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Edaphic patchiness influences grassland regeneration from the soil seed-bank in mountain grasslands of central Argentina

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Abstract The soil seed-banks in the main natural vegetation patches that make up mountain grasslands on granite substrates in central Argentina were studied. The main natural vegetation types are moist swards, tall-tussock grasslands and stony grasslands. Ten compound soil samples from each community at two soil depths (0–5 and 5–10 cm) were taken. The density of soil seed-banks was highest in moist swards, intermediate in stony grasslands and lowest in tall-tussock grasslands. Low levels of similarity were found between the established vegetation and total soil seed-bank in tall-tussock grasslands and stony grasslands, but the similarity was higher in swards. In all three communities the seed-bank was most frequently transient in nature. Short-term persistent and long-term persistent seed-banks were less frequent. Regeneration from the seed-banks after disturbance is expected to differ among communities on different edaphic patches. On the basis of the density and longevity of the soil seed-banks and the similarity to the established vegetation, potential for *in situ* regeneration should be lower in tall-tussock grasslands, intermediate in stony grasslands and higher in moist swards.

Key words: community regeneration, granite grasslands, persistent seed-banks, spatial heterogeneity, transient seed-banks.

INTRODUCTION

Soil seed-banks play an important role in plant community dynamics and regeneration (Harper 1977; Bakker *et al.* 1996; Bertiller & Aloia 1997). Furthermore, in today's increasingly fragmented environments, knowledge of seed reservoirs in the soils of natural communities should provide useful tools for conservation and restoration efforts (Bekker *et al.* 1998; Bakker & Berendse 1999). Species not represented in the seed-bank are particularly vulnerable to elimination from standing vegetation (Brown & Oosterhuis 1981; Fenner 1985; O'Connor 1991). Furthermore, community regeneration from the seed-bank following a disturbance is an important aspect of ecosystem resilience (*sensu* Leps *et al.* 1982). Three aspects are relevant in the regeneration of natural communities: (i) the density of the seed-banks; (ii) the relationship between the established vegetation and the seed-banks; and (iii) the persistence of seeds in the soil. All these aspects, but particularly seed density, are influenced by climatic factors, soil structure, chemical composition and moisture regimen (Cavers & Benoit 1989; Semenova & Onipchenco 1994; Kaoru & Tilman 1996).

In relatively stable tall-tussock grasslands, (Thompson *et al.* 1998) there are often differences in species composition between the standing vegetation and the seed-bank. This is attributed to the fact that in these systems, species that are abundant in the standing vegetation are often rare or absent in the soil seed-bank (Chippendale & Milton 1934; Champnes & Morris 1948; Major & Pyott 1966; Abrams 1988; D'Angela *et al.* 1988; Bakker 1989). This is not the case for more frequently disturbed habitats. In some wetland communities with seasonal water-level fluctuations, the composition of the established vegetation and that of the soil seed-bank below tend to coincide (Keddy & Reznicek 1982; Parker & Leck 1985; Leck & Simpson 1987). At the other extreme, Houle and Phillips (1988) found a significant association between species presence in the seed-banks and presence in the standing vegetation in water-stressed communities growing on granite outcrops.

Another important aspect of community regeneration dynamics is the seed-bank strategy of the component species. On the basis of a seasonal wide-ranging survey of the germinable seed-bank of British plant communities, Thompson and Grime (1979) grouped

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the species into those with persistent and those with transient seed-banks. Relative to transient seed-banks, the species with persistent seed-banks have dormant seeds that tend to be smaller, and are important in population maintenance during unfavourable years (Graham & Hutchings 1988). In general, dominant species in communities subjected to periodic natural or anthropogenic disturbance produce large numbers of seeds that persist in the soil for a long time (persistent seed-banks); whereas the dominants of more stable communities tend to produce smaller numbers of seeds, which remain viable in the soil for a short time (transient seed-banks; Thompson *et al.* 1993, 1998; Warr *et al.* 1993). The longevity of seeds in the soil bank can be estimated by comparing the composition of the established vegetation with that of the seed-banks in the top soil and deeper soil layer (Bakker 1989; Thompson *et al.* 1993, 1997).

