Viable seed banks under grazing and exclosure conditions in montane mesic grasslands of Argentina

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Abstract

Grazing by large herbivores affects the composition of established vegetation and seed banks. Montane Pampas grasslands are highly productive and have evolved with the influence of grazing by native herbivores. Thus we proposed, firstly that grazing by feral horses would increase seed bank diversity, without changing seed density in grazed areas and secondly that there is a greater similarity between the seed bank and aboveground vegetation in exclosure areas. The study area is located in sub-humid montane grassland in mid-eastern Argentina. Sampling took place at the beginning and end of summer in 2008 and 2009, in three one-year-old exclosures and grazed areas. Soil and litter samples were collected and established vegetation cover was visually recorded in every area. Each sample was elutriated and sieved. Seed composition was recorded using a dissecting microscope. Seed density and species richness of the samples was analyzed using ANOVA and species composition was analyzed by multivariate analysis. Grazing reduces the seed density and richness of grasses, but forb species are not affected. The seed density of grasses increases in soil samples at the end of summer, while the density of forb species does not change. Similarity between the established vegetation and the seed bank was low. Grazing affects seed bank composition which could limit restoration time after the removal of herbivores. However, grass seed availability increases considerably during a short period after exclosure establishment, showing high potential for recovery in sub-humid grasslands.

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1. Introduction

Seed banks are a key component for the persistence of communities, particularly when these are subject to regular disturbances (Bakker et al., 1996). In grassland communities, disturbances take place on different spatial and temporal scales and may be produced by the activity of burrowing mammals, large grazing herbivores, wild fires and droughts, among others. Seed banks are important for recolonization after a large-scale disturbance period; but are also important for recolonization after small-scale disturbances that generate gaps in the vegetation structure (Thompson, 2000). Additionally, vegetation composition in grasslands may be driven by seed bank composition (Grime and Hillier, 2000). Floristic similarity between the seed bank and established vegetation will provide insight information regarding the recovery of a community after disturbance (Amiaud and Touzard, 2004; Kinloch and Friedel, 2005; Schmiede et al., 2009), restoration after biological invasions (Cuevas and Zalba, 2010; Drake, 1998) or during succession after abandonment (Bossuyt and Hermy, 2004), which may improve management and restoration techniques. In a review on the relation between seed banks and standing vegetation, Hopfensperger (2007) found that grassland ecosystems showed more similarity between seed banks and vegetation (54%), than in the case of forest or wetland ecosystems.

Grazing by large herbivores affects seed density, species richness and seed bank composition (Oesterheld and Sala, 1990; Peco et al., 1998; Watt and Gibson, 1988). It also changes the species abundance in established vegetation (Cingolani et al., 2003; Loucougaray et al., 2004; Loydi and Distel, 2010; Sala et al., 1986) and reduces seed production (O’Connor and Pickett, 1992; Pehrsson, 1988). Consequently, species presence in the seed bank...
changes with grazing (Bertiller, 1992; Márquez et al., 2002; Milberg, 1995). The intensity and direction of this effect is related to the response of grasslands to grazing, which depends on their evolutionary history of grazing and productivity (Milchunas et al., 1988). In highly productive grasslands, grazing increases species richness in the established vegetation and soil seed bank (see for example Donelan and Thompson, 1980; Gibson and Brown, 1991; Haretche and Rodríguez, 2006; Marco and Páez, 2000; McDonald et al., 1996). On the other hand, seed bank density usually remains the same (Márquez et al., 2002; McDonald et al., 1996; Milberg and Hansson, 1994), although it may also decrease (Ortega et al., 1997) or increase (Donelan and Thompson, 1980; Marco and Páez, 2000) in response to grazing, depending on the plant functional groups present (Haretche and Rodríguez, 2006).

Nevertheless, these types of productive grasslands are generally resilient to grazing by large herbivores, if they are maintained under certain thresholds of disturbance intensity (Cingolani et al., 2005).

