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Seed bank dynamics in tall-tussock grasslands along an altitudinal gradient

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Abstract. We studied the germinable soil seed bank of tall-tussock grasslands along an altitudinal gradient in the mountains of central Argentina. We selected 10 sampling plots at three altitudinal levels (1200 m, 1600 m and 2200 m). We assessed the composition of the established vegetation and took ten compound soil samples (0 - 5 cm depth) at each plot in autumn and spring. The soil samples were sieved, chilled, and incubated in a glasshouse to assess the composition of the seed bank. The similarity between the composition of the seed bank flora and that of the established vegetation was low throughout the gradient. Most species did not change their seed bank strategy along the gradient. Seed bank richness and density increased with altitude. Most species had a persistent seed bank at all altitudinal levels, and the proportion of such species increased with altitude. These results suggest that a cold climate directly and/or indirectly favours the formation of seed banks and seed persistence in the soil.

Keywords: Argentina; Diaspore bank; Seed persistence; Soil seed bank.

Nomenclature: Zuloaga et al. (1994); Zuloaga & Morrone (1996, 1999).

Introduction

Seed banks can be classified into two fundamental types: transient and persistent (Thompson & Grime 1979). Persistent seed banks may function as a type of genetic memory of a population (Brown & Venable 1986; Levin 1990) and play an important role in community dynamics and regeneration (e.g. Bakker et al. 1996; Bakker & Berendse 1999; Funes et al. 2001). Seed bank density and species richness have been reported to change along temporal (succession) and spatial (altitude, latitude) gradients (Thompson 1978; Warr et al. 1993). For example, Milton (1939) and Thompson (1978, 1985) showed that seed bank density decreases with altitude. This is because at high altitudes there is a predominance of slow-growing and long-lived species and environmental conditions (short growing season) are less favourable to seed production (Archibold 1984; Thompson 1992). These ideas were reinforced by the results of Ortega et al. (1997) who found that richness and density of seed bank decreased with altitude in Spanish mountain grasslands. If the dominant species at high altitudes do not form a persistent seed bank, the similarity between the composition of established vegetation and seed bank should decrease with altitude (Peco et al. 1998).

However, an alternative hypothesis has been proposed. In cold climates (e.g. high mountains or high latitudes) several factors could contribute to the maintenance of many seeds in the soil (Archibold 1984; Cavieres & Arroyo 2001). The diversity of both seed predators and fungi tends to be low in high-mountain habitats (McGraw & Varvek 1989), and low temperatures are associated with low embryonic metabolic rates and slow consumption of seed reserves, favouring seed longevity (Murdoch & Ellis 2000), and thus the formation of persistent seed banks (Cavieres & Arroyo 2001). Seeds of species with a persistent seed bank remain in the soil for long periods (Thompson et al. 1997). This high carry-over of soil seeds from year to year should increase the total seed bank density toward higher altitudes. If this assumption is correct, seed bank density should increase with altitude.

At a finer scale of analysis, it is debatable whether the seed bank strategy of a species tends to remain constant along altitudinal gradients. In ten contrasting habitats, Thompson & Grime (1979) showed that the seed bank strategy of a given species did not change. They suggested that seed bank strategy is independent from the environment. However, Ortega et al. (1997) and Funes et al. (2001) reported different seed bank strategies in different populations of the same species, in relation to changing micro-environmental conditions at the local scale.

Here we examine the variations in richness and density of soil seed banks and the relationship between the composition of the established vegetation and seed banks of tall-tussock grasslands at different altitudes in central Argentina. In order to demonstrate if cold climate promotes the formation of a persistent seed bank, we distinguished between transient and persistent seed bank fractions (*sensu* Thompson & Grime 1979). We specifically aimed to (1) compare the composition of the established vegetation and that of the seed bank in tall-tussock grasslands; (2) classify the species present in the seed bank according to their persistence strategy; (3) investigate whether the strategy of a given species remains constant or changes at different altitudes.

Material and Methods

Study area

The study area is located in the Córdoba mountains, central Argentina (ca. 31°35' S, 64°45' W) and includes an altitudinal gradient from 1200 m to 2200 m a.s.l. Mean annual rainfall is between 800 and 850 mm, and mainly concentrated to the warm season (Funes & Cabido 1995), but there are sharp changes in mean annual temperature, from 13.1 °C at the lowest to 8 °C at the highest altitude. The number of frost-free months decreases from four at the lowest to zero at the highest altitude (Díaz et al. 1998). At the highest altitude ice needles are common in the soil during the cold season, and snow is not uncommon in winter or early spring (Cabido et al. 1987). Capitanelli (1979) reported evidence of peri-glacial activity at the highest level of the gradient during the last Ice Age.