The natural grasslands on granite substrates in the mountains of central Argentina have a mosaic-like spatial pattern. The mosaic consists of vegetation patches with a distinct structure and floristic composition (Acosta *et al.* 1992). These communities are associated with different soil types and soil moisture regimes. The three main communities are (i) moist swards on hydromorphic soils subjected to waterlogging at least during the rainy season; (ii) tall-tussock grasslands on mesic sites with relatively well-developed soils; and (iii) stony grasslands on shallow soils subjected to extreme variation in moisture and temperature throughout the year (Cabido *et al.* 1987).

In the present study, we document the spatial variations in the composition and density of the soil seed-banks of a granite grassland of central Argentina. We specifically aimed to:

1. Describe the soil seed-banks of the three types of communities (as mentioned previously) with varying soil types and water availability.
2. Compare the composition of the established vegetation and that of the seed-banks within patches.
3. Classify the seed-banks according to the strategies of species, taking into account the relationship between their occurrence in the established vegetation and in different soil layers.

METHODS

Study area

The study area is located in the central part of Pampa de Achala, in the Córdoba mountains, central Argentina (approximately 31°35′S, 64°45′W; 2100 m a.s.l.). The climate of the region is subhumid, with short, cool summers and long, cold winters (Capitanelli 1979). The mean annual temperature is 8°C, and the mean annual rainfall is 840 mm, falling mostly in the warm season.

The vegetation consists of a mosaic of different plant communities, described in detail by Cabido (1985; Fig. 1). The soil moisture regime is the main environmental factor determining the spatial distribution pattern of plant communities (Cabido 1985; Cabido *et al.* 1987; Table 1).

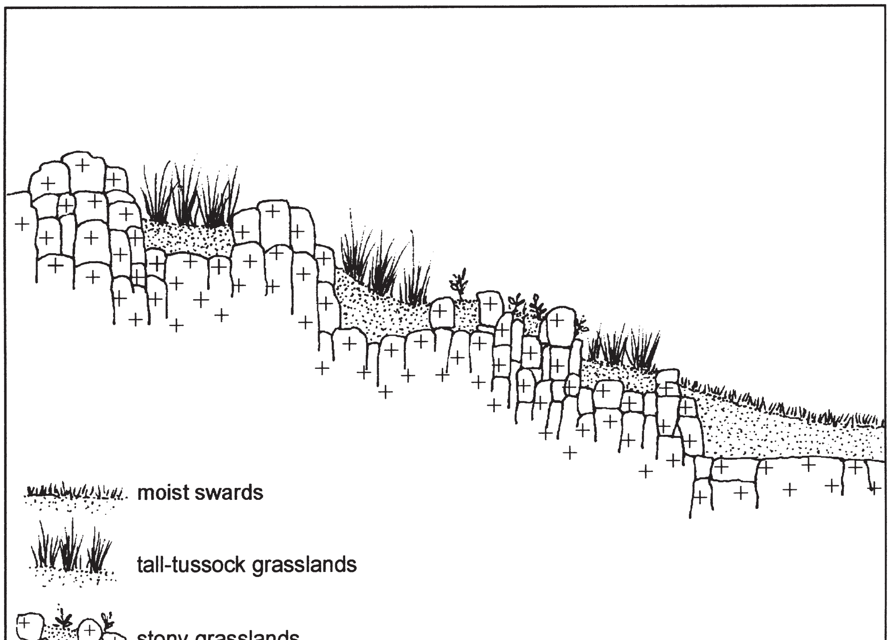

Fig. 1. Diagrammatic representation of the three main plant communities at Pampa de Achala, in the mountain grasslands from central Argentina.

