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Seed bank dynamics of *Lachemilla pinnata* (Rosaceae) in different plant communities of mountain grasslands in central Argentina

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We studied the soil seed bank of *Lachemilla pinnata* (Ruiz & Pav.) Rothm. (Rosaceae) in the main vegetation patches that make up mountain grasslands on granitic substrate in central Argentina: moist swards, tall-tussock grasslands and stony grasslands. Ten compound soil samples from each community at two soil depths (0–5 cm and 5–10 cm) were taken. In general, the density of the germinable seed bank of *L. pinnata* was larger in autumn after the seed rain, increased with its relative cover in the established vegetation, and sharply decreased with soil depth. The seed bank of *L. pinnata* was classified as short-term persistent. Its density was higher in moist swards, where it was abundant and could produce flowers and fruits, than in stony grasslands where its cover was very low, or tall-tussock grasslands, where no flowering events were recorded. On those bases, moist-sward patches are expected to play a more important role than, tall-tussock grasslands or stony grasslands in the maintenance of local populations of *L. pinnata*.

Keywords: *Lachemilla pinnata*, mountain grassland, seed banks, vegetation patches

INTRODUCTION

Understanding persistent seed banks is the key to many aspects of practical land management for agriculture or conservation, and to the effective conservation of many rare species (Thompson *et al.* 1993). Management, which permits intermittent regeneration from a persistent seed bank is crucial to the survival of many rare or declining species (Keddy & Reznicek 1982, Rowell *et al.* 1982). Furthermore, in the increasingly disturbed environments created by modern land use, knowledge of seed reservoirs in the soils of natural communities will provide useful tools for conservation. In particular, species not represented in the seed bank are particularly vulnerable to elimination from the standing vegetation (Brown & Oosterhuis 1981, Fenner 1985).

In Northern Hemisphere temperate grasslands, plants which are common in the standing vegetation often show low seed numbers or are absent in the seed bank (Chippendale & Milton 1934, Champnes & Morris 1948, Major & Pyott 1966, Abrams 1988, D'Angela *et al*. 1988, Bakker 1989).

The dynamics of soil seed populations is likely to depend on multiple factors, including density of local seed rain, seed predators and chemical and physical factors that affect seed dormancy and survival (Roberts 1981, Baskin & Baskin 1989, Thompson 1992). Although seeds of many species can survive in the soil for long periods, the density of viable seed declines exponentially when local seed rain is prevented (Roberts & Feast 1973, Roberts 1981, Williams 1984).

Many studies of grassland seed banks have involved sampling on a single event, a practice that fails to reveal the rich variety of seed bank dynamics. Intensive sampling over a whole year has revealed that seeds of many species can only be found in the soil for a relatively short period, while others may show seasonal peaks of abundance but are present throughout the year (Thompson 1992). On the basis of a seasonal wide-ranging survey of the germinable seed bank of British plant communities, Thompson and Grime (1979) grouped the species into those showing persistent or transient seed banks. The species with persistent seed banks have dormancy and smaller seeds than those with transient banks, and are important in population maintenance in unfavourable years (Graham & Hutchings 1988). On the other hand, the best assessment of the longevity of seeds in the soil can be obtained from burial experiments, but it is possible to estimate the longevity on the soil seed banks from indirect evidence. This can be achieved by comparing the established vegetation with the seed banks in the top soil and deeper soil layer (Bakker 1989, Thompson *et al*. 1993, Thompson *et al.* 1997).

Lachemilla is a genus widely distributed in the neotropics. *Lachemilla pinnata* (Ruiz & Pav.) Rothm. is a common montane species, whose range extends from the Peruvian and Bolivian Andes to the North-Western and Central mountains of Argentina. It is highly selected by domestic and native grazers, and possesses high forage quality (Ringuelet 1941). When heavily grazed it forms a dense cover which does not die back during the winter, helping to protect the soil in areas where the risk of erosion from weathering and livestock trampling is high (Pucheta *et al*. 1998). In our study area, Díaz *et al.* (1994) found that *L. pinnata* did not flower in tussock-grassland communities, but it did in neighbouring sward patches on hydromorphic soils. These phenological differences between community patches should be reflected in the seed bank dynamics of this species.

The aims of this paper were to document (1) the seasonal dynamics of *Lachemilla pinnata* seed bank in different plant communities; and (2) its relative abundance in the seed bank and in the standing vegetation.

The nomenclature follows Hunziker (1984) and the author abbreviations follow Brummitt and Powell (1992).

METHODS

Study area

The study site is located in Pampa de Achala, Córdoba mountains, central Argentina (31°35´S, 64°45´W) at 2 100 m elevation. The climate of the region is humid, with short, cool summers and long, cold winters (Pucheta *et al*. 1998). Mean temperature of coldest and warmest months are 5 and 11.4°C, respectively, and the mean annual rainfall is 840 mm, concentrated mainly in the summer.

