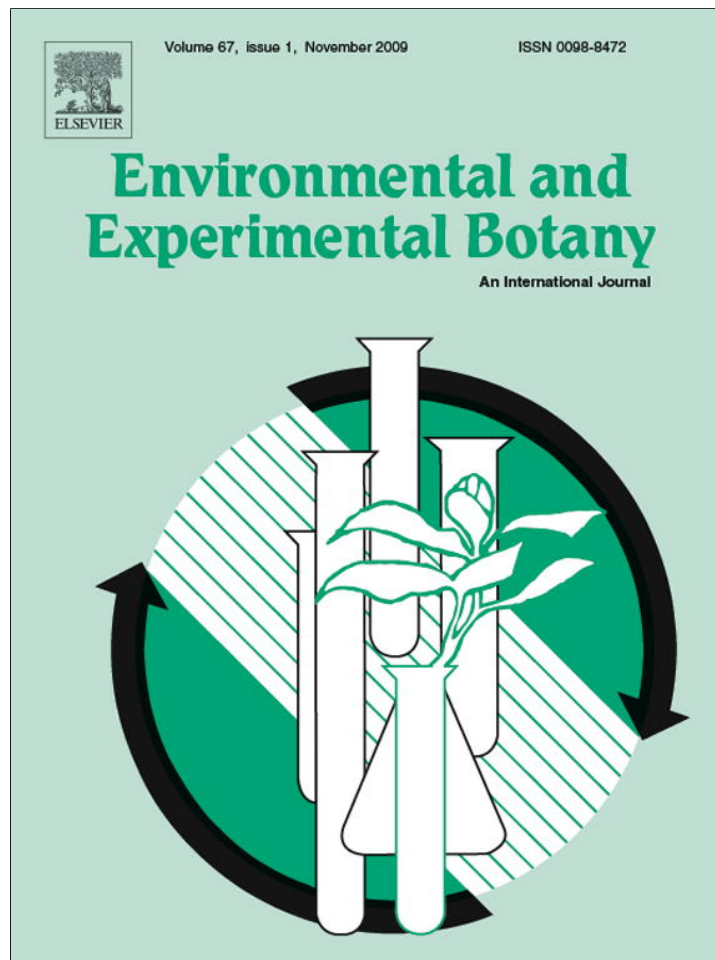


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## Soil seed bank in and between vegetation patches in arid Patagonia, Argentina

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## ABSTRACT

This study was conducted at two sites, 1.5 km from 1 to another in arid Argentina (39°S, 69°W). Vegetation is distributed in patches. Four microenvironments can be identified in the soil surface of these patches, and the bare interspaces among them. Hypotheses were that (1) at any time during the sampling periods, buried (viable + damaged) seeds of the most common vegetation in the patches, *Larrea divaricata* Cav., *Atriplex lampa* Gill ex Moquin, *Stipa neaei* Nees ex Steudel and *Leymus erianthus* (Phil.) Dubcovsky, are present in the soil seed bank at all four microenvironments within any vegetation patch and its associated interspace, and (2) natural plant recruitment from the soil seed bank occurs for *L. divaricata*, *A. lampa*, *S. neaei*, *L. erianthus*, *Bromus tectorum* L. and *Poa lanuginosa* Poir. Lamarck in all study microenvironments. In undisturbed field areas, 32 soil samples were periodically taken using an auger in 1999. Viable and damaged seeds contained in the soil organic matter were counted for *L. divaricata*, *A. lampa*, *S. neaei*, and *L. erianthus*. In a further study, emergence and subsequent growth of *L. divaricata*, *A. lampa*, *S. neaei*, *L. erianthus*, *B. tectorum* and *P. lanuginosa* from the soil seed bank were evaluated in the various microenvironments; permanent plots (0.04 m<sup>2</sup>) were placed on each of the two study sites using four vegetation patches and their associated interspaces per site. Results supported the first hypotheses only for *L. divaricata* and *A. lampa*. However, natural recruitment from the soil only included *S. neaei* and *P. lanuginosa* through asexual, and *B. tectorum* through sexual reproduction. Despite the presence of buried seeds of *L. divaricata* and *A. lampa* in microenvironment 4 during most of the sampling period, bare interspaces among vegetation patches can be naturally vegetated through sexual reproduction by *B. tectorum*, during years of abundant, higher than long-term, annual precipitation.