In Pampas grassland, grazing by large herbivores increases plants diversity, promoting different plant groups, such as forbs, rosettes and non-native species (Chaneton et al., 2002; de Villalobos and Zalba, 2010; Loydi and Distel, 2010; Loydi et al., 2010; Rusch and Oesterheld, 1997; Sala et al., 1986). In particular, montane grasslands in the Ventania system have evolved with the influence of grazing by native herbivores such as ‘guanacos’ (Lama guanicoe) and ‘Pampas Deer’ (Ozotoceros bezoarticus) (Bilenca and Miñarro, 2004; Hudson, 1929); and have a relatively high productivity (between 370 and 580 g m⁻² year⁻¹ according to Pérez and Frangi, 2000). Also, they had shown to be more or less resilient to grazing by large herbivores (Loydi et al. in press). However, seed bank density and composition under grazing situations, and its relation to the established vegetation, are unknown for these grasslands. This information could be useful for decision making involved in grassland restoration (Fenner, 2000).

Higher species richness and lower seed production in grazed areas might affect seed bank composition. According to this information the following hypotheses are proposed:

1. grazed areas have a higher species richness, but a lower seed density, in the seed bank than ungrazed areas (exclosures).
2. there is a higher similarity in the species composition between seed bank samples and aboveground vegetation for exclosed areas than for grazed areas.

Therefore, we proposed:

1. to compare seed density and species richness in seed bank samples between grazed and exclosed areas, and
2. to analyze the similarity between established vegetation and seed bank composition under different grazing treatments.

2. Methods

2.1. Study area

The study area is located in mid-eastern Argentina (between 38° 02′ and 38° 04′ S and 61° 57′ and 62° 00′ W) in the Ernesto Torquati Provincial Park (ETPP). Piedmont valleys, with 3–11% slopes and occasional rocky outcrops dominate the study area. Climate is temperate and sub-humid (Burgos and Vidal, 1951). Average annual air temperature is 14 °C, and average annual precipitation is 800 mm, concentrated in the spring and summer. Snow occasionally falls during the winter (Burgos, 1968).

Soils in the study area are classified as litics hapludols and argidols with a high content of organic matter (ca. 7%) on the superficial horizons (Cappannini et al., 1971; Frangi et al., 1980). In the absence of grazing, the community is dominated by herbaceous species with low abundance of small shrubs. The grass canopy may reach 50–60 cm in height, dominated by Piptochaetium hackelii, Nassella melanosperma and Briza subaristata (Frangi and Bottino, 1995). Nomenclature in this work follows Zuloaga and Morrone (2007).

ETPP has a long history (>30 years) of heavy, continuous, year round grazing by feral horses. These occupy ca. 20 km² in area, reaching a maximum of 32.5 horses per km² during 2002 (Scorolli and Cazorla, 2010). The population has been reduced since then (Loydi and Zalba, 2009) and is currently ca. 7.25 horses per km² (Smorzeňuk, 2008).

2.2. Sampling design

Sampling took place in January and April of 2008 and 2009, in three 20 x 20 m exclosures, constructed in December 2006; and in three grazed areas adjacent to each exclosure but separated by at least 30 m. At the time of sampling the exclosed areas were ca. one year old (2008) and two-years old (2009). These sampling dates were chosen to accomplish better characterization of the seed bank, since cool-season species in the area release their seeds at the beginning of summer, while warm-season species do so at the end of summer. At each sampling date 30 samples were taken, five in every grazing or exclosure condition in all three areas. Each pair of grazing/exclosure was considered as a block, and seed bank samples are nested within it. Soil samples consisted of a soil core (10 cm diameter and 5 cm deep) and included the litter above it. Both fractions (soil and litter) were separated in the field. Seeds on the surface of the soil were considered as in the litter fraction. At the same time, the established vegetation was sampled using a 1 m² plot next to the soil sample. Vegetation cover for every species present was visually recorded using a modified Braun–Blanquet scale (Sutherland, 1996).

Each soil sample was dried for 20 days before processing. Each dried soil sample was elutriated as many times as necessary for it to pass through a set of graduated stacked sieves of 15 cm diameter with mesh of 1 mm (N’18), 0.71 mm (N’25), 0.5 mm (N’35) and 0.25 mm (N’60) (Gross, 1990; Malone, 1967). Visible rocks, tubers, turions and rhizomes were carefully removed after washing off the soil. After elutriation, samples were allowed to air-dry for 72 h. All material retained in each of these sieves was observed under a dissecting microscope in order to extract and count the seeds. Each seed was determined to the genus or species level using a reference catalog, consisting of seeds collected from established vegetation in the study area. Seeds were considered to be viable when they resisted light hand pressure with tweezers (D’Angela et al., 1988; Roberts and Ricketts, 1979). Thereafter, seeds were classified into the following two categories: (1) viable seeds, which included all entire firm seeds (after applying pressure with tweezers) and germinated seed (with a visible radicle), and (2) unviable seeds, which included broken, burnt, empty and dead seeds (soft seeds after applying pressure with tweezers) (Busso and Bonvissuto, 2009). Only viable seeds were considered for analysis.