Data collection

Within the central portion of the Achala Plateau, 10 different patches of each of the three communities mentioned previously were selected. The selection was made on the basis of the vegetation and landscape map of Cabido *et al.* (1981) and was designed to maximize representation of the patches of each community type as well as to ensure proper interspersion, and to avoid areas close to roads, paths, animal pens and dwellings. The sizes of the patches ranged from approximately 50 to 500 m^2 and each patch was considered a replicate. Ten compound soil samples were collected from randomly selected points within each of the 10 different patches in early May 1996. Samples were taken with a bore 4 cm in diameter. Sampling was carried out immediately after the community had set seed (Díaz *et al.* 1994). Therefore, the seed-bank included elements of the newly dispersed (transient seed-bank) and older components of the buried seed-bank (persistent seed-bank; Thompson & Grime 1979). Two soil depths were sampled: 0–5 and 5–10 cm. Plant fragments and stones were removed by sieving soil samples through 1 cm, 2 mm and 250 μm mesh sieves (Ter Heerdt *et al.* 1996). Soil samples were chilled in a refrigerator at 5°C for 1 month in order to break the seed dormancy of many temperate species (Houle & Phillips 1988; Kaoru & Tilman 1996; McDonald *et al.* 1996). The soil was then spread over a 2 cm thickness of sterilized sand in plastic trays of 15 cm × 15 cm. All trays were placed in a greenhouse at random positions under a 20–30/10–15°C day/night temperature regime. The soil samples were maintained at field capacity. As a control against contamination, additional trays containing autoclave-sterilized soil were included.

The germinable seed-bank in the soil was evaluated by counting the seedlings emerging from the soil samples. Although trays were kept in the greenhouse for 12 months, no new germination was observed after 4 months. Whenever possible, seeds were identified at an early stage and removed from the trays. When flowers and or fruits were required for correct identification, seedlings were transplanted to separate pots and grown on natural unfertilized soil within the same greenhouse. The majority of seedlings were identified to species level, with the exception of *Carex* and *Cyperus* seedlings. The germination method with cold stratification is considered the most appropriate for studying the composition of species in the soil seed-bank, particularly in natural systems with high floristic richness (Gross 1990).

Although the actual area sampled per community was 0.1258 m^2, seed density was expressed as number of seeds per m^2 for comparability with published studies.

The established vegetation was recorded in 12 10 cm × 10 cm quadrats placed at random within each of the vegetation patches where the soil seed-bank samples were taken.

Seed-bank classification

The seed-banks were classified according to Thompson *et al.* (1997). The seed-banks of species present in the established vegetation and absent from the seed-bank or present only in the upper soil layer, were classified as transient. When seeds were present in both soil layers, they could be either transient or persistent. If most of the viable seeds of a species were in the 5–10 cm soil layer, the seed-bank of the species was considered to be long-term persistent. If viable seeds were recorded more frequently in the 0–5 cm soil layer, the soil seed-bank of a species was classified as short-term persistent; whereas if viable seeds numbers were equal in the two soil depths, the seed-bank was classified as long-term persistent. Although the rate at which the seeds of a given size and shape move down through the soil profile in different soil types is not necessarily constant, this method has been widely used to compare seed soil banks of contrasting habitats (Thompson *et al.* 1997).

Data analysis

The relationship between the presence/absence of species in the germinable seed-bank and in the established vegetation in each community was

Table 1. Major characteristics of the three different communities of mountain grasslands of central Argentina (Cabido *et al.* 1987)

	Moist swards	Tall-tussock grasslands	Stony grasslands
Drainage	Poor	Imperfect	Excessive
Soil organic matter (%)	20–30	8–12	2–4
Vegetation cover (%)	100	90–100	20–50
Vegetation height (cm)	10	70–90	25–35
Dominant species	*Lachemilla pinnata* *Eleocharis albibracteata*	*Deyeuxia hieronymi* *Festuca tucumanica*	*Sorghastrum pellitum* *Stipa juncoides*

evaluated by using the Sørensen coefficient (Warr *et al.* 1993; Peco *et al.* 1998). Differences in germinable seed-bank richness and density among the three communities were tested by using the Mann–Whitney non-parametric test (Sokal & Rohlf 1995).