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## 1. Introduction

The occurrence of patches of vegetation alternating with patches of (almost) bare soil is a common feature in arid and semi-arid grazing systems throughout the world (Ludwig et al., 2004; Erickson et al., 2005). Knowledge of ecological processes in these vegetation patches and their associated nude interspaces is then essential since these systems cover nearly 30% of the earth's land surface (FAO, 2005). Plant patches modify the local microenvironment and resource availability. The soil beneath plant canopies accumulates biomass, organic matter and nutrients, and the majority of seeds either settles in the neighbourhood of the mother plants or is redeposited by winds (Ellner and Shmida, 1981; Jiménez and Armesto, 1992; Vinton and Burke, 1995).

Grazing leads to ecosystem changes such as the reduction of palatable plant cover, the increase of shrubs, the increase of bare soil and the increase of wind and water erosion of soils. These processes increase the spatial and temporal heterogeneity of plant and soil

resources affecting the availability of seeds and microsites for plant emergence and establishment (Schlesinger et al., 1990; Trilca and Rittenhouse, 1993).

Our study was conducted in the Monte Austral Neuquino (MAN), within the Monte Phytogeographical Province in south-western Argentina, where vegetation is arranged in patches. Soil surface microenvironments may be identified in and around vegetation patches. Characteristics of these soil surface microenvironments appear to perpetuate the existence of long-lived perennial shrubs, perennial grasses, *Bromus tectorum* L. and annual herbs (Blackburn, 1975; Eckert et al., 1978). These grasslands have been extensively grazed by sheep since the beginning of this century. Grazing has reduced the cover of perennial grasses and some shrubs leading to changes in the floristic structure and spatial organization of vegetation, such as fragmentation of large patches, extinction of grass patches and formation of new incipient vegetation patches (Bisigato and Bertiller, 1997). These processes probably affect the spatial structure of the soil seed bank which, as in other desert ecosystems (Kemp, 1989), may be controlled by local plant distributions.

Previous studies at the research site have determined that seed rain of the shrubs *Larrea divaricata* and *Atriplex lampa*, and the perennial grasses *Stipa neaei* and *Leymus erianthus*, reaches

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all four microenvironments in and among the vegetation patches (Bonvissuto and Busso, 2007a). These species differ in seed morphology (Bonvissuto and Busso, 2007a). In a field seeding study, Bonvissuto (2006) reported that plant establishment of these species and *Poa ligularis* was unsuccessful in the bare, plant uncovered microenvironments, but it was highly successful under the shrub canopies. The only exception was in *P. ligularis* which did not emerge at the soil surface in any of the study microenvironments. In addition, all these species, but *P. ligularis*, germinated under various temperature and water availability conditions in a germination growth chamber study (Bonvissuto and Busso, 2007b). These field and growth chamber investigations made us to exclude *P. ligularis* from the soil seed bank study. Bonvissuto (2006) suggested that unusual years of high, above-average precipitation might allow shrub establishment in the interspaces among vegetation patches; thereafter, these shrubs would allow the subsequent formation of new vegetation patches in the nude interspaces. Subsequently, a major question to be answered in our study was to determine the size and viability of the soil seed source of *L. divaricata*, *A. lampa*, *S. neaei* and *L. erianthus* (i.e., the size and viability of the soil seed bank) for the potential formation of new vegetation patches in the interspaces during unusual, high precipitation years. Other studies have demonstrated that unusually high precipitation years are necessary for shrub germination and establishment in semiarid rangelands of central Argentina (Peláez et al., 1996).

Common plant species in the vegetation patches, included in this field study, are *L. divaricata*, *A. lampa*, *S. neaei*, *L. erianthus*, *Poa lanuginosa* and *B. tectorum* (Bonvissuto et al., 2001, 2008; Bonvissuto and Busso, 2007a,b). They have a wide distribution in the American Continent, including Argentina (Valentine and Norris, 1964; Passera and Borsetto, 1989; Johnson and Mayeux, 1992; Gandullo, 2004). This makes the results of our study interesting from the standpoint of increasing knowledge on these species and their associated ecological system. *B. tectorum* is the main invasive, exotic annual grass at the study site (Bonvissuto et al., 2001; Gandullo, 2004). This is similar to that reported by Young et al. (1999) for the semiarid rangelands of the Intermountain West Region in the USA.

Successional changes may cause large differences between the soil seed bank and the aboveground floristic composition (Thompson, 2000). Then, we also wanted to determine the soil seed bank contribution of the study species to plant recruitment using permanent field plots within field enclosures to domestic livestock.