2.3. Statistical analysis

Seed density and species richness under grazing and exclosure situations were compared using one-way ANOVA with a block design (n = 3). These analyses were performed for the total sample (soil + litter fractions) and for both fractions separately, for every sampling date. On the other hand, the response of the seed density and species richness in each sampled fraction (litter/soil) and seed type (grass/forb) was tested with a nested ANOVA with a block design (n = 3). Every sample was divided into four nested levels: (1)
treatment: exclosure or grazing, nested within block; (2) sub-sample: every sample \((n = 5)\) taken in the field, nested within treatments; (3) fraction: soil or litter, nested within subsamples; and (4) seed type: grass or forb, nested within fractions. All factors were fixed, except for the sub-sample level that was not analyzed as it was a random factor. If the interaction terms between the different levels were statistically significant, ANOVA analyses were performed for each level separately. For these, the interaction terms were analyzed for the least hierarchy level (4, seed type) through the highest hierarchy level (1, treatment). In every case data were rank transformed prior to analysis (Conover and Iman, 1981; Zar, 1999).

To assess the differences in the species composition of vegetation recorded, and the soil and litter samples, we used a non-metric

<table>
<thead>
<tr>
<th>Seed density (seeds.m(^{-2}))</th>
<th>Total</th>
<th>F((1,2))</th>
<th>p</th>
<th>Soil</th>
<th>F((1,2))</th>
<th>p</th>
<th>Litter</th>
<th>F((1,2))</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ex</td>
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<td>Ex</td>
<td>Gr</td>
<td></td>
<td>Ex</td>
<td>Gr</td>
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</tr>
<tr>
<td>January 2008</td>
<td>19,353</td>
<td>11,204</td>
<td>16.90</td>
<td>0.05</td>
<td>6366</td>
<td>4812</td>
<td>18.96</td>
<td>0.05</td>
<td>12,987</td>
</tr>
<tr>
<td>April 2008</td>
<td>14,396</td>
<td>12,163</td>
<td>1.12</td>
<td>0.40</td>
<td>10,347</td>
<td>8946</td>
<td>1.74</td>
<td>0.30</td>
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<tr>
<td>January 2009</td>
<td>30,719</td>
<td>18,691</td>
<td>5.56</td>
<td>0.10</td>
<td>14,447</td>
<td>10,856</td>
<td>8.20</td>
<td>0.10</td>
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<td>April 2009</td>
<td>14,752</td>
<td>16,866</td>
<td>0.15</td>
<td>0.70</td>
<td>12,333</td>
<td>13,556</td>
<td>1.81</td>
<td>0.30</td>
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<tr>
<td>Species richness ((\text{species.sample}^{-1}))</td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>January 2008</td>
<td>47.3</td>
<td>44.0</td>
<td>0.92</td>
<td>0.40</td>
<td>35.7</td>
<td>33.0</td>
<td>0.84</td>
<td>0.45</td>
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<tr>
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<td>44.0</td>
<td>41.3</td>
<td>4.00</td>
<td>0.15</td>
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<td>34.0</td>
<td>3.66</td>
<td>0.15</td>
<td>31.0</td>
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<tr>
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<td>52.3</td>
<td>44.3</td>
<td>21.33</td>
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<td>45.3</td>
<td>36.3</td>
<td>11.57</td>
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<tr>
<td>April 2009</td>
<td>46.7</td>
<td>42.0</td>
<td>2.48</td>
<td>0.25</td>
<td>42.3</td>
<td>39.0</td>
<td>1.10</td>
<td>0.40</td>
<td>19.3</td>
</tr>
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</table>

