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We studied the seed bank and above-ground vegetation in a replicated field experiment with sites ungrazed for 22 years as well as three different grazed sites in seminatural grasslands in central Argentina. We examined the relationship between vegetation and seed bank composition, and tested 3 hypotheses predicting decrease in seed bank richness, decrease in seed bank abundance, and divergence of seed bank species composition from vegetation composition during succession. Grazing changed species abundance and the vertical structure of the vegetation but did not cause loss of species. Most of the taxa in the seed bank occurred in the vegetation. Seed bank richness, diversity, and abundance decreased significantly during grassland succession following cessation of grazing. Although in general the most abundant species in the vegetation at each site were also dominant in the respective seed bank, seed bank and vegetation composition differed greatly after cessation of grazing. The seed bank at sites undisturbed over the long term does not appear to be an important source of seedling recruitment after disturbance in these grasslands.

Keywords: *Soil seed bank; mountain pastures; seminatural grassland; vegetation composition; grazing; Argentina.*

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Introduction

Changes in species richness, diversity, and hierarchical and spatial structure are common responses of seminatural grassland communities to grazing (Collins 1987; Belsky 1992). Patterns of change in species richness and diversity have frequently been interpreted in relation to the intermediate disturbance hypothesis (Connel 1978), which predicts that species richness is maximized at intermediate levels of disturbance. Another hypothesis, the initial floristic composition model (Egler 1954), predicts that overall plant species richness will decrease during succession.

It has been argued that the soil seed bank may play a significant role in seedling recruitment after disturbances on seminatural grasslands (Milberg 1993; Kalamees and Zobel 1997), be a minor recruitment source compared with regrowth from vegetative parts (Viragh and Gerencser 1988; Ghermandi 1997), or vary in its significance depending on the season and topography (Bertiller 1996). Attempts to relate vegetation changes to seed production and seed viability during secondary succession can be found in several hypotheses proposed to explain seed bank characteristics, including that (1) seed bank richness (Symonides 1986; Pickett and McDonnell 1989; Roberts and Vankat 1991) and diversity (Numata et al 1964) decrease during succession; (2) total seed bank abundance decreases from earlier to later successional stages (Thompson 1978; Symonides 1986; Pickett and McDonnell 1989), and (3) the species composition diverges from the composition of the vegetation during succession (Numata et al 1964).

We compared the species composition of the soil seed bank and above-ground vegetation and tested the hypotheses formulated above for successional seed banks in a replicated field experiment with two 22-year-old ungrazed sites and grazed sites in seminatural grasslands in central Argentina. In these grasslands, vegetation at ungrazed sites shows a higher, more closed canopy and lower photosynthetic photon flux density (PPFD) at soil level than at grazed sites, although it is possible to find sites with intermediate characteristics at intermediate levels of disturbance (Marco 1995). Consequently, the study made a distinction between grazed sites with differing vertical structures of vegetation.