Hypotheses of this study were that (1) at any time during the sampling period, buried (viable + damaged) seeds of *L. divaricata*, *A. lampa*, *S. neaei* and *L. erianthus* are present in the soil seed bank at all four microenvironments within any vegetation patch and its associated microenvironment, and (2) natural plant recruitment from the soil seed bank occurs for *L. divaricata*, *A. lampa*, *S. neaei*, *L. erianthus*, *B. tectorum* and *P. lanuginosa* in all study microenvironments. Specific objectives were (1) to determine the magnitude of the soil seed bank (viable + damaged seeds) of *L. divaricata*, *A.*

*lampa*, *S. neaei* and *L. erianthus* in different microenvironments of the vegetation patches which characterize the study site (spatial variability), and (2) to evaluate plant recruitment from the natural soil seed bank at all four study microenvironments. Since samplings were conducted at different times during the growing season, and given that all seed banks have a seasonal variation determined by the processes of seed inputs and outputs in any ecosystem, the seasonal dynamics of the soil seed bank (temporal variability) was also characterized.

## 2. Materials and methods

### 2.1. Study area and study sites

This research was conducted in the shrubby steppe of *L. divaricata* Cav. and *A. lampa* Gill ex. Moquin, near the town of Picún Leufú, Province of Neuquén, within the MAN. As in other arid and semi-arid environments of the world, vegetation at this study site had a scattered distribution and a patchy structure (Ludwig et al., 2004; Erickson et al., 2005). *L. divaricata* and *A. lampa* are the major shrub species, and *S. neaei* Nees ex Steudel and *L. erianthus* (Phil.) Dubcovsky (syn: *Elymus erianthus* Phil., Dubcovsky et al., 1997) are the most abundant perennial grasses in any vegetation patch.

Studies were conducted at two sites (39°20–32'S; 69°19–30'W) distant 1.5 km from one another. One site was nearby a New Road while the other site was close to an Old Road. At each site, four vegetation patches and their associated, nude interspaces were chosen, and four study microenvironments (Fig. 1) were identified within each patch. Bonvissuto (2006) provides a detailed description of each microenvironment.

Rangelands in the MAN, surrounding the town of Picún Leufú, have been exposed to continuous, uncontrolled grazing by goats, sheep and cattle since the early 1900s (Bonvissuto, 2006). Forage production of these rangelands is often limited partially due to the scarce precipitation in these areas [long-term mean annual precipitation: 137.2 mm (1928–1950) = Italconsult Argentina, 1966]. Thus, these rangelands have been led to a similar structure and spatial arrangement of the vegetation at both study sites (Bonvissuto et al., 1999), and allowed us to pool the soil seed bank data obtained from both study locations for subsequent interpretation.

### 2.2. Climate

In Picún Leufú, the average annual precipitation for 1928–1950 and 1999–2005 were 137.2 and 200 mm, respectively. Extremes of annual precipitation between 1928 and 1950 were 62.7 and 245.3 mm (Morello, 1958). Most precipitation occurs during winter and spring, and the least during summer. Average daily maximum and minimum temperatures in January are 28 and 15 °C, and 7 and 2 °C in July. Mean annual wind speed is 13 km h<sup>-1</sup> (Servicio

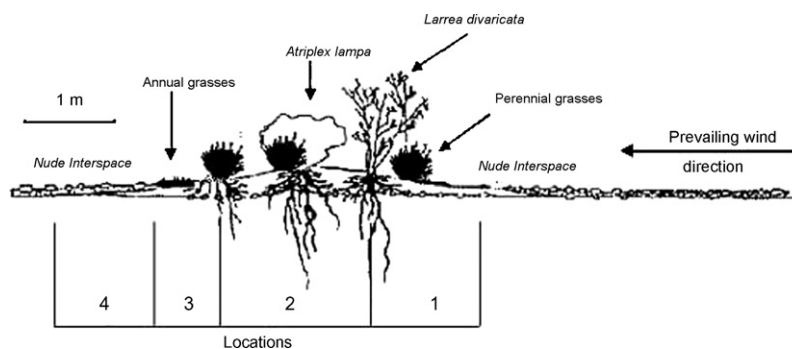


Fig. 1. Vegetation patch description. The microenvironment of annual and perennial grasses, *Larrea divaricata* and *Atriplex lampa* is indicated in the patch.

Meteorológico Nacional, 1958). November and December (spring) and January (early summer), have the greatest wind speeds, with a mean of 17 km h<sup>-1</sup> at 2 m above soil level.

