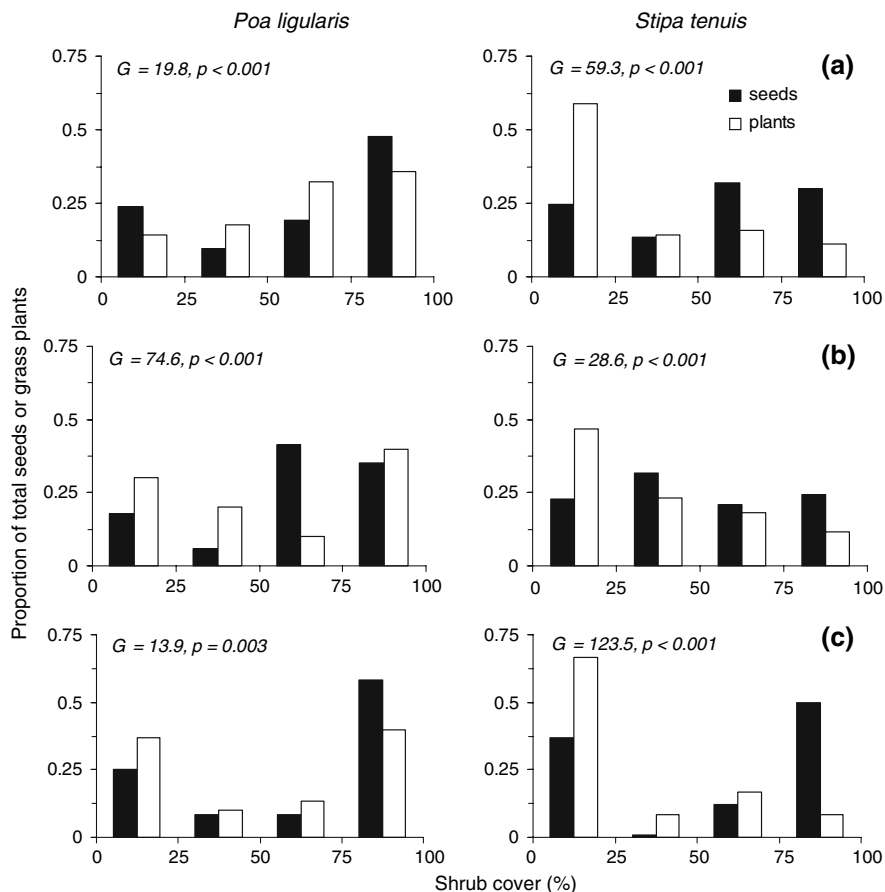
distribution of grass plants of this species with respect to the cover of shrub patches between EX and H sites ($G = 4.71$, $p = 0.194$) but plant distribution of *S. tenuis* in L differed from that in EX and H sites ($G = 8.08$, $p = 0.044$; $G = 21.61$, $p < 0.001$, respectively). The plants of this species were more frequent at the patches with the lowest shrub cover at both EX and H than at L sites (Fig. 2). Accordingly, the distribution of grass plants with respect to the cover of shrub patches significantly differed between species at each site ($G = 95.75$, $p < 0.001$; $G = 53.77$, $p < 0.001$; $G = 79.34$, $p < 0.001$ for EX, L, and H, respectively) (Fig. 2).

Spatial pattern of the GSB of perennial grasses with respect to grass plants and the cover of shrub patches

The distribution of seeds of *P. ligularis* with respect to the cover of the shrub patches at EX sites

significantly differed from that at L ($G = 26.1$, $p < 0.001$) and H sites ($G = 10.11$, $p = 0.034$) and between these latter ($G = 55.21$, $p < 0.001$). However, we found the largest proportion of seeds of this species at transect segments of high shrub cover at all sites. The distribution of seeds of *P. ligularis* with respect to the shrub cover significantly differed from that of the plants at the three sites. We found more seeds than expected at both the lowest and the highest categories of shrub cover at EX sites. In contrast, we found more seeds than expected only at high shrub covers at L (50–75% shrub cover) and H sites (75–100% shrub cover) (Fig. 2). The distribution of seeds of *S. tenuis* with respect to the cover of shrub patches at EX sites significantly differed from that at L ($G = 23.22$, $p < 0.001$) and H sites ($G = 52.82$, $p < 0.001$) and between these latter ($G = 86.81$, $p < 0.001$). The most homogeneous seed distribution with respect to the shrub cover categories was observed at the L site and the most heterogeneous distribution at the H site. The distribution of seeds of

this species with respect to the cover of shrub patches significantly differed from that of the plants. We found more seeds of *S. tenuis* than expected at high covers of shrub patches at all sites (50–100, 25–100, and 75–100% shrub cover for EX, L, and H, respectively) (Fig. 2). Accordingly, the distribution of seeds with respect to the cover of shrub patches significantly differed between species at each site. At EX and L sites, *S. tenuis* showed a more homogeneous distribution of seeds with respect to the shrub cover categories than *P. ligularis* ($G = 16.17$, $p = 0.001$; $G = 53.24$, $p < 0.001$, respectively). At H sites, both grass species showed different but heterogeneous seed distributions ($G = 27.64$, $p < 0.001$) (Fig. 2).