The local vegetation consists of a mosaic of different plant communities, described in detail by Cabido *et al*. (1989) (Fig. 1). Soil moisture regime is the main environmental factor determining their spatial patterns (Cabido 1985, Cabido *et al*. 1987). *Lachemilla pinnata-Eleocharis albibracteata* swards occupy the wettest extreme. Soils in this type of community are very poorly drained. Total vegetation cover is always 100%, of which over 65% corresponds to *L. pinnata* and *E. albibracteata*. *Deyeuxia hieronymi* tall-tussock grasslands is the most widespread community in the study area. Soils are well to imperfectly drained, generally deep, with a loam to clay-loam texture. This community generally presents a three-layered structure, with the top layer being dominated by the perennial tall tussock grass *D. hieronymi*, and the intermediate and lower layers dominated

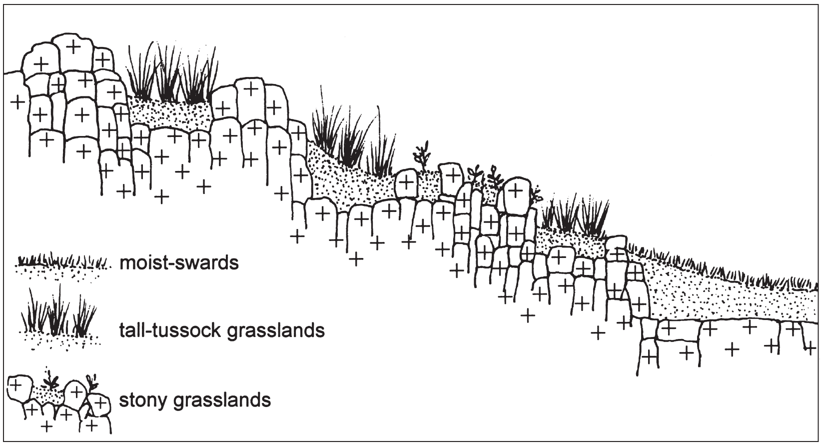

Fig. 1. Diagrammatic representation of the three main communities of Pampa de Achala high-mountain grasslands (central Argentina).

by *Agrostis montevidensis* and *L. pinnata*, respectively. The driest extreme, represented by rock outcrops and steep, rocky slopes where well to excessively drained shallow stony soils occur or where no soil has developed, is occupied by *Sorgastrum pellitum* and *Stipa juncoides* stony grasslands.

Data collection

Ten compound soil samples from 10 different patches of each of the three communities mentioned above were collected at 9-week intervals, from March 1996 to January 1997. Each compound sample consisted of 10 soil cores taken with a 4 cm diameter bore, and then pooled and thoroughly mixed. Two soil depths were considered: 0–5 cm and 5–10 cm. Compound soil samples were sieved through 1 cm, 2 mm and 250 μm mesh sieves, thus removing plant fragments and stones (Ter Heerdt *et al.* 1996). In order to break seed dormancy, we treated them by chilling (Houle & Phillips 1988, Kaoru & Tilman 1996, McDonald *et al.* 1996). Compound soil samples were placed in a refrigerator at 5°C for one month, and then the soil was spread over 2 cm of sterilised sand in 15 × 15 cm plastic trays. Each try corresponded to one compound soil sample. All trays were placed in a greenhouse in two randomised blocks. The temperature in the greenhouse was kept at 25–30°C during the day and 10–15°C during the night. The soil cores were maintained at field capacity. As a control against contamination, four additional trays containing sterilised soil were included in each set of soil samples. Trays were placed in greenhouse during 12 months.

The germinable-seed bank in the soil (GSB) of *Lachemilla pinnata* was evaluated by counting the number of seedlings emerging from the soil cores. The established vegetation was sampled using twelve 10 × 10 cm sqares in each stand from where soil samples were taken. Presence-absence data were combined to give frequency values of *L. pinnata* for each community.

Data analysis

The correlation of the *Lachemilla pinnata* seed density (no. seed m^{-2}) and the frequency of established vegetation in each community was evaluated using a non-parametric test (Spearman). Means of seed density in the three communities at each date and soil depth were tested for significant differences using the non-parametric Kolmogorov-Smirnov test (Sokal & Rohlf 1995).

RESULTS

The total density of *Lachemilla pinnata* in the GSB was higher in moist swards than in tall tussock grasslands or stony grasslands at both soil depths and during the whole annual cycle (Fig. 2). Differences between the three were significant for all seasons at 0–5 cm depth ($p < 0.001$), but only in March and May at 5–10 cm depth ($p < 0.05$). Seed density (no. seeds m^{-2}) in each community along the annual cycle decreased significatly with soil depth (Fig. 2). No seeds were found in stony grassland in the deepest layer.