### 2.3. Vegetation

The shrubby steppe vegetation of the dominant *L. divaricata* and the co-dominant *A. lampa* occupies approximately 1,080,000 hectares in the MAN. This steppe is usually present either in plain areas or in those with very little slope (<5%) (Movia et al., 1982). Three strata can be found within each of the vegetation patches in this steppe (Movia et al., 1982): (1) *L. divaricata*, *Bougainvillea spinosa* (Cav.) Heimerl, *Monttea aphylla* (Miers) Bentham et Hooker and *Larrea cuneifolia* Cav. are present with a mean height of 1.50 m, but which can be reduced to 0.80 m on stony or fine-textured soils, (2) the second stratum varies between 0.70–1.00 m, and is characterized by the presence of *A. lampa* (0.5–0.8 m height). This species is present either on sandy mounds [together with *Prosopis alpacato* Philippi, *Schinus polygamus* (Cav.) Cabr., *Lycium chilense* Miers (ex Bertero), *Chuquiraga erinacea* D. Don and *Fabiana peckii* Niederlein] or alone in the interspaces, (3) small shrubs [*Acantholippia seriphioides* (A. Gray) Moldenke, *Gutierrezia solbrigii* Cabr., *Verbena seriphioides* Gilles and Hook, *Senecio aff. filaginoides* DC., *Cassia aphylla* Cav. and *Grindelia chiloensis* (Corn.) Cabr.], and perennial [*S. neaei*, *P. lanuginosa* Poir. ap. Lamarck, *P. ligularis* (Nees ap. Steudel), *Stipa speciosa* (Trinius et Ruprecht), and *L. erianthus*] and annual grasses (*Schismus barbatus* Thellung, *Plantago patagonica* Jacquin and *B. tectorum*) form the third stratum, which is 0.05–0.60 m height. *Schismus barbatus* and *P. patagonica* are ephemeral species about 0.05 m height and do not have a plant cover greater than 15%. Abundance of *B. tectorum* within the herbaceous layer is associated with years of above-average precipitation (Rickard, 1965; Bonvissuto et al., 2001, 2008).

### 2.4. Soils

Aridisols dominate the area. There are mostly old structural plains. Landscape is controlled by the topography of the underlying mantle. It includes Typic Paleortids, Petrocalcic Calciorids, Petrocalcic Paleargids and Typic Torriorthents, with shallow and saline phases (Ferrer and Irisarri, 1989). According to the soil classification (Soil Survey Staff, 1975) no water is available during long periods. However, a slight tendency to the Mediterranean type could be observed, with greater humidity during the winter (Morello, 1958). When temperature is sufficient for plant growth, soil water potentials are  $\leq -1.5$  MPa most of the time (Bonvissuto and Busso, 2006). During the warm season, a continuous period of three or more months with plant available moisture does not occur (Soil Survey Staff, 1975). In addition, little of the scarce rain infiltrates the soil, especially in the interspaces between vegetation patches, and most of it is lost to runoff (Bonvissuto, 2006).

### 2.5. Sampling methods

(i) *Soil seed bank*: In undisturbed field areas, soil samples were taken using an auger of 9 cm diameter and 5 cm depth. Sampling volume was 318 cm<sup>3</sup> in each microenvironment of the vegetation patch. Sampling was conducted in April, August and December 1999. The total number of samples was 1 sample/microenvironment  $\times$  4 microenvironments/vegetation patch  $\times$  4 vegetation patches/site  $\times$  2 sites  $\times$  3 sampling dates = 96 samples. The soil seed bank was evaluated following the technique of Mayor (1996). Soil samples were passed through a screen of 5.4 mesh size to eliminate branches and stones, and were then treated with Malone's solution (Malone, 1967) to disperse the soil and allow flotation of the

organic matter. All floating material was passed through a screen tower of various mesh sizes. From greatest (0.85 mm) to lowest (0.25 mm) mesh openings, screens were of 30, 42 and 102 mesh size in the tower. The organic material retained in each of these screens was observed under a magnifying glass to extract and count the seeds.

Undamaged seeds which resisted a light hand pressure were considered viable by Roberts and Ricketts (1979) and D'Angela et al. (1988). Thereafter, seeds were classified into the following two categories: (1) viable (entire) seeds, which included those firm (after applying pressure with a tweezer) and germinated (with visible radicle), and (2) damaged seeds, which included broken, burnt, empty and dead seeds (soft seeds after applying pressure with a tweezer), as well as those with broken seminal coats. The number of seeds in each category was counted for each of the four study species.