Tall-tussock natural grasslands represent the most widespread vegetation type in the study area. The structure of these grasslands is similar along the gradient, with the dominant tall-tussock species being replaced by others morphologically equivalent as altitude increases (Acosta et al. 1992). The canopy is often three-layered, with the top layer (ca. 120 cm high) dominated by the perennial grasses *Festuca hieronymi* and *Stipa tenuissima* at lower and *Deyeuxia hieronymi* and *Festuca tucumanica* at medium and higher altitudes (Acosta et al. 1992).

Data collection

We selected ten different patches of tall-tussock grasslands at three altitudinal levels, 1200 m, 1600 m and 2200 m. The selection was made on the basis of the vegetation and landscape map of Cabido et al. (1987) and was designed to maximize representation of the patches of grassland communities as well as proper interspersion, and to avoid areas close to roads, paths, pens and dwellings. The sizes of the patches ranged from ca. 50 m^2 to ca. 500 m^2 and each patch was considered a replicate. Within the patches both vegetation and environmental factors were homogeneous (Acosta et al. 1992). Ten compound soil samples were collected from randomly selected points within each of the ten different patches. We sampled 5-cm deep cores with a diameter of 4 cm, taking into account that most viable seeds are located within the first few cm (Funes et al. 2001).

In order to differentiate the persistent fraction of the seed banks, we collected the samples in autumn (May 1996) after the seed rain, in order to capture both the transient seed bank of the present year and the persistent seed bank of previous years (assuming that seeds of species with a persistent seed bank remain in the soil for >1 yr, Thompson et al. 1997) and in spring (October 1996) after seed germination but before the production of new seeds, when only the persistent fraction of the seed bank should be present in the soil (Warr et al. 1993; Milberg 1995; Bakker et al. 1996). The soil samples were sieved through 1-cm, 2-mm and 250-mm mesh sieves, in order to remove plant fragments and stones (ter Heerdt et al. 1996; Funes et al. 1999, 2001). They were then chilled in a refrigerator at 5 °C for one month in order to break seed dormancy (Houle & Phillips 1988; Funes et al. 2001). It should be noted that chilling is likely to affect part of the seeds with a transient seed bank. The soil was then spread over 2 cm of sterilized sand in 15 cm × 15 cm plastic trays which were placed in a glasshouse at a 20 - 30 °C / 10 - 15 °C day/night temperature regime. The trays were distributed in the glasshouse at random positions, and watered daily. As a control against contamination, eight additional trays containing autoclave-sterilized soil were kept under the same conditions.

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 mo, no new germination was observed after 4 mo. 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 into separate pots and grown on natural unfertilized soil within the same greenhouse. Most of the seedlings were identified to species level, with a few exceptions (e.g. *Conyza* spec.). 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). The number of seeds per core were converted to number per m^2.

The established vegetation was recorded by placing 12 quadrats of 10 cm × 10 cm at random within each of the patches where the soil seed bank samples were taken. We recorded the presence of all species within each quadrat.

In this study, we classified the seed banks into only two categories, transient or persistent (Bekker et al. 1998), taking into account their annual dynamics through the comparison of autumn and spring seed occurrence (Ortega et al. 1997). Species that only appeared in autumn have *transient* seed banks (Types I and II); species that were present both in autumn and spring have *persistent* seed banks (Types III and IV) (Thompson & Grime 1979). Following Bakker et al. (1996), species with < 3 seeds per community were omitted.

Data analysis

Differences in germinable seed bank richness and density among tall-tussock grasslands at different altitudes were tested with Kruskal-Wallis (Sokal & Rohlf 1995) and the multiple comparison method for *a posteriori* analysis (Marascuilo & McSweeney 1977). In order to understand the seasonal variation of seed banks, we calculated (Ortega et al. 1997) the seed bank depletion as:

$$\frac{\text{(No. seeds per plot in autumn – No. seeds per plot in spring)}}{\text{No. seeds per plot in autumn}} \quad (1)$$

We used Sørensen's coefficient (Warr et al. 1993; Peco et al. 1998) to evaluate the relationship between the presence/absence of species in the germinable seed banks and in the established vegetation of each community.

Results

Species richness and density of soil seed bank

In total 73 species (including species with < 3 seeds per community) belonging to 27 families germinated from the soil samples. The dominant plant families were *Asteraceae* (19 species) and *Poaceae* (16 species). The species richness of the seed bank changed significantly with altitude both in autumn and spring (Fig. 1a) ($p \leq 0.01$ and $p \leq 0.001$, respectively; Kruskal-Wallis test). In autumn the highest levels showed significantly more species than the other two levels. In spring this trend was more gradual (Fig. 1a).
Soil seed bank density increased with altitude both in autumn and spring (Fig. 1b), although this trend was significant only in spring, when only persistent seeds are present in the soil ($p \leq 0.0001$; Kruskal-Wallis test):

	1200 m	1600 m	2200 m
Autumn	2103 ± 280	2289 ± 196	2880 ± 271
Spring	780 ± 186	1480 ± 247	2738 ± 201

The depletion of the seed bank from autumn to spring was more marked with decreasing altitude (Fig. 2). The highest and medium levels of the gradient showed a more homogeneous seasonal pattern in seed bank density than the lowest level.