After the seed rain (May 1996), the GSB of *Lachemilla pinnata* increased in all three communities (Fig. 2), but that increase was significant only in the case of moist swards. In that community it reached a density peak in early May (2 769 ± 361 seeds m^{-2}). Its density sharply decreased in winter (August 1996) (800 ± 187 seeds m^{-2}), and in late spring and early summer (January 1997) new seeds are added to the bank.

As expected, the frequency of *Lachemilla pinnata* was different in the established vegetation

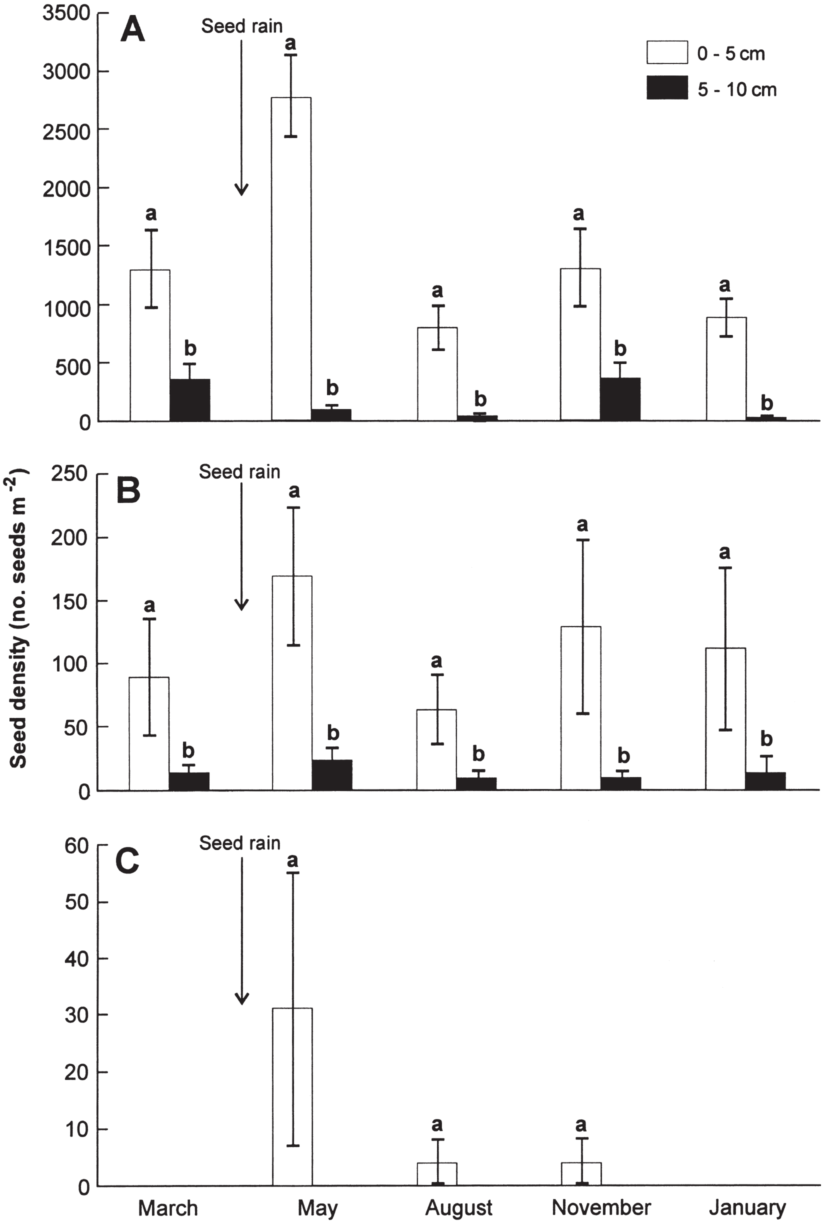

Fig. 2. Germinable seed bank (GSB, no. seeds m^{-2}) and standard error ($n = 10$) of *Lachemilla pinnata* at 0–5 cm and 5–10 cm depth in different plant communities and seasons. — A: Moist swards. — B: Tall-tussock grassland. — C: Stony grassland. — Different letters indicate significant differences ($p < 0.05$) among mean values of the GSB between 0–5 cm and 5–10 cm soil layers in each sampling date. Note differences in scale shown in A, B and C.

of the three patches considered. We also found a strong correlation between its frequency in the established vegetation and in the GSB (Fig. 3).

DISCUSSION

The most important single factor determining the size of *Lachemilla pinnata*'s GSB was the seed rain itself (Fig. 2). Bertiller (1992) and Bertiller and Coronato (1994) found similar results in the grasslands of *Festuca pallescens*, in NW Patagonia.