(ii) *Plant recruitment*: In a further study, seedling emergence and subsequent growth of the study grass and shrub species from the soil seed bank was evaluated. Four vegetation patches at each of the two study sites were selected and excluded from domestic herbivory. Within each vegetation patch, permanent plots (0.10 m  $\times$  0.40 m) were located in the four study microenvironments (2 sites  $\times$  4 vegetation patches/site  $\times$  4 microenvironments/vegetation patch = 32 plots). Any standing vegetation was carefully removed from the plots at the study initiation (March 2000). Neither juvenile nor adult shrubs were present in the plots at this time. On December 2000 and October 2001, all individuals of all species which established in the plots were harvested, dried at 70 °C during 72 h and weighed. Density was measured by counting the number of individuals of any given species per unit surface area.

### 2.6. Statistical analysis

Since the dataset included zeros, and then we could not assume normal distribution and equal variance, data were transformed following Sokal and Rohlf (1984):

$$\sqrt{x + 0.5},$$

where  $x$  = either (1) number of viable and buried (viable + damaged) seeds in the soil seed bank or (2) plant recruitment biomass and density of *S. neaei*, *P. ligularis* or *B. tectorum*.

ANOVA were performed for each study variable. Means were compared with Fisher's protected LSD at 5% when  $F$  tests were significant at that level (Steel and Torrie, 1981). Untransformed data are referred to in the text and tables.

## 3. Results

### 3.1. Soil seed bank

The frequency distribution of total study species seeds per sample had a highly leptokurtic pattern. That is, some samples had many seeds, but most had very few, if any. In the shrub species, the amount of damaged seeds was often greater than the viable (entire) number at all four microenvironments and sampling dates (Table 1). In the sampling volume, only 17 and 9%, of the 191 *L. divaricata* seeds and 455 *A. lampa* seeds, respectively, were entire with the remainder damaged. Eight of the 10 *S. neaei* seeds were entire and, of the two *L. erianthus* seeds, one was entire and the other damaged. *S. neaei* only had viable seeds in microenvironments 2–4 in April.

Except in April, viable and buried seed number were greater ( $p < 0.05$ ) in microenvironment 3 (August) or microenvironment 2 (December) than in the bare, uncovered interspaces (microenvironment 4) (Table 2).

**Table 1**

Numbers of viable or damaged seeds per sampling volume (318 cm<sup>3</sup>) at all four microenvironments in *L. divaricata*, *A. lampa*, *S. neaei* and *L. erianthus* during April, August and December 1999.

	Microenvironment	<i>Larrea divaricata</i>		<i>Atriplex lampa</i>		<i>Stipa neaei</i>		<i>L. erianthus</i>	
		Viable	Damaged	Viable	Damaged	Viable	Damaged	Viable	Damaged
April	1	0	3.1 ± 1.7	0.5 ± 0.3	1.7 ± 0.7	0	0	0	0
	2	0	0.6 ± 0.3	0	1.4 ± 0.5	0.4 ± 0.2	0	0	0
	3	0.1 ± 0.1	2.1 ± 1.2	0.4 ± 0.2	4.9 ± 1.9	0.2 ± 0.2	0	0	0
	4	0.6 ± 0.2	0.7 ± 0.6	0.1 ± 0.1	1.4 ± 0.5	0.4 ± 0.3	0.2 ± 0.2	0.1 ± 0.1	0
August	1	0.5 ± 0.3	0	0.4 ± 0.3	6.2 ± 1.6	0	0	0	0
	2	0	2.7 ± 0.8	0	10.9 ± 1.7	0	0	0	0
	3	0.5 ± 0.3	1.6 ± 1.1	1.5 ± 1.3	11.1 ± 3.1	0	0	0	0
	4	0	0	0	0.1 ± 0.1	0	0	0	0
December	1	0.1 ± 0.1	0	0.1 ± 0.1	4.1 ± 2.5	0	0	0	0
	2	1.9 ± 0.8	6.6 ± 4.9	1.4 ± 0.6	6.0 ± 1.4	0	0	0	0
	3	0.2 ± 0.2	1.9 ± 1.3	0.5 ± 0.3	3.2 ± 0.4	0	0	0	0.1 ± 0.1
	4	0	0.4 ± 0.3	0	0.9 ± 0.2	0	0	0	0

Values are the mean of  $n = 8 \pm 1$  standard error.