Discussion

We found differences in the GSB of coexisting perennial-grass species of the Patagonian Monte under different intensities of grazing disturbance. *Stipa speciosa* did not form a GSB at any site and year, which agree with studies in other ecosystems of Argentina (Ghermandi 1997; Mayor et al. 2003). This fact may be due to a very low seed rain and/or high seed losses after seed maturation and dispersal (Thompson 2000). In general, species with highly xerophytic traits and large seeds like *S. speciosa* (Pazos et al. 2007) have low fecundity in terms of number of seeds produced per plant as a consequence of the trade-off between seed size and seed number (Moles et al. 2004). Previous studies showed that a lower proportion of plants of *S. speciosa* reached the fruiting phenological stage, mostly in dry years, in relation to the other two grass species in a growing period (Campanella and Bertiller in press; Bertiller et al. 1991) suggesting a reduced seed production in *S. speciosa* at community level. In addition, large-seeded species generally experience higher rates of pre- and post-dispersal seed predation by ants, birds, and rodents soon after seed maturation and primary dispersal than small-seeded species (Thompson 2000; Traba et al. 2006). Seed losses by granivory were the most important factor determining the declining of the soil seed bank of perennial grasses in the central Monte (Marone et al. 1998a, b). The fruit maturation and dispersal period of *S. speciosa* extends from December to February–March approximately (late

spring to summer) (Campanella and Bertiller in press), which is the period of maximum ant activity in the study area, while birds are the most important seed eaters throughout the year (Saba and Toyos 2003). Seed losses to deep burial seem less probable because of the large seed size and the scarce rainfall in the summer period that hinder seed burial by the wetting of the hygroscopic awn (Chambers and MacMahon 1994; Guo et al. 1998). The low preference by herbivores of this species makes also little probable large pre-dispersal seed losses due to herbivore consumption of reproductive tissues (Pazos et al. 2007).

The other two species (*Poa ligularis* and *S. tenuis*), more mesophytic and with smaller seeds than *S. speciosa*, formed different GSB. The GSB of *P. ligularis* was smaller than that of *S. tenuis* and it was not affected by grazing pressure. This could be firstly related to the similar low abundance and size of the plants of this species at the three study sites (O'connor and Pickett 1992). In addition, the avoidance of herbivore consumption of reproductive tissues through the concentration of mature plants under dense shrub canopies with high anti-herbivore defences may contribute to maintain seed production under high grazing pressure as has been observed elsewhere (Milchunas and Noy-Meir 2002). These results are in accordance with Pazos et al. (2007) who reported the concentration of plants of *P. ligularis* under shrub patches at different grazing pressures, probably due to its strong mesophytic character and the high preference by herbivores.

In contrast, *Stipa tenuis* showed a GSB 10- and 8-fold larger than that of *P. ligularis* at EX and L sites, respectively. This agrees with results reported by Mayor et al. (2003) for other region of Argentina where these species also coexist. These results partially support the hypothesis that the dominance and higher colonization ability of *S. tenuis* in relation to the other two study species in the Patagonian Monte could be due to a high potential of sexual reproduction and the subsequent seedling recruitment (Bisigato and Bertiller 1997; Pazos et al. 2007). Moreover, our findings showed that increasing grazing pressure led to both reduced size of the GSB and decreased abundance and size of the plants of *S. tenuis* which, in turn, were more abundant than those of *P. ligularis* in patches with low shrub cover. Probably, *S. tenuis* located at the open inter-patch microsites were more exposed to herbivores than

those protected under shrubs (Bisigato et al. 2005). Accordingly, removal of vegetative and reproductive tissues by herbivores could reduce the vigor of the grazed plants, the seed rain, and the size of its GSB (O'connor and Pickett 1992).