Fig. 1. Interaction plot between seed density in grazed (continuous line) and exclosed areas (dashed line) in different fractions (soil/litter). Plots (a) to (d) grass seed density, (e) to (h) forb seed density. (a) and (e): January 2008; (b) and (f): April 2008; (c) and (g): January 2009; (d) and (h): April 2009. Treatment effects (T) (exclosure/grazing), sampled fraction (C) (soil/litter) and their interaction (T*S) are detailed in the box. ns \(p > 0.10\), \(^*\) \(p < 0.10\), \(^{**}\) \(p < 0.05\), \(^{***}\) \(p < 0.01\).
multidimensional scaling (NMS) (Legendre and Legendre, 1998). Seed density values were transformed to percentage and January and April samples were pooled for each year. All data were arc-sine square root transformed before analysis. The NMS was conducted using the Sørensen-distance measure, two dimensions and a starting configuration by random number. For the final solution 52 iterations were required. Graphic representations of the analysis are associated with a certain stress level (Kruskall’s stress), which is a goodness-of-fit for the sample’s position in a two dimensional plot. Kruskall’s stress level below 15% is acceptable (Clarke, 1993), although this depends on the variable’s number and the number of calculated dimensions (Legendre and Legendre, 1998). Kruskall’s stress was evaluated with a Monte Carlo (randomization) test (McCune and Mefford, 1999). Differences between established vegetation and seed bank composition were assessed with a multi-response permutation procedure (MRPP) using Euclidian distance (McCune and Grace, 2002). Plot scores of the aboveground vegetation and seed bank composition were assessed with a multi-response permutation procedure (MRPP) using Euclidian distance (McCune and Grace, 2002). We evaluated the groups differentiation in the MRPP using the A-value, since statistical significance for this test has been challenged (McCune and Mefford, 1999). An A-value >0.3 is considered very high for community ecology and we used this value as a grouping threshold. Significant indicators of the groups test with MRPP were identified through Indicator Species Analysis (Dufrêne and Legendre, 1997).

Univariate analyses were performed with the basic package for R program (R Development Core Team, 2010). For multivariate analysis we used PC-ORD 5.33 (McCune and Mefford, 2006).

3. Results

3.1. Grazing effect on seed density and species richness in seed banks

Total seed bank samples showed up to ca. 56,000 seeds per square meter and a minimal value of ca. 2400 seeds per square meter. Grazing did not statistically affect the seed density in the total samples, nor in soil or litter fractions, except for the seed density on January 2008, when it was lower in the soil fraction on grazed areas (Table 1). We found seeds belonging to 103 species. Of these, 98 (95%) were determined to species or genus level. Species

Fig. 2. Interaction plot between seed species richness in grazed (continuous line) and exclosed areas (dashed line) in different fractions (soil/litter). Plots (a) to (d) grass seeds density, (e) to (h) forb seed density. (a) and (e): January 2008; (b) and (f): April 2008; (c) and (g): January 2009; (d) and (h): April 2009. Treatment effects (T) (exclosure/grazing), sampled fraction (C) (soil/litter) and their interaction (T*C) are detailed in the box. ns = p > 0.10, * = p < 0.10, ** = p < 0.05, *** = p < 0.01.
richness varied between 21 and 52 species per sample, but there was no statistical difference between grazed and exclosed situations for the total samples, nor in the soil or litter fractions; except for January 2009 when species richness was higher for the total sample in the exclosure areas (Table 1).

The interaction terms among seed types (grasses/forbs), sample fractions (litter/soil) and treatments (grazing/exclosure) were statistically significant in ANOVA ($p < 0.01$) which indicates that grass and forb seeds in the soil and litter fractions respond differently to grazing. Thus, grass and forb seeds were considered separately in all subsequent analyses. In these analyses, the interaction terms between treatment and sample fractions were not significant (except in April 2009), indicating that grass seeds responded in the same way in both the litter and soil samples, in relation to treatment. The same is valid for forb seeds. Therefore, these ANOVA analyses were used to make conclusions about the effects of treatments on the soil or litter fractions.

Grass seed density was higher in exclosures than in grazed areas ($p < 0.05$) (Fig. 1a–d). It was also higher in the litter fraction in January 2008 ($p < 0.01$) and in the soil samples in April 2008 and 2009 ($p < 0.01$). On the other hand, forb seed density did not differ between the grazed and exclosed areas ($p > 0.05$) (Fig. 1e–h). However, it was higher in soil samples than in litter for all sampling dates ($p < 0.01$), except for January 2008.