The nomenclature follows Cabrera (1963, 1965, 1966, 1967, 1969, 1970) and Correa (1984a, b, 1988).

RESULTS

Seed-bank composition and density

A total of 63 species germinated from the soil samples. Species richness was highest in tall-tussock grasslands, intermediate in stony grasslands and lowest in moist swards (Fig. 2a). Seed-bank richness decreased significantly with soil depth in all three communities ($P \leq 0.01$; mean values given in Fig. 2a). The most abundant species found in a single community was the annual grass *Muhlenbergia peruviana*, representing 60% of the seeds in the soil bank of stony grasslands.

The germinable seed-bank density was highest in moist swards, intermediate in stony grasslands and lowest in tall-tussock grasslands (Fig. 2b). Significant differences were found among the three communities when the seed-banks were compared, taking into account both soil layers (0–10 cm; Fig. 2b). These differences can be attributed to the seed-banks in the 5–10 cm soil layer, where significant differences were found between all three communities, as there was no significant difference between moist swards and stony grasslands in the seed-banks at 0–5 cm depth.

Seed-bank density decreased significantly with soil depth in all three communities ($P \leq 0.01$; mean values in Fig. 2b).

Established vegetation and soil seed-banks

Low similarities between the established vegetation and the total soil seed-bank (Sørensen coefficient) were found in tall-tussock grasslands (20%) and stony grasslands (21%), but the similarity was highest in moist swards (45%). In moist swards, many dominant species in the seed-bank (e.g. *Lachemilla pinnata*) were also present in the established vegetation. In tall-tussock grasslands, the dominant species in the established vegetation (e.g. *Festuca tucumanica*) were absent from the seed-banks.

Seed-bank classification

In all three communities, transient seed-bank was the most frequently found category, followed by short-term persistent and long-term persistent strategies (Table 2).

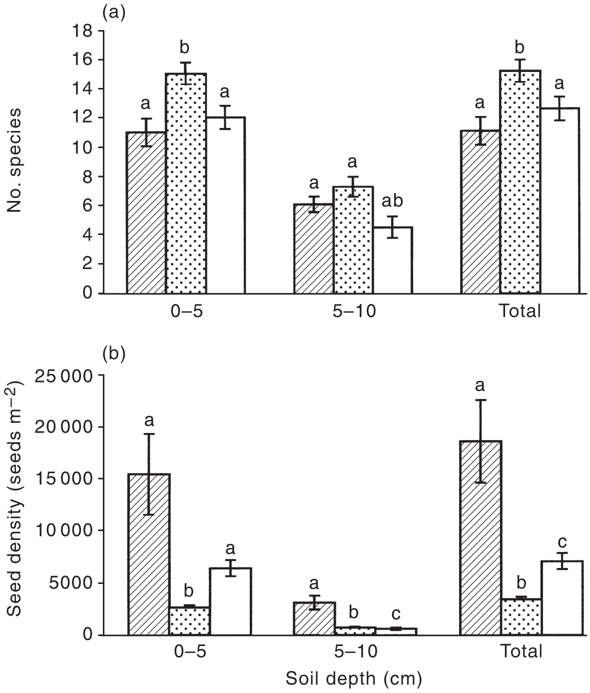

Fig. 2. Seed-bank (a) richness and (b) density (no. seeds m^{-2}), plus SE ($n = 10$) for two different soil depths, and total soil profile in three different plant communities in the granite mountain grasslands of central Argentina. Different letters indicate significant differences ($P \leq 0.05$) between the mean values of seed-bank richness/density of all three communities. (▨), Moist swards; (⬚), tall-tussock grasslands; (□), stony grasslands.