Considering the changes observed in its pre- and post-dispersal sizes, with seed replenishment clearly occurring after seed rain, the GSB of *Lachemilla pinnata* may be classified as type III *sensu* Thompson and Grime (1979). According to the classification by Thompson *et al.* (1997), *Lachemilla pinnata* shows a short-term persistence seed bank strategy, since its seeds were present at both soil depths (5–10 cm) but the bank density was

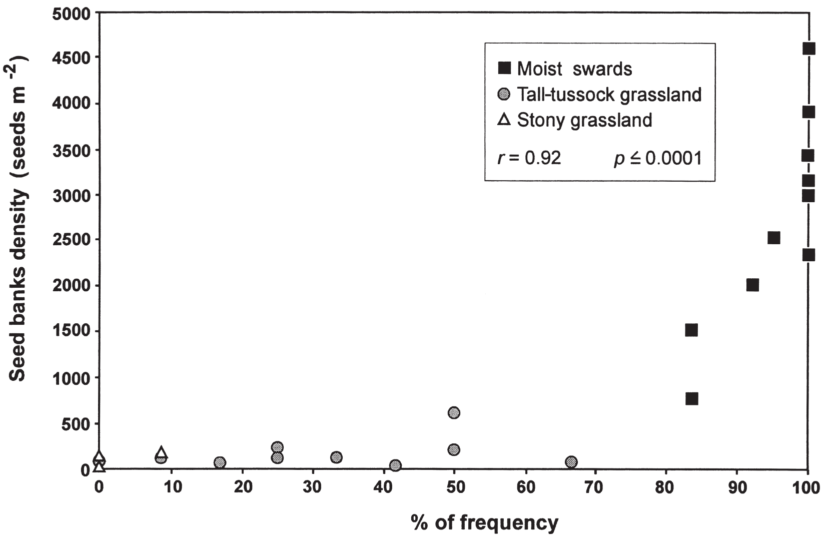

Fig. 3. The relationship between seed bank density recorded after the seed rain and aboveground frequency of *Lachemilla pinnata* in different plant communities in a mountain grassland of Central Argentina. Correlation according to Spearman rank. Since *L. pinnata* is absent both in the GSB and established vegetation in seven stony grasslands sites, only three triangles are displayed in the figure.

higher in the upper layer.

The bigger size of *Lachemilla pinnata*'s GSB found in the moist swards in every season could be related with the species importance in the standing vegetation. *Lachemilla pinnata* was one of the dominants in this community, it was unlikely to be overcompeted by other species, and showed abundant flowering and fruiting (Díaz *et al.* 1994). Bertiller (1992) found similar patterns for *Carex patagonica*, whose GSB was related to its abundance in the standing vegetation.

Although *Lachemilla pinnata* was very frequent in tall-tussock grasslands, it was scarcely represented in their soil seed bank. This could be due to the strong dominance effect exerted by the tall and dense grasses *Festuca tucumanica* and *Deyeuxia hieronymi*, which apparently prevents flower and fruit production by *L. pinnata* (Díaz *et al.* 1994), thus preventing local seed rain. Roberts and Feast (1973) observed that the weed seed bank diminished exponentially when seed rain was prevented. In tall-tussock grasslands, the *L. pinnata* GSB is likely to be showing a similar behaviour. The few seeds found in the soil bank in tall-tussock grasslands could have been dispersed from neighbouring communities or originated in past seed rains in which disturbances could have diminished tall grasses dominance and allowed flowering and seed set by *L. pinnata*. Further exploration is needed, however, to confirm this hypothesis.

The decrease in seed density with soil depth agrees with many previous findings at the whole-community level (Rice 1989, Ghermandi 1992, Bakker *et al.* 1996), although some authors (e.g., Milberg 1995) have reported a bigger seed bank size at greater depth. At the species level, there are examples (e.g. *Taraxacum officinalis*, *Thalictrum flavum*, *Carex nigra*) known to have larger seed banks at 5–10 cm than at lower soil depths (McDonald *et al.* 1996).

In unfavourable years, a persistent seed bank might reduce the risk of local extinction (Houle & Phillips 1988). In the grassland studied, the restoration of *Lachemilla pinnata* populations from seed banks following disturbance is likely to be different depending on which community is considered. Restoration possibilities will be lower in stony grasslands, intermediate in tall tussock grasslands and higher in moist swards. But, because these communities tend to form a mosaic over the landscape, tall-tussock grasslands and stony grasslands are likely to receive part of the seed rain that originated in moist swards. This suggests that moist swards may play an important role as genetic reservoirs of this important forage species, and therefore should receive particular attention in regional conservation efforts.

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