Grass seed richness in the seed bank was higher in exclosures than in grazed areas for all sampling dates ($p < 0.05$) (Fig. 2a–d). Also it was higher in the litter samples for January 2008 ($p < 0.05$) and in soil samples for the rest of the sampling dates ($p < 0.05$). However, forb species richness did not differ between the exclosed and grazed areas ($p > 0.10$) (Fig. 2e–h). Nevertheless, forb species richness was generally higher in the soil fraction than in the litter samples ($p < 0.01$), except for January 2008.

3.2. Similarity between the composition of established vegetation and seed banks

The NMS-Ordination had a final stress of 14.43, which is significantly smaller than the stress expected by chance (Monte–Carlo test, $p < 0.01$). This ordination showed a separation between the seed bank samples and above-ground vegetation relevés (Fig. 3). There was some grouping in the vegetation surveys depending on the grazing treatment and sample year ($A > 0.70$, $p < 0.01$). While the first year vegetation relevés did not differentiate according to the treatments, relevés from the second year grouped according to grazing conditions. This pattern was not observed in the seed bank samples, where all the samples formed a unique group. Nevertheless, soil and litter seed bank samples from the exclosures were located between the seed bank samples from grazed areas and the established vegetation relevés. Indicator species analysis showed several species that are more related to these four groups (i.e. established vegetation in the first year, exclosure vegetation in the second year, grazed area vegetation in the second year and seed bank samples) (Table 2).

4. Discussion

The seed bank density varied widely between years, treatments and analyzed fractions. Grassland in the study area is shown to have similar or slightly higher seed densities than in other natural or semi-natural grasslands in Argentina (Bertiller, 1992; Haretche and Rodríguez, 2006; Marco and Páez, 2000; Márquez et al., 2002) and around the world (Aboling et al., 2008; Jakobsson et al., 2006; Kalamees and Zobel, 1998; Sternberg et al., 2003). Species richness was also high compared with other grassland ecosystems (Aboling et al., 2008; Funes et al., 2003; Jakobsson et al., 2006; Marquez et al., 2002; Schmiede et al., 2009; Sternberg et al., 2003) and the variation between years, treatments and fractions was smaller.

The species richness in the exclosed and grazed areas was not consistent with the proposed hypothesis of higher richness in grazed areas. Seed density also remained the same. Grazing does not affect, or even reduce, seed species richness. This is contrary to what happens in the established vegetation, where species richness was increased by grazing (Loydi and Distel, 2010). However, when we considered different components of the vegetation, we found that there was a higher density and richness of grass seeds in the exclosures. Perennial grasses are dominant in these areas (de Villalobos and Zalba, 2010; Loydi and Distel, 2010) and usually their seeds tend to fall around the parent plants (Cheplick, 1998), which is reflected in the seed bank. Grass seeds were more common in the litter fraction during January, becoming reduced by April. Litter may act as a natural seed trap after release from the mother plants (Ruprecht and Szabó, 2011). After trapping, predation of seed during the summer (Murillo et al., 2007), or its incorporation to the soil fraction during this period (Fenner and Thompson, 2005), may explain the diminished seed density in litter samples. On the contrary, forb seed density and species richness did not change between the grazed and exclosed areas. However seed content was two to three times higher in the soil fraction than in the litter fraction. Many forb species in the study area have small and more or less isodiamic seeds (A. Loydi, personal observation). While many large seeded species are caught in a litter cover, small seeds may percolate through the litter cover (Donath and Eckstein, 2010). They may become buried in the soil constituting a permanent soil seed bank (Bekker et al., 1998; Funes et al., 1999; Thompson et al., 1998).

A higher similarity between the composition of the established vegetation and seed bank exclosed areas than in grazed areas, as proposed, was not observed. In general, similarity between seed bank samples and vegetation relevés was low, as reported for other grasslands (Funes et al., 2001; Peco et al., 1998; Schmiede et al., 2009). However, samples from the exclosures had higher grass seed density, giving this a lower distance in the NMS to the established vegetation than for grazed areas. On the contrary,
unpalatable grasses that are dominant in grazed areas are not characteristic in seed bank samples. Many forb species are annual species and these were more abundant in the seed bank samples than in the vegetation relevés, which is probably due to the high seed production of this kind of plant (Grime, 2001) and their scattered aboveground biomass and cover (Frangi and Bottino, 1995).