The spatial patterning of the GSB of *P. ligularis* mimicked that of the mature plants, i.e., the major proportion of germinable seeds were located under shrub patches at all sites. This could be the consequence of the limited seed dispersal in this species. Although it possesses small and light seeds which can be easily wind dispersed after detachment from the mother plant (Willson and Traveset 2000; Fernández et al. 2002), the presence of long sticky hairs probably facilitates the rapid attachment of seeds to shrub plants, soil particles and/or the litter layer under shrubs (Chambers 2000). In contrast, the high proportion of plants of *S. tenuis* in patches of low shrub cover was not consistent with the spatial distribution of its seeds, which were either homogeneously distributed among patches with variable shrub cover or highly frequent at patches with the highest shrub cover, depending on the grazing pressure. Previous works in the study area (Bertiller 1998; Bisigato and Bertiller 2004a) found the largest density of seeds of perennial grasses near established grass plants of *S. tenuis* located outside shrub patches. However, our study provides evidence of high relocation of seeds after dispersal that accumulate under shrubs and probably represent the tail of the seed shadow (Willson and Traveset 2000). Spatial relocation of seeds may be due to higher wind velocities at open interpatch spaces than under closed shrub canopies (Chambers and MacMahon 1994; Marone et al. 1998a). Thus, despite their larger size and the anchorage appendages (hygroscopic awns and stark spikelet stalks), seeds of *S. tenuis* were dispersed farther or were more mobile after reaching the soil surface than those of *P. ligularis*. Horizontal movements of awned grass seeds have also been reported in other studies (Cheplick 1998; Chambers 2000).

Our findings indicate that differences in the GSB would be reflected in the recruitment dynamics of the three perennial-grass species. In the case of the most xerophytic and deep-rooted *S. speciosa* (Bertiller et al. 1991), the lack of a GSB would indicate that the persistence of its populations could mainly depend on its perenniality, as occurs with other grass species in other ecosystems of the world (Moles et al. 2004).

Probably, new recruits would emerge from the scarce seeds that are not exposed to seed predation in microsites located under shrub patches (Fernández et al. 2002; Pazos et al. 2007). The matching between the spatial patterns of mature plants and GSB of *P. ligularis* suggest that the persistence of its populations under grazing disturbance strongly depend on the presence of spiny shrubs acting as biotic refuges, as has been observed in other arid and semi-arid ecosystems (Milchunas and Noy-Meir 2002). This hypothesis is also partially supported by previous studies indicating that peripheries of dense shrub patches are preferential safe microsites for the establishment of perennial grasses (Bisigato and Bertiller 2004b). Thus, seed dispersal and recruitment of *P. ligularis* would involve a positive feedback that reinforces the aggregated spatial patterning of mature plants (Aguiar and Sala 1999). This would not be the case of *S. tenuis*, since the spatial pattern of plants and seeds suggest that the spatial pattern of recruitment would be dissociated from shrub patches. The high reproductive output of this species may compensate the eventual seed losses and/or the failed recruitment at not favorable microsites or years. Bisigato and Bertiller (2004a) showed that seedling survival of this species did not differ among different microsites when seed availability was not limiting. This suggests that dense leaf pubescence and the short plant-stature would confer to seedlings of this species high stress tolerance to withstand the harsh environmental conditions in the open inter-patch spaces (Grace 1998) thus colonizing vacant microsites outside shrub canopies (Pazos et al. 2007).

We conclude that the size and the spatial patterning of the GSB of the dominant perennial-grass species in the arid Patagonian Monte were related not only to seed and plant traits but also to the spatial distribution of plants and their exposure to grazers. Several hypotheses regarding the recruitment dynamics of these species emerged from these results. To test them, research under field conditions and manipulative experiments should be focused on the comparative assessment of seed production and seed dispersal potential, and the long term fate of both seeds and seedlings of the three species.

References

Aguiar MR, Sala OE (1999) Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends Ecol Evol 14:273–277

Augustine DJ, McNaughton SJ (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. J Wildl Manage 62:1165–1183

Bertiller MB (1996) Grazing effects on sustainable semiarid rangelands in Patagonia: the state and dynamics of the soil seed bank. Environ Manage 20:123–132

Bertiller MB (1998) Spatial patterns of the germinable soil seed bank in northern Patagonia. Seed Sci Res 8: 39–45

Bertiller MB, Ares JO, Bisigato AJ (2002) Multiscale indicators of land degradation in the Patagonian Monte, Argentina. Environ Manage 30:704–715

Bertiller MB, Beeskow AM, Coronato F (1991) Seasonal environmental variation and plant phenology in arid Patagonia (Argentina). J Arid Environ 21:1–11

Bisigato AJ, Bertiller MB (1997) Grazing effects on patchy dryland vegetation in northern Patagonia. J Arid Environ 36:639–653

Bisigato AJ, Bertiller MB (2004a) Seedling recruitment of perennial grasses in degraded areas of the Patagonian Monte. J Range Manage 57:191–196

Bisigato AJ, Bertiller MB (2004b) Temporal and micro-spatial patterning of seedling establishment. Consequences for patch dynamics in the southern Monte, Argentina. Plant Ecol 174:235–246

Bisigato AJ, Bertiller MB, Ares JO, Pazos GE (2005) Effect of grazing on plant patterns in arid ecosystems of Patagonian Monte. Ecography 28:561–572