Table 2. Number of species (including both the established vegetation and the soil seed-bank; percentages indicated in parentheses) showing different seed-bank strategies in three different plant communities in the granite mountain grasslands of central Argentina (full data available upon request)

Strategy	Moist swards ($n = 42$)	Tall-tussock grasslands ($n = 95$)	Stony grasslands ($n = 74$)
Transient	28 (67)	75 (79)	59 (80)
Short-term persistent	10 (24)	14 (15)	10 (13)
Long-term persistent	4 (9)	6 (6)	5 (7)

Several species showed different seed-bank strategies in the different communities in which they were present (e.g. *L. pinnata*, *Crassula peduncularis*, *Bulbostylis juncoides*, *Gamochaeta simplicicaulis*, *Juncus achalensis*, *Eragrostis lugens*).

DISCUSSION

Seed-bank composition and density

The total number of germinable seeds in the whole soil profile was largest in moist swards and smallest in tall-tussock grasslands. For alpine communities, Semenova and Onipchenco (1994) reported that the largest number of seeds was also found in wetter sites, but then the number decreased progressively from mesic to xeric habitats. In the present study, seed numbers were higher in xeric sites (stony grasslands) compared with mesic sites (tall-tussock grasslands).

Stony grasslands had a higher seed-bank density than tall-tussock grasslands. This was mainly the result of the large contribution of *M. peruviana* (mean ±SE, 3911 ± 258 seeds m^{-2}), an annual grass reaching the highest frequency in the established vegetation in the stony grasslands.

The moist swards showed the lowest species richness in the seed-banks, which is in agreement with the findings of other wetland studies (van der Valk & Davis 1976; Ungar & Woodell 1993). The low species richness (in both the established vegetation and the soil seed-bank) at these sites could be related to waterlogging (Bekker *et al.* 1998). According to Grubb (1987), comparatively few genotypes can tolerate persistent waterlogging. Waterlogging appears to be one potentially limiting factor, which a comparatively low number of tolerant genotypes have evolved to withstand.

The high seed-bank density found in moist swards is in accordance with results obtained in similar communities (van der Valk & Davis 1976). However, in the present study, this high density was not due to the presence of large numbers of annuals, as was reported by Ungar and Woodell (1993) and Leck and Simpson (1995). Rather, the very dense seed-banks of the Córdoba moist swards were strongly dominated by perennial species such as *C. peduncularis*, *L. pinnata*, and *J. achalensis*.

Tall-tussock grasslands showed the lowest seed-bank density. This may be related to the strong dominance exerted by the tall-tussock grasses *Deyeuxia hieronymi* and *F. tucumanica* in the established vegetation. This effect seems to strongly limit the sexual reproduction of some subordinate species (Díaz *et al.* 1994), thus preventing the local seed rain of many species in this community. Robert and Feast (1973) have observed that the size of the seed-banks diminishes exponentially when seed rain is absent.

The decrease in seed density observed in the present study in relation to soil depth is in agreement with the results reported for many grasslands at the community level (Rice 1989; Bakker *et al.* 1996; McDonald *et al.* 1996; but see Milberg 1995).

Established vegetation and soil seed-banks

We found a low similarity between the established vegetation and that of total soil seed-banks in tall-tussock grasslands and stony grasslands, but not in moist swards. The data confirm the results obtained in different temperate tall-tussock grasslands of the world, in which no association has been found between the composition of seed-banks and that of standing vegetation (Chippendale & Milton 1934; Champnes & Morris 1948; Major & Pyott 1966; Abrams 1988; D'Angela *et al.* 1988; Bakker 1989; Warr *et al.* 1993). This may be the result of the small contribution to the soil seed-bank of the dominant species in the established vegetation, especially *D. hieronymi*. This suggests that vegetative spread might be the main regeneration strategy of the dominant grasses in these grasslands.

In accordance with the results reported for different wetlands from the Northern Hemisphere (Parker & Leck 1985; Leck & Simpson 1987), the moist swards of the study area showed a positive association between established vegetation and soil seed-bank compositions. Species with high frequency in the established vegetation, such as *L. pinnata*, *Eleocharis albibracteata* and *J. achalensis*, were also present in the soil seed-bank in this community.