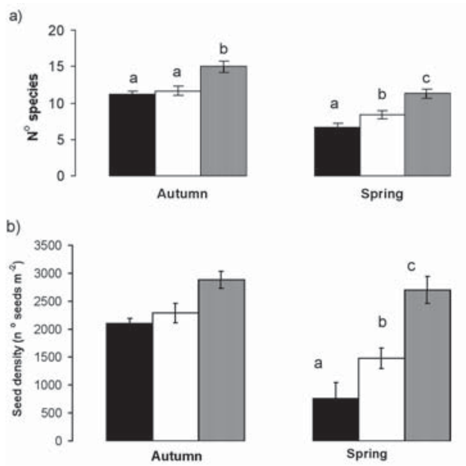

Fig. 1. Seed bank richness (**a**) and density (**b**) mean ± SE (n = 10) in tall-tussock grassland communities along an altitudinal gradient in Central Argentina. Letters indicate significant differences ($p \leq 0.05$, multiple comparison test) among mean values. Black = 1200 m; white = 1600 m; hatched = 2200 m.

Established vegetation and soil seed bank

At all altitudes, and both in autumn and spring, the Sørensen similarities between the established vegetation and the soil seed bank were low:

Autumn			Spring		
1200 m	1600 m	2200 m	1200 m	1600 m	2200 m
25%	21%	22%	19%	20%	20%

119 species (excluding species that occurred in < 3 quadrats) present in the vegetation were absent from the seed banks at all three altitudes (App. 1). Moreover, 29 species occurring in the seed bank were absent in the established vegetation. The common tall-tussock species in the vegetation at all three altitudes (e.g. *Festuca tucumanica*, *F. hieronymi*, *Paspalum cromyorrhizon*) were absent from the seed bank. Only two taxa (*Alchemilla pinnata* and *Carex* spec.) were important both in the established vegetation (frequency > 30) and in the seed bank.

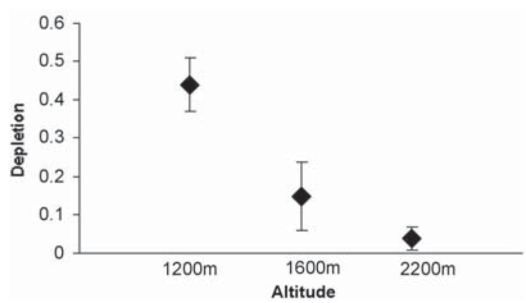

Fig. 2. Seed bank depletion (mean ± SE, n = 10) from autumn to spring in tall-tussock grasslands along an altitudinal gradient in central Argentina.

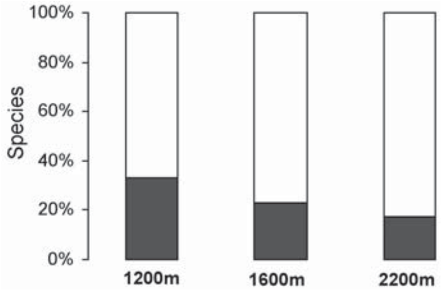

Fig. 3. Proportional representation of different seed bank strategies in tall-tussock grasslands at 1200 m (n = 20), 1600 m (n = 35) and 2200 m (n = 34) in central Argentina. Species with < 3 seeds per community were excluded from the analysis. Black = transient seed banks and white = persistent seed banks.

Seed bank strategies

Persistent seed banks was the most frequent strategy at all three altitudes. Moreover, the proportion of species with persistent seed banks showed a trend to increase with altitude, whereas that of species with transient seed banks decreased with altitude (Fig. 3). Out of 58 species classified (excluding species with < 3 seeds per community), 28 (48%) were present in at least two sites. When the seed bank strategies of these species were compared, only two species, *Paronychia setigera* and *Plantago tomentosa,* representing 6% of the total, showed different seed bank strategies at different altitudes (App. 1).

Discussion

Seed bank composition and density

Seed bank richness increased with altitude, a result that does not agree whit that by Ortega et al. (1997). The grasslands at the lower altitude in their Spanish Mediterranean gradient were dominated by annual species and those at the upper level were dominated by perennial species. Annual species usually supply seeds to the soil bank (Marañón 1995), whereas perennial species (specially the dominants in the established vegetation) tend to be absent in the seed bank, probably because vegetative spread is their main regeneration strategy (Ortega et al. 1997; Funes et al. 2001). Also, the more favourable climatic conditions at the lower level could enhance the activity of seed predators (see below). Therefore, the lower species richness in seed banks at lower altitudes may be explained by both low input of seeds and high levels of predation on them. Central Argentina grasslands, are dominated by perennial species at all altitudinal levels, so in this case greater predation is the most likely explanation for the lower species richness in seed banks observed at lower altitudes.