Description of the study site

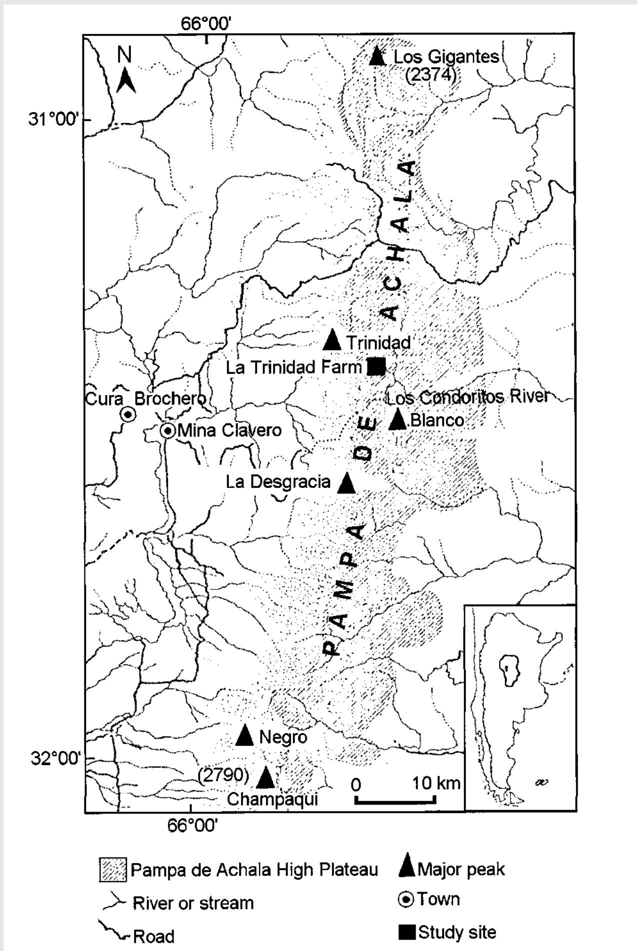
The grassland studied is situated in a National Park in Pampa de Achala, a broad granite plateau in the high mountains of central Argentina (32° S, 64° W), with an average altitude of 2100 m (Figure 1). The climate is humid (840 mm rainfall per year) and seasonal, with a short summer and frequent frosts and snowfalls in winter. The Pampa de Achala is characterized by extensive livestock grazing, primarily cattle and sheep, with an average density of 1 animal/ha. Grazing has a long history in the area, having prevailed at least since the end of the 18th century (Río and Achával 1904). Patchy vegetation has developed, composed of interspersed patches of different grassland communities on disturbed sites, with tall grasslands of *Deyeuxia hieronymi* on undisturbed or less disturbed sites (Luti et al 1979; Marco 1995). Soil depth is another possible but secondary source of vegetation differences in species composition and abundance (Luti et al 1979).

Methods

Study site

Two cattle exclosures of 1 ha each were installed 4 km apart at 2 study sites in 1973 as part of a long-term experiment established to assess vegetation changes after grazing cessation (Luti 1986). The exclosures were installed

FIGURE 1 Map of the study area. The average altitude of Pampa de Achala High Plateau is 2200 m. Altitudes of major peaks are in parentheses.



at 2100 m in sites with homogeneous gentle slopes and representative patchy vegetation. Grasslands adjacent to the exclosures remained subject to grazing (Luti 1986).

The current study, conducted in 1995, compared the seed bank and above-ground vegetation in the exclosures (hereafter referred to as ungrazed) with the immediately adjacent grazed grasslands. The ungrazed sites had developed homogeneous tall grasslands 1 m high, dominated by *Deyeuxia hieronymi* (Luti 1986) (Figure 2). Successional stages after cessation of grazing have been well characterized for the area (Luti 1986; Marco 1995). Grazed grasslands were classified as follows, using species composition and vegetation structure as selection criteria (Marco 1995): (a) tall grassland, dominated by large *Deyeuxia hieronymi* tussocks (tall grazed) (b) grassland of medium height, with smaller *Deyeuxia hieronymi* tussocks interspersed with short turf (medium grazed), and (c) short turf, dominated by small herbs and grasses (short grazed).

Ungrazed and grazed sites represent an increasing gradient of disturbance by grazing, considering biomass destruction, from ungrazed to short grazed sites (Collins 1987). Above-ground vegetation in exclosures and on grazed sites is referred to here as vegetation types. To minimize the possible effect of soil depth on vegetation composition, sites with shallow soils were avoided. Because of their small size (mean size 65 m^2), 2 patches of each grazed vegetation type (sampling sites) immediately adjacent to each exclosure were used

FIGURE 2 General view of the Pampa de Achala High Plateau. Granite outcrops and patchy grassland are visible in the background. An example of ungrazed tall grassland dominated by *Deyeuxia hieronymi* can be seen in the foreground.

TABLE 1 Number of seedlings and species richness (S) (mean ± standard deviation) and species diversity (*H'*) recorded for each vegetation type in the seed bank. For the number of seedlings and species richness, different letters within a column indicate significant differences between ungrazed and grazed sites using Friedman two-way ANOVA and a posteriori multiple comparison ($P < 0.05$), used to determine the number of seedlings and species richness. Differences found when comparing only grazed sites using the same method were not significant ($P > 0.05$, comparisons not shown). For species diversity, different letters within the column indicate significant differences found when comparing all vegetation types (Hutcheson's test).