**Table 2**

Numbers of viable or buried seeds per sampling volume (318 cm<sup>3</sup>) of the study shrub plus grass species at different sampling dates in all four microenvironments.

Seeds	Microenvironments	Dates		
		April	August	December
Viable	1	0.12 aa	0.22 aa	0.06 aa
	2	0.09 aa	0 ba	0.81 bb
	3	0.19 aa	0.50 aa	0.19 aa
	4	0.31 aa	0 ba	0 aa
Buried (viable + damaged)	1	1.34 aa	1.78 aba	1.09 aa
	2	0.59 aa	3.4 ba	3.97 bb
	3	1.94 aa	3.69 aa	1.50 aa
	4	0.91 aa	0.03 ba	0.31 aa

Values are the mean of  $n = 32$ . Within each seed condition (viable or buried) and sampling date, different letters within a column to the left of the comma indicate significant differences ( $p < 0.05$ ) among microenvironments, and those to the right of the comma indicate significant differences ( $p < 0.05$ ) among dates.

The greatest ( $p < 0.05$ ) numbers of viable and buried seeds were found on microenvironment 2 in December (Table 2). However, when referring to the date in a descriptive way, the greatest soil seed bank in the sampling volume was measured at different times during the year in the different species. The greatest soil seed bank was observed in August (89 seeds) in *L. divaricata*, in May (242 seeds) in *A. lampa*, in December (10 seeds) in *S. neaei*, and in August and December (2 seeds total) in *L. erianthus*. From a total of 8 samples in microenvironment 4, one for each vegetation patch, 1 seed of *A. lampa* was recognized in May, 7 seeds of *A. lampa* and 3 of *L. divaricata* were found in August, and in December there were 12 seeds of *A. lampa* and 11 seeds of *L. divaricata*.

The number of viable and buried seeds was greater ( $p < 0.05$ ) in the shrub than in the grass species (Table 3).

Each of the microenvironments was analyzed separately to study the spatial distribution of the soil seed bank. In *L. divaricata* + *A. lampa*, 0.78, 0.71, 0.42 and 0.11 viable seeds m<sup>-2</sup> were found in microenvironments 2, 3, 1 and 4, respectively. Adding seeds collected in the sampling volume for all 3 sampling dates, 890 seeds m<sup>-2</sup> were found under the shrub protection (microenvironment 2) and 269 seeds m<sup>-2</sup> in the bare interspaces among vegetation patches (microenvironment 4) for all species. This comes out to a three-fold difference in size between both soil seed banks. This information shows a clear tendency in the size of the soil seed

**Table 3**

Numbers of viable or buried (viable + damaged) seeds per sampling volume (318 cm<sup>3</sup>) of *L. divaricata*, *A. lampa*, *S. neaei* and *L. erianthus* at the vegetation patches in arid Patagonia.

	Viable	Buried
<i>L. divaricata</i>	0.33 a	1.99 a
<i>A. lampa</i>	0.41 a	4.74 a
<i>S. neaei</i>	0.08 b	0.10 b
<i>Leymus erianthus</i>	0.01 b	0.02 b

Each value is the mean of  $n = 96$ . Within each column, different letters indicate significant differences at  $p < 0.05$ .

bank among microenvironments in the study vegetation patches and surrounding vegetation bare interspaces. Regarding *S. neaei* + *L. erianthus*, 6 seeds were found in microenvironment 4, 3 seeds in each of the microenvironments 2 and 3, and no seeds were found in microenvironment 1.

### 3.2. Plant recruitment

Regarding the 0.04 m<sup>2</sup> plots, installed to determine plant recruitment from the soil seed bank in the various microenvironments, diverse results were obtained depending on the microenvironment in the vegetation patch. In December 2000, it was determined that

**Table 4**

Aboveground biomass (g dry matter 0.04 m<sup>-2</sup>) of *S. neaei* and *Poa lanuginosa* which grew into the 10 cm × 40 cm plots through vegetative reproduction (December 2000). Number of individuals of both species was not counted because of their rhizomatous growth habit.

	Microenvironment 1	Microenvironment 2	Microenvironment 3	Microenvironment 4
Exclosure on the New Road Harvested species: <i>S. neaei</i>	0.07 ± 0.07 a	0.76 ± 0.51 a	0 a	0 a
Exclosure on the Old Road Harvested species: <i>P. lanuginosa</i>	0.42 ± 0.31 a	2.29 ± 2.06 a	0.74 ± 0.28 a	0 a

Each value is the mean of  $n = 4 \pm 1$  standard error. Within a row, values followed by the same letter are not significantly different at  $p < 0.05$ .