We found a tendency of seed bank density to increase with altitude both in autumn and spring. However, this tendency was significant only in spring, when the persistent fraction, but not the transient fraction, of the seed bank is present in the soil. This could be due to two factors. First, the cold climatic conditions at the highest extreme of the gradient may promote low embryonic metabolic rates and slow consumption of seed reserves, favouring seed longevity (Murdoch & Ellis 2000) and slowing down germination (Milberg 1995). In this context, the formation of persistent seed banks will be favoured (Cavieres & Arroyo 2001) and thus promote a high carry-over of soil seeds from year to year (MacGraw & Vavrek 1989; Cavieres 1999). Second, the relatively warm conditions at lower altitudinal levels may favour the activity of post-dispersal seed predators, especially rodents, that are an important factor of seed bank depletion (Louda 1989; Cavieres 1999; Edwards & Crawley 1999). Small mammals have been found to be particularly abundant at intermediate altitudinal levels, such as the lowest point in our gradient (Md. Nor 2001). Our finding that seed bank depletion from autumn to spring was highest at the lowest level of the gradient (low carry over) is also consistent with these speculations. The patterns found by Milton (1939) and Thompson (1978, 1985) for perennial grasslands and Ortega et al. (1997) for annual and perennial grasslands, whereby seed bank density falls as altitude increases, were not repeated in this study either.

Established vegetation and soil seed bank

We found a low degree of similarity between the composition of established vegetation and that of soil seed banks along the gradient. Our data confirm the results obtained in different temperate tall-tussock grasslands of the world, where a very low degree of association has been found between the composition of seed banks and that of the standing vegetation (Major & Pyott 1966; Abrams 1988; D'Angela et al. 1988; Bakker 1989; Warr et al. 1993). In our case, this may be the result of the small contribution to the soil seed bank of the common species in the established vegetation at the highest and intermediate altitudes (especially *D. hieronymi*), and the absence of *Festuca tucumanica* at the highest and intermediate levels and *F. hieronymi* and *Paspalum cromyorrhizon* at the lowest level. This suggests that vegetative spread might be the main regeneration strategy of the common grasses in this kind of grassland at all altitudes (Funes et al. 2001). The pattern found here disagrees with that reported by Peco et al. (1998) on mountains of central Spain. They showed a high similarity (75%) between the established vegetation and seed bank composition at the lowest level of the gradient and a lower similarity (50%) at the upper level. The established community at the lowest level in these Spanish grasslands is dominated by annual species. The strong association between the composition of the established vegetation and that of the seed bank in annual grasslands is well known (Leck & Simpson 1987; Ungar & Woodell 1993).

Seed bank strategies

The proportion of different seed bank strategies (transient and persistent) detected in the gradient studied agreed with the observations made by Ortega et al. (1997). The percentage of species with persistent seed banks increase with altitude. This also agrees with the suggestions of MacGraw & Vavrek (1989) and Cavieres & Arroyo (2001), that a cold climate contributes to the maintenance of seed viability and persistence in the soil. According to Thompson & Grime (1979), the seed bank strategy is a species' inherent trait, i.e., it is expected to be the same in all the different habitats where a species can thrive. However, Ortega et al. (1997) and Funes et al. (2001) reported different seed bank strategies in different populations of the same species, in relation to changing local (micro-environmental/edaphic) conditions. Cavieres & Arroyo (2001) showed that *Phacelia secunda* becomes more prone to form a persistent seed bank as altitude increases along a gradient in the Andes of central Chile. They concluded that the cold climate in high mountains promotes seed persistence in the soil. Moreover, for many species, seed germination requirements change with altitude (Trillo & Carro 1993; Meyer et al. 1995; Baskin & Baskin 1998), which suggests that the seed bank dynamics of a given species may be responsive to the modulating effect of the environment, at least to some degree. In this study, however, only two species out of the 28 growing in at least two different altitudes changed their seed bank strategy along the altitudinal gradient. Therefore our results give new support to the Thompson & Grime's (1979) hypothesis. However, and in the light of previous results by Ortega et al. (1997), and Funes et al. (2001) it is possible that seed bank strategy remains constant at the regional level (i.e. in the face of changing climatic conditions), but not at the local level (i.e. under different edaphic conditions, such as soil water-logging). This remains to be tested.

The results reported in this study support the idea that, in perennial grasslands, increasing altitude favours seed bank richness and density and persistence of seeds in the soil. This could be the result of two processes: on the one hand, direct effect of climatic conditions on seed longevity, and on the other hand, their indirect effect mediated by decreased predation.

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