Vegetation type	Number of seedlings	Species richness (S)	Species diversity (*H'*)
Ungrazed	83.50 ± 50.20[a]	6.50 ± 2.11[a]	0.61[a]
Tall grazed	312.50 ± 147.77[b]	25.50 ± 4.03[b]	0.89[b]
Medium grazed	290.50 ± 155.85[b]	24.00 ± 2.83[a]	1.05[c]
Short grazed	732.50 ± 178.83[b]	15.50 ± 4.95[a]	0.62[a]

to determine seed bank and above-ground vegetation. Although sampling from the edges of each site was avoided as much as possible, the likelihood of seed dispersal among the sites cannot be discarded, as patches of different vegetation types were in close proximity and were relatively small. Interspersion and the size of the vegetation patches were representative of grasslands in the Pampa de Achala (Marco 1995). On the other hand, seed immigration from other sites was improbable in the ungrazed exclosures because of their greater size when compared with grazed sites. To avoid influence from the grazed sites, sampling sites were located in the center of each exclosure. Nomenclature of taxa followed Cabrera and Zardini (1978).

Seed bank study

Ten quadrats of 1 m^2 (a total of 20 quadrats per vegetation type) were selected randomly in late winter at each sampling site; 16 regularly located soil cores 5 cm in diameter and 5 cm deep were taken in each quadrat. The soil cores were crumbled and combined to form a single sample, with a volume of 400 cm^3, including litter when present. Each sample was air dried and stored at −2°C for 5 months. Cold storage can increase seed germination (Grime et al 1980). Half of each sample volume (200 cm^3) was evenly spread over a 2-cm layer of sterile sand in a plastic tray (15 × 20 cm). After watering, the trays were randomly arranged in a room under a 25°C/16-hour light and 15°C/8-hour dark cycle. Light was provided by fluorescent and tungsten lamps (minimum PPFD 30 $\mu mol/m^2/s$ at tray level). Emerging seedlings were identified and removed over a 6-month period. After seedling emergence stopped, the soil in each tray was stirred and stored 3 weeks at 2°C. Germination was monitored for another 3 months under the same conditions as previously. Unidentified seedlings were replanted for later identification. Seedlings in bad condition were removed and identified at the lowest taxonomic level possible.

Vegetation study

In spring, above-ground vegetation was sampled for species composition and abundance at the same sampling sites used for the seed bank study in 10 randomly located 50- × 50-cm quadrats subdivided into 25 small subquadrats, avoiding the 1-m^2 quadrats used for the seed bank sampling. In each of the subquadrats, species presence/absence was recorded, with frequencies ranging from 0 to 25 per species per quadrat. To estimate the vertical structure, litter cover, vegetation height (differentiated into four strata), and vegetation cover per stratum were measured as interception percentages in six linear transects of 6 m, each located randomly at each sampling site, avoiding the quadrats used for the seed bank sampling. With this method, the percentage of the transect covered by each stratum was measured over the transect, yielding results that can exceed 100% when all strata are considered.

Data analysis

For each analysis performed, data from the 2 patches sampled for each grazed vegetation type adjoining each exclosure were totaled. As a result, the final design for statistical analysis had 2 replicates of each vegetation type, including the ungrazed sites (exclosures).

The number of seedlings and species in the seed bank and the number of species in the above-ground vegetation were compared using Friedman two-way ANOVA and a posteriori multiple comparison to determine differences between ungrazed and grazed sites and between the different types of grazed sites.

The species diversity of seed bank and vegetation was calculated for each vegetation type as

$$H' = -\Sigma\, pi \log pi,$$

where *pi* is the relative frequency of species *i* (Shannon and Weaver 1949). Statistical differences in diversity were determined using the test proposed by Hutcheson (1970).

The multiresponse permutation procedure (MRPP, Brewer and Platt 1994; Steinauer and Collins 1995) was used to compare the composition and abundance of species in the seed banks of all four vegetation types. A similar analysis was conducted using the vegetation data. This technique has the same aim as a MANOVA test but does not depend on assumptions of normality and homogeneity of variances required for parametric analysis. Parametric assumptions were not made in the seed bank and vegetation data sets. MRPP calculates average Euclidean distances (similarities) among observations within each group (vegetation type in this case). An observed weighted average (Delta) of the mean Euclidean distances is then calculated for all groups. A small value for Delta indicates a tendency for observations to cluster within groups. Multiple random permutations are then calculated to determine whether Delta is unusually small. Spearman rank correlations were performed with the seed bank and above-ground vegetation data for species richness and abundance.