**Table 5**  
Biomass (either plant<sup>-1</sup> or 0.04 m<sup>-2</sup>) and density of *Bromus tectorum* (October 2001) within the 0.10 m × 0.40 m plots located in the Old Road enclosures. Plants growing at the patch periphery and the interspaces among patches, with higher light availability, were in a more advanced phenological stage than those growing underneath the shrubs. There were no individuals of *B. tectorum* in the New Road enclosures.

	Microenvironment 1	Microenvironment 2	Microenvironment 3	Microenvironment 4
g dry matter plant <sup>-1</sup>	0.004 ± 0.002 a	0.004 ± 0.001 a	0.012 ± 0.002 a	0.033 ± 0.005 a
Number of plants 0.04 m <sup>-2</sup>	2.00 ± 1.15 c	21.75 ± 8.25 b	68.00 ± 8.83 a	7.50 ± 2.6 bc
g dry matter 0.04 m <sup>-2</sup>	0.015 ± 0.009 a	0.104 ± 0.038 ab	0.821 ± 0.192 c	0.231 ± 0.061 b

Each value is the mean of  $n = 4 \pm 1$  standard error. Within each row, values followed by different letters are statistically different at  $p < 0.05$ .

plots had been occupied by sprouts of *S. neaei* and *P. lanuginosa*, both with rhizomes, through asexual reproduction (Table 4). There was no vegetation coming from the soil seed bank. In the vegetation patches located beside the new road, the only species that came up, which was harvested, was *S. neaei*. Although the absolute amounts of shoot dry matter differed with microenvironment in the vegetation patch by a factor of at least 10 (Table 4), no significant differences ( $p > 0.05$ ) were found among them in this species. In the vegetation patches located over the old road, the harvested species was *P. lanuginosa*. Once again, the amount of shoot dry matter in the sampling area (0.04 m<sup>2</sup>) was >3 times greater in microenvironment 2 than in the other microenvironments; however, differences were not significant ( $p > 0.05$ ) among them (Table 4).

In October 2001, abundant presence of *B. tectorum* was observed in the plots located in the different microenvironments of the vegetation patches (Table 5). Plant weight was similar ( $p > 0.05$ ) in all microenvironments (Table 5). However, plant densities were greatest ( $p < 0.05$ ) at microenvironment 3, intermediate ( $p < 0.05$ ) at microenvironment 2, and lowest ( $p < 0.05$ ) at microenvironments 1 and 4 (Table 5). As a result, the greatest ( $p < 0.05$ ) dry matter production in *B. tectorum* in the sampling surface area used (0.04 m<sup>-2</sup>) was determined in microenvironment 3 (Table 5).

## 4. Discussion

### 4.1. Soil seed bank

As in most arid ecosystems, the frequency distribution of seeds in soil samples showed a leptokurtic form, since most samples had a few or no seeds and only a minor proportion had a large number of seeds. This general spatial pattern may be in part the result of the relatively short seed dispersal distances that characterize the majority of desert plants (Ellner and Shmida, 1981).

At any time during the sampling period, either in agreement with hypothesis (1) for the shrub species, or in disagreement with it for the perennial grasses, buried seeds were mostly present in the soil seed bank at all four microenvironments within any vegetation patch and its associated microenvironment. One factor which can affect the magnitude of the soil seed bank during the year is shrub and grass phenologies, which change during it (Giorgetti et al., 2000). González Arzak (1995), for example, compared phenological data with seed abundance in the soil bank. In our investigation, shrubs had seeds in the soil bank in various seasons during the year. The greatest soil seed bank in *L. divaricata* was observed in December. This is coincident with its phenology (González Arzak, 1995; Giorgetti et al., 2000). In December, *L. divaricata* plants exhibit flowers and fruits, and continue having fruits until July, time when its total dispersal is completed. *A. lampa* showed flowers and fruits in November, and residuals fruits on plants until August. This is why the greatest soil seed bank in *A. lampa* was in mid-winter. In contrast, annual seed both production and dispersal are much more constrained in time for the grass than for the study shrub species (Giorgetti et al., 2000). This helps to explain why shrubs are present in the soil seed bank during most of the year, while persistence of the perennial grass species in it is limited to specific months during

a 12-month-period. *S. neaei*, displayed the greatest soil seed bank in April, time when its remaining fruits came to an end. *L. erianthus* showed a reduced soil seed bank. This species exhibited seed dispersal in December. Additionally, continuous, selective foraging of grass seeds during the year by ants and rodents (Mayor et al., 2003) contribute to explain the absence of grass seeds in the soil seed bank during most part of the year. Our observations are in agreement with the great seasonal and annual variability in the soil seed banks which have been described for other desert and semi-desert regions (Coffin and Lauenroth, 1989; Kemp, 1989).