Published information on the seed-banks of stony grasslands is extremely limited, which makes comparisons difficult. However, Houle and Phillips (1988) reported a positive association between the standing vegetation and the seed-bank composition in depressions on granite exposures in Georgia piedmont (USA). However, we found a low similarity between the established vegetation and the total seed-bank.

Seed-bank strategies

The proportion of transient, short-term and long-term persistent seed-banks detected in each community agreed with the observations of Bakker *et al.* (1996). The soil seed-banks of the majority of species were classified as transient, whereas a small number of them were short-term and long-term persistent seed-banks. Species with persistent seed-banks (especially long-term, but also short-term) are important for community persistence and regeneration following disturbance, and therefore highly relevant to management (Vyvey 1986; McDonald *et al.* 1996). In the present study, persistent seed-bank species were represented in moist swards by above-ground dominants (e.g. *L. pinnata*, *E. albibracteata* and *J. achalensis*). In contrast, species with persistent seed-banks were mostly absent from the established vegetation of tall-tussock grasslands (e.g. *G. simplicicaulis*, *Linaria texana*, *Veronica peregrina*). The stony grasslands represented an intermediate example, in which some species with persistent seed-banks were present (e.g. *M. peruviana*) and some were absent (e.g. *Mollugo verticillata*, *L. texana*) in the established vegetation.

The species with long-term persistent seed-banks have more or equal numbers of seeds in the lower soil layer relative to the upper soil layer. This may be explained in part by their shape and size (Thompson *et al.* 1993; Milberg 1995; Thompson *et al.* 1997). Species with small and compact seeds tend to move deeper into the soil and thus evade predation more easily. The two species that are more abundant in the lower soil layer, *J. achalensis* and *C. peduncularis*, both produce small seeds (Funes *et al.* 1999b).

According to Thompson and Grime (1979), the seed-bank strategy is an inherent trait of a species; that is, it is expected to be the same in the various habitats in which a species can thrive. In the present study, several species showed different seed-bank strategies in the different communities analysed. Other authors have reported different seed-bank strategies of different populations of the same species, in relation to changing environmental conditions (Ortega *et al.* 1997).

Implications for restoration ecology

In years with particularly unfavourable climatic conditions, or following severe disturbance, a persistent seed-bank might reduce the chance of extinction for a population on a site (Houle & Phillips 1988; van der Valk & Pedersen 1989; Strykstra *et al.* 1998; Bakker & Berendse 1999; Funes *et al.* 1999a). The possibilities of community regeneration *in situ* are strongly related to the ability of the component species to form a persistent soil seed-bank (Bakker *et al.* 1996). For example, in British grasslands (McDonald *et al.* 1996) and Swedish dry alvar grasslands (Bakker *et al.* 1996), the regeneration of natural communities from the seed-bank is low, because the more abundant species in the established vegetation are absent from the seed-bank.

In the case of the Córdoba granite grasslands, regeneration from the seed-banks after disturbance (e.g. related to land use or climate change) is expected to differ among communities developed on different edaphic patches. On the basis of soil seed-bank density, longevity and similarity to the established vegetation, potential for *in situ* regeneration should be lower for tall-tussock grasslands, intermediate for stony grasslands and higher for moist swards. This means that the heterogeneity observed by Acosta *et al.* (1992) in the established vegetation on granite substrate is reflected in the soil seed-banks. This heterogeneity in regeneration potential has important implications for conservation. Several investigators have stressed the importance of spatial heterogeneity in maintaining the biodiversity of established vegetation (Pickett & Thompson 1978; Pickett & White 1985; Ostfeld *et al.* 1997) and highlighted its role in the conservation and restoration of natural ecosystems (Pickett *et al.* 1997). Although less explored, soil seed-banks also show heterogeneity at different spatial scales (Inglis 2000). The results of the present study illustrate the strong influence of spatial heterogeneity at the local scale on the maintenance of a rich species pool in grassland soil seed-banks.

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