TABLE 2 Number of seedlings of each species in the seed bank in each vegetation type. The number of soil samples in which a species occurred is shown in parentheses. Data from the two study sites have been aggregated. A species is listed if the actual total count of seedlings was higher than two. Taxa identification was done at the lowest possible taxonomic level. Life history (A = annual, B = biennial, P = perennial) is reported if known. The signs ‡ and † indicate the presence of a species in a vegetation type in more (‡) or less (†) than 5 sampled quadrats (out of 20 quadrats per vegetation type).

Species	Life history	Vegetation type			
		Ungrazed	Tall grazed	Medium grazed	Short grazed
Forbs					
Alchemilla pinnata	P	—†	8 (5)‡	10 (6)‡	21 (10)‡
Apium leptophyllum	P	—†	1 (1)‡	8 (4)†	—
Chenopodium ambrosioides	A-B	—	2 (2)	1 (1)	1 (1)
Conyza bonariensis	A	—	1 (1)	—	—
Eryngium nudicaule	P	—‡	—†	1 (1)†	—†
Gamochaeta filaginea	B	12 (10)†	213 (19)†	63 (16)†	41 (14)†
Gentiana spp.	A	2 (2)†	6 (6)	47 (16)†	28 (11)†
Geranium magellanicum	A	52 (10)†	23 (10)‡	32 (7)	44 (8)
Glandularia dissecta	P	—	—†	1 (1)	15 (3)
Oxalis chrysantha	P	—	—†	—	3 (2)
Plantago myosurus	P	—	17 (9)†	1 (1)†	23 (6)†
Relbunium richardianum	P	6 (3)†	5 (2)†	16 (3)†	42 (9)†
Stellaria spp.	—	—	3 (2)	3 (2)	22 (8)
Taraxacum officinale	P	—	—†	1 (1)†	†
Veronica persica	A	—	1 (1)†	—	1 (1)†
Unidentified Compositae	—	—	1 (1)	15 (7)	—
Dicotyledonous 1	—	—	3 (3)	4 (3)	7 (4)
Dicotyledonous 2	—	—	12 (7)	45 (9)	2 (1)
Grasses and graminoids					
Agrostis montevidense	A	—†	3 (1)†	—†	—
Briza subaristata	P	—†	23 (11)†	10 (4)†	—†
Bromus auleticus	P	—†	6 (5)†	7 (5)†	—†
Cyperus spp.	P	—	—	3 (3)†	—
Deyeuxia hieronymi	P	82 (18)‡	76 (14)‡	4 (3)‡	—‡
Festuca lilloi	P	‡	5 (3)‡	†	—†
Juncus achalensis	P	7 (5)	167 (15)†	100 (16)‡	142 (16)‡
Muhlenbergia peruviana	A	1 (1)†	9 (7)†	144 (14)‡	935 (19)‡
Piptochaetium montevidense	P	—	1 (1)	8 (5)†	7 (4)†
Bulbostylis tenuispicata	B	—	7 (6)	41 (5)†	120 (10)†
Stipa nidulans	A	—†	—†	—†	3 (2)
Stipa spp.	—	—	2 (1)†	—	—
Unidentified Gramineae 1	—	—	7 (5)	8 (3)	4 (1)
Gramineae 2	—	—	9 (5)	3 (2)	—

Results

Seed bank

A total of 3318 seedlings representing 47 species were recovered from the soil samples. The second germination period revealed few additional seedlings and no new species. The total number of seedlings in the upper 5 m of the soil increased significantly with grazing intensity (Friedman two-way ANOVA $T1 = 9.20$, df = 3, $P < 0.05$, and a posteriori multiple comparison) (Table 1), although grazed sites did not differ from each other. The total number of species in the seed bank was significantly lower on the ungrazed sites than on the tall grazed sites ($T1 = 9.20$, df = 3, $P < 0.05$, and a posteriori multiple comparison) (Table 1) but did not differ significantly from total numbers on the other grazed sites. There was no difference among the grazed sites.