Thus similarity between the composition of the established vegetation and seed bank was slightly lower for grazed areas. For example, Aristida spagazzinii is an unpalatable grass (Rúgolo de Agrasar et al., 2005) which is dominant in grazed areas. For example, Aristida spagazzinii is an unpalatable grass (Rúgolo de Agrasar et al., 2005) which id dominant in grazed areas (Loydi and Distel, 2010), although its presence in the seed bank was practically nil. Soliva sessilis is an annual forb species, frequent on degraded grassland (Cabrera, 1963). Its presence in the seed bank was important, especially in grazed areas, although it was not found in vegetation relevés during this study. Similarly, some other forb species showed low cover in the established vegetation, but their abundance in the seed bank was considerable (e.g. Oxalis, Relbunium and Silene spp.). All these species are small as adult plants, but they produce a high number of seed.

Vegetation relevés formed three different groups. Samples from 2008 did not differ between grazed and exclosed areas, showing that one-year of exclosure is not sufficient to induce a change in the vegetation composition. This group is especially characterized by a few rosette species (e.g Chaptalia, Hololechthus, Hypochaeris and Pffafia). However, in the second year (2009), the exclosures were dominated by a few grass species, characteristic of late seral communities in these grasslands (Frangi and Bottino, 1995), whereas grazed areas were especially characterized by a high abundance of A. spagazzinii. Differences between grazed areas in both sample years may be related to the moderate drought conditions during 2009, which probably reduced the growth of forb species (Loydi et al. in press).

### 4.1. Conclusions

Grazing in the Ventania system montane grasslands not only affects the composition of aboveground vegetation (de Villalobos and Zalba, 2010; Loydi and Distel, 2010) but also that of the seed banks. In particular the seed density of dominant grass species is reduced, which might limit restoration time, especially in cases where local extinction takes place (Suding et al., 2004). However, a short time after the removal of herbivores (<3 years) seed availability had increased, showing high potential for the recovery of this type of grassland. Moreover, after grazing abandonment, ruderal species with high seed production are suppressed by grassland species with lower growth rates and seed production, but with larger seeds (Grime et al., 1988). The reduction of forb species caused by grazing exclusion may be mediated by competitive suppression by grasses (Dickson and Busby, 2009; Distel et al., 1996; Yelenik and Levine, 2010). This may induce a decrease in the forb biomass and subsequently in their seed production (Bekker et al., 2000). Grazing suppression might lead to a reduction in plant diversity above- and below-ground and so grazing intensity should be managed in order to promote plant diversity without compromising the survival of the most preferred species.

Knowledge of the relationship between the soil seed bank and established vegetation will provide useful information for the restoration and succession of communities (Bossuyt and Hermy, 2004; Carter and Ungar, 2002; Grandin, 2001; Hözel and Otte, 2004; Leck, 2003; Schmiede et al., 2009), response to disturbance (Amaud and Touzard, 2004) and to invasive species (Drake, 1998).
In general, similarity between seed banks and vegetation increase during the age of the system (Hopfensperger, 2007), especially in grassland where the seeds have a short dispersal distance (Desaint et al., 1997) and are clustered around parent plants (Henderson et al., 1988). The present study shows that grazing is a major factor affecting seed bank composition and it may induce changes so that the composition of seed banks differs from that of the established vegetation. However, in the mountain pampas grasslands these changes seem to be reversible.

Acknowledgment

This work was funded by Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET) and Universidad Nacional del Sur, Argentina. Dr. Jacqui Shykoff and one anonymous reviewer offered shrewd comments, that significantly improved the manuscript. Rosemary Scoffield revised the English. All help is gratefully acknowledged.

References

Carter, C.T., Ungar, I.A., 2002. Aboveground vegetation, seed bank and soil analysis with the age of the system (Hopfensperger, 2007), especially in grassland where the seeds have a short dispersal distance (Desaint et al., 1997) and are clustered around parent plants (Henderson et al., 1988). The present study shows that grazing is a major factor affecting seed bank composition and it may induce changes so that the composition of seed banks differs from that of the established vegetation. However, in the mountain pampas grasslands these changes seem to be reversible.

References