Campanella MV, Bertiller MB (2008) Plant phenology, leaf traits, and leaf litterfall of contrasting life forms in arid Patagonian Monte, Argentina. J Veg Sci (in press). doi 10.3170/2007-8-18333

CENPAT (2003) Meteorological Station of the Oceanography and Meteorology Research Unit, Centro Nacional Patagonico (CONICET). http://www.cenpat.edu.ar

Chambers JC (2000) Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: implications for restoration. Ecol Appl 10:1400–1413

Chambers JC, MacMahon JA (1994) A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annu Rev Ecol Syst 25:263–292

Cheplick GP (1998) Seed dispersal and seedling establishment in grass populations. In: Cheplick GP (ed) Population biology of grasses. Cambridge University Press, Cambridge, pp 84–105

Correa MN (1971–1999) Flora Patagónica. Colección Científica. Instituto Nacional de Tecnologia Agropecuaria (INTA), Buenos Aires

Correa MN (1978) Flora Patagónica, parte III: Gramineae. Colección Científica. Instituto Nacional de Tecnologia Agropecuaria (INTA), Buenos Aires

Csontos P (2007) Seed banks: ecological definitions and sampling considerations. Community Ecol 8:75–85

Ellner S, Schmida A (1981) Why are adaptations for long-range seed dispersal rare in desert plants? Oecologia 51:133–144

Fernández RJ, Golluscio RA, Bisigato AJ, Soriano A (2002) Gap colonization in the Patagonian semidesert: seed bank and diaspore morphology. Ecography 25:336–344

Ghermandi L (1997) Seasonal patterns in the seed bank of a grassland in north-western Patagonia. J Arid Environ 35:215–224

Grace J (1998) Plant water relations. In: Crawley MJ (ed) Plant ecology, 2nd edn. Blackwell Science, Oxford, pp 28–50

Guo Q, Rundel PW, Goodall DW (1998) Horizontal and vertical distribution of desert seed banks: patterns, causes, and implications. J Arid Environ 38:465–478

Gutterman Y (1993) Seed germination in desert plants. Springer-Verlag, Berlin

Kemp PR (1989) Seed banks and vegetation processes in deserts. In: Leck MA, Parker VT, Simpson RL (eds) Ecology of soil seed banks, Academic Press, San Diego, California, pp 257–281

León RJC, Bran D, Collantes M, Paruelo JM, Soriano A (1998) Grandes unidades de vegetación de la Patagonia extra andina. Ecologia Austral 8:125–144

Marone L, Cueto VR, Milesi FA, Lopez de Casenave J (2004) Soil seed bank composition over desert microhabitats: patterns and plausible mechanisms. Can J Bot 82:1809–1816

Marone L, Rossi BE, Horno ME (1998a) Timing and spatial patterning of seed dispersal and redistribution in a South American warm desert. Plant Ecol 137:143–150

Marone L, Rossi BE, Lopez de Casenave J (1998b) Granivore impact on soil-seed reserves in the central Monte desert, Argentina. Funct Ecol 12:640–645

Mayor MD, Bóo RM, Peláez DV, Elía OR (2003) Seasonal variation of the soil seed bank of grasses in central Argentina as related to grazing and shrub cover. J Arid Environ 53:467–477

Milchunas DG, Noy-Meir I (2002) Grazing refuges, external avoidance of herbivory and plant diversity. Oikos 99: 113–130

Moles AT, Falster DS, Leishman MR, Westoby M (2004) Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. J Ecol 92:384–396

Norusis MJ (1997) SPSS advanced statistics 7.5. SPSS Inc., Chicago

O'connor TG, Everson TM (1998) Population dynamics of perennial grasses in African savanna and grassland. In: Cheplick GP (eds) Population biology of grasses. Cambridge University Press, Cambridge, pp 333–365

O'connor TG, Pickett GA (1992) The influence of grazing on seed production and seed banks of some African savanna grasslands. J Appl Ecol 29:247–260

Pazos GE, Bisigato AJ, Bertiller MB (2007) Abundance and spatial patterning of coexisting perennial grasses in grazed shrublands of the Patagonian Monte. J Arid Environ 70:316–328

Saba SL, Toyos A (2003) Seed removal by birds, rodents and ants in the Austral portion of the Monte Desert, Argentina. J Arid Environ 53:115–124

Soil Survey Staff (1998) Keys to soil taxonomy. US Department of Agriculture, Washington

Thompson K (2000) The functional ecology of soil seed banks. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities, 2nd edn. CAB International, Wallingford, pp 215–235

Traba J, Azcárate FM, Peco B (2006) The fate of seeds in Mediterranean soil seed banks in relation to their traits. J Veg Sci 17:5–10

Willson MF, Traveset A (2000) The ecology of seed dispersal. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities, 2nd edn. CAB International, Wallingford, pp 85–110