Table 2 lists the number of seedlings of each species in the seed bank. Five seedling species remained unidentified, but they presented only few seedlings.

Seedlings of *Gentiana achalensis* and *Gentiana parviflora* were counted as a single species (*Gentiana* spp.). Only 6 species were present in all f vegetation types, including the 2 most abundant taxa, *Muhlenbergia peruviana* and *Juncus achalensis,* which accounted for 70 and 12%, respectively, of the total seedlings recorded.

Ungrazed and short grazed sites showed significantly lower diversity values than tall and medium grazed sites, which in turn differed from each other (Table 1). Dominant species in the seed bank also varied with disturbance intensity. The most abundant grasses were the perennial *Deyeuxia hieronymi* (ungrazed and tall grazed sites) and the annual *Muhlenbergia peruviana* (medium and short grazed sites). The perennial graminoid *Juncus achalensis* dominated the seed bank on the grazed sites. Seeds of the biennial forb *Gamochaeta filaginea* were very abundant on the ungrazed, tall, and medium grazed sites.

Results of the MRPP analysis showed a statistically significant effect of vegetation type on seed bank composition (Table 3). The MRPP analysis also evidenced a tendency of heterogeneity in the seed bank composition to increase with disturbance intensity, from a mean Euclidean distance of 4 for the ungrazed sites to 63 for short grazed sites (Table 3).

Vegetation

There were significant differences in vegetation composition between vegetation types. The groups showed small Euclidean distances and a small Delta, indicating homogeneity within vegetation types (Table 3). Species richness of the above-ground vegetation did not differ significantly between ungrazed and grazed vegetation types ($T1 = 6$, df = 3, $P > 0.05$, and a posteriori multiple comparison) (Table 4). The grazed sites did not differ from each other. Ungrazed sites showed the lowest diversity value and short grazed sites the highest

TABLE 3 Analysis of the effect of vegetation types on seed bank and vegetation composition using multiresponse permutation procedures (MRPP). The effect of a vegetation type is measured in terms of Euclidean distances among groups.

	Mean Euclidean distance	
Vegetation type	**Seed bank**	**Vegetation**
Ungrazed	4.371	15.636
Tall grazed	13.288	12.834
Medium grazed	16.875	19.253
Short grazed	63.045	10.614
Test statistic	-13.538	-15.451
Delta	24.909	14.584
***P* Delta**	0.00001	0.00001

TABLE 4 Analysis of the effect of vegetation type on species vegetation richness (S) and diversity (*H'*). For the number indicating species richness, different letters within the species richness column designate significant differences between ungrazed and grazed sites using Friedman two-way ANOVA and *a posteriori* multiple comparison ($P < 0.05$). Differences found when comparing only grazed sites using the same method were not significant ($P > 0.05$, comparisons not shown). For species diversity, different letters within the column indicate significant differences obtained when comparing all vegetation types (Hutcheson's test).

Vegetation type	Species richness (*S*)	Species diversity (*H'*)
Ungrazed	26.50 ± 0.71^a	0.78^a
Tall grazed	27.50 ± 2.83^a	1.01^b
Medium grazed	28.50 ± 2.11^a	1.07^b
Short grazed	21.50 ± 2.81^a	1.19^c

(Table 4). Dominant species varied with disturbance intensity. The most abundant species on the ungrazed and tall grazed sites was *Deyeuxia hieronymi*. The perennial forb *Alchemilla pinnata, Muhlenbergia peruviana,* and the perennial graminoid *Carex boliviensis* were the dominant species on the medium and short grazed sites. The vegetation types showed different vertical structures, with tall and medium grazed sites showing a more complex structure than ungrazed and short grazed sites. Litter covered 30% of the ungrazed sites but was almost absent in the other vegetation types (Figure 3).

Seed bank and vegetation

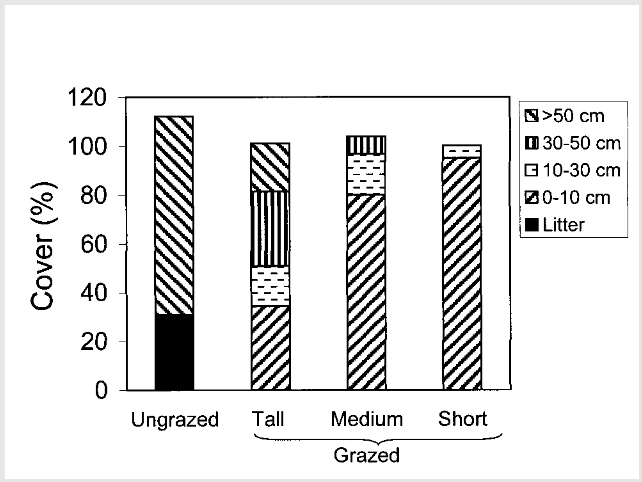
Most of the identified seedling species in the seed bank also occurred in the vegetation, except the weedy forbs *Chenopodium ambrosiodes, Conyza bonariensis,* and *Stellaria* spp. (Table 2). Conversely, of the 37 species present in the vegetation, 8 were not detected in the total seed bank. *Glandularia dissecta, Oxalis chrysantha,* and *Stipa nidulans* occurred both in the vegetation and in the seed bank but in different vegetation types (Table 2). For at least one vegetation type (eg, *Gentiana* spp. on tall grazed sites), 15 species were detected in the seed bank but not in the vegetation (Table 2). On the other hand, 12 species occurred in the vegetation but were not detected in the respective seed bank in at least 1 vegetation type (eg, *Alchemilla pinnata* on the ungrazed sites) (Table 2). In general, some of the most abundant species in each vegetation type were also dominant in the respective seed bank. Correlations between aboveground vegetation and the seed bank were negative (−0.217 for species richness and −0.619 for species abundance).

Discussion and conclusions

Vegetation changes

Changes in vegetation composition due to grazing are common on grasslands in North America (Collins et al 1995), South America (Sala et al 1986), and elsewhere (Belsky 1992; Milberg 1995). In the mountains of central Argentina, floristic changes resulting from grazing have also been previously reported (Luti 1986; Marco 1995). Species richness and diversity (H') in grassland prairies are expected to be enhanced by grazing

FIGURE 3 Cover percentage of different strata in the vegetation of each site.



because of reductions in the dominance of tall grasses (Collins and Barber 1985). In the present study, grazing was found to tend to decrease or eliminate the dominance of the tall tussock grasses, although species richness did not differ along the grazing disturbance gradient. A previous study in the area showed that the number of species and the degree of diversity both increased greatly in sites subject to intense burning, when compared with grazed and ungrazed sites (Marco 1995). Considering the less extreme ranking of disturbance intensity proposed in this study, neither the intermediate disturbance hypothesis (Connel 1978) nor the initial floristic composition model (Egler 1954) is appropriate to describe the effects of grazing. Collins et al (1995) evaluated both hypotheses using long-term experiments on a North American tall-grass prairie and found that patterns in species richness could be explained by a combination of the two hypotheses.

We conclude that, in the grassland studied, grazing at current intensity levels changed species abundance and vertical vegetation structure but did not cause loss of species at the spatial scale examined.

Seed bank and vegetation changes

Seed bank richness and diversity: Seed bank richness and diversity decrease during succession. Since later successional species tend to produce fewer seeds with smaller viability periods than earlier successional species (Harper 1977) and seeds produced by the later species may lose viability with time, seed bank richness and diversity may decrease in later successional stages.

In this study, the number of taxa in the seed bank and diversity were both significantly lower in the exclosures, where the dominance of large tussock grasses in the vegetation precluded or diminished seed production in subordinate species such as *Alchemilla pinnata* and *Gentiana* spp. (Marco 1995). Coupled with this effect, the great litter cover might also have prevented the seeds from reaching the soil surface, thus increasing seed losses in the ungrazed sites due to survival failures. In spite of the greater number of seed species present, diversity was also low on the most disturbed sites due to the presence in the vegetation of short-lived or perennial small species that produce high quantities of seeds, such as *Muhlenbergia peruviana, Bulbostylis tenuispicata,* and *Juncus achalensis.* Seed bank richness decreased on abandoned grazed grasslands compared with sites still grazed in a chronosequence representing successional series in Sweden (Bakker et al 1996). In contrast, seed bank richness did not decrease during succession in an experimental study on a Swedish seminatural grassland with ungrazed sites during a period of 18 years (Milberg 1995).

Seed bank abundance: Seed bank abundance decreases from earlier to later successional stages. In the present study, total seed bank abundance decreased with succession after cessation of grazing, probably for the same reasons given for the seed bank richness hypothesis. On the other hand, seed bank abundance did not decrease during succession on seminatural grasslands with ungrazed sites 18 years old (Milberg 1995) or on 6- and 10-year-old Patagonian grasslands (Bertiller 1996; Ghermandi 1997) nor did it increase on abandoned Estonian grasslands (Kalamees and Zobel 1997).

Seed bank species composition: The seed bank species composition diverges from that of the vegetation during succession. Differences in seed production and seed viability in the soil, coupled with differential germination and/or survival conditions during succession, may explain the expected divergence in seed bank and above-ground vegetation composition.

Although in general the most abundant species in the vegetation in each vegetation type were also dominant in the respective seed bank, seed bank and vegetation composition in this study differed greatly after cessation of grazing. In contrast, Milberg (1992, 1995) and Bakker et al (1996) found that successional changes in the vegetation were similar to those in the seed bank, suggesting that seeds were short-lived in the soil. On the ungrazed sites in the present study, only 7 of the 28 taxa in the vegetation were present in the seed bank. *Juncus achalensis* was the only species present in the seed bank that was not detected in the vegetation on the ungrazed sites. Seeds of some *Juncus* species have been found in the seed bank even without being present in the vegetation, indicating they have persistent soil seed banks (Milberg 1995). The only 3 species not detected in the vegetation but present in the seed bank (although exclusively on the grazed sites and in small numbers) are considered weedy species (Cabrera and

Zardini 1978). Seeds of weeds are commonly found on sites with an agricultural past (Rice 1989). The grassland studied has a prolonged history of grazing, but soil cultivation has been infrequent. A period of 22 years without disturbance seems to be long enough to eliminate *Chenopodium ambrosiodes, Conyza bonariensis,* and *Stellaria* spp. from the seed bank, as well as *Taraxacum officinale* and *Veronica persica,* the other 2 weeds found in the seed bank and in grazed vegetation in this study.

Clearly, seed banks on this grassland can be related to vegetation changes due to grazing. Since grazing did not cause loss of species at the vegetation level, the changes recorded in the seed bank following cessation of grazing are related mainly to different opportunities for seed production and seedling recruitment for distinct species, depending on grassland successional stages. Alterations in microenvironmental variables and resource levels are common on grasslands disturbed by grazing (Reichman et al 1993). Light quality and intensity at soil level are directly related to vertical structure in herbaceous communities (Deregibus et al 1985; Hirose and Werger 1995), which is altered by grazing on seminatural grassland (Collins 1987; Marco 1995; this study). Light quality and quantity are important factors involved in flowering processes (Vince-Prue 1983). Secondary effects of grazing, such as urine deposition, may promote changes in grassland structure by modifying nitrogen availability (Steinauer and Collins 1995). Light quality and quantity, water, and nitrates are factors stimulating germination in many species, although they are not involved in dormancy induction and release (Vince-Prue 1983).

Management implications

The results of this study have important implications for conservation and economic management of the altitudinal grassland of central Argentina. Species of interest in terms of conservation, such as the endemic *Gentiana achalensis* (Seckt 1929), or of economic importance for natural forage, such as *Alchemilla pinnata* (Ringuelet 1941), require a certain degree of disturbance to produce and accumulate persistent soil seed banks (Marco 1995; this study). At the community level, moderate disturbance enhances both seed bank richness and abundance. In the case of the Pampa de Achala, the seed bank on sites that remained undisturbed over the long term does not appear to be a significant source of seedling recruitment after disturbance, supporting results from other studies of seminatural grasslands (Bakker 1989; Bakker et al 1991; Milberg 1992, 1995; Bakker et al 1996; Bertiller 1996; Ghermandi 1997; Bekker et al 1997; but see also Kalamees and Zobel 1997). In conclusion, a management system with moderate grazing levels on this grassland might ensure the maintenance of populations and communities, both at seed bank and at vegetation stages.

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