In agreement with hypothesis 1 for the shrub species, and to a lesser extent for the grass *S. neaei*, buried seeds were mostly present in the soil bank at all four microenvironments within any vegetation patch and its associated microenvironment. However, such hypothesis did not apply to the perennial grass *L. erianthus*. Accordingly, the soil seed bank of the steppe of *L. divaricata*, *A. lampa* and *Stipa* spp. was patchily distributed in agreement with the spatial pattern of the aboveground vegetation, a characteristic already observed in other desert ecosystems (Kemp, 1989; Kinucan and Smeins, 1992; Zammit and Zedler, 1994). In December 1999, both shrub species showed a leptokurtic distribution for the number of viable and damaged seeds in the soil bank from microenvironment 2 (where aboveground biomass of *L. divaricata* + *A. lampa* was the greatest = mean ± 1 S.E.; 816.6 ± 51.9 g m<sup>-2</sup>) to microenvironment 4 (where there was no aboveground biomass neither for the shrub nor the grass species). Nelson and Chew (1977) reported 13 times more seeds under the canopies of *Larrea* sp. and *Lycium* sp. than in the open spaces (interspaces among shrubs). Reichman (1984) reported 13,400 seeds m<sup>-2</sup> under the protection of *Larrea* sp. plants, and 5600 seeds m<sup>-2</sup> in the open spaces, i.e., a relationship of 2.4 to 1 between the seed banks at both microenvironments. These results are similar to those obtained in this investigation.

The greater patch aboveground biomass of the two major shrub species (*L. divaricata* + *A. lampa* = 816.6 ± 51.9 g m<sup>-2</sup>) compared to that of *S. neaei* + *L. erianthus* (24.9 ± 2.8 g m<sup>-2</sup>) contributes to explain the greater viable and buried soil seed banks in the shrub than in the grass species. *L. erianthus*, other than the aboveground biomass of *P. lanuginosa* (0.01 ± 0.01 g m<sup>-2</sup>), showed the lowest aboveground biomass (0.89 ± 0.89 g m<sup>-2</sup>) among all grass species in the vegetation patch and its associated vegetation bare interspace. This low aboveground plant biomass, and the fact that plants of *L. erianthus* showed almost no seed production (Bonvissuto and Busso, 2007a), help to explain the extremely low presence of viable and damage seeds in the soil bank for this grass species.

In microenvironment 2 (890 seeds m<sup>-2</sup>), under the protection of *L. divaricata* and *A. lampa*, three times more seeds were found than in the interspaces (269 seeds m<sup>-2</sup>) between vegetation patches for all study species and sampling dates. Seed banks in bare soil were smaller than those beneath the external crown of vegetation patches.

In microenvironment 4 (interspaces among vegetation patches), extremely small numbers of viable *L. divaricata* and *A. lampa* seeds were present in the soil seed bank. These results are similar to those of Bertiller (1998) who reported that seeds of long-lived shrubs were scarce and infrequent in the soil seed banks of a study site located 40 km west of Puerto Madryn, Argentina (42° 39' S, 65° 23' W,

115 m a.s.l.). She reported that the larger seeds of long-lived perennials were more likely to be predated than the smaller seeds of annual dicots. This, and the low seed both production and retention in the study shrub species (Giorgetti et al., 2000) might be some of the causes to explain their small numbers in the soil seed bank at the bare interspaces (see also Kemp, 1989; Chambers, 1993). After seeding *L. divaricata*, no germination occurred in microenvironment 4 in any of the 8 study vegetation patches. In *A. lampa*, only 1 seed germinated, which did not survive, out of 128 seeds broadcasted in that microenvironment (Bonvissuto, 2006). Soil temperatures at this time in the interspaces among vegetation patches (microenvironment 4) used to reach 50 °C at 5 cm depth during summer (Bonvissuto, 2006). Also, soil moisture contents at this microenvironment were about 1% at 5 cm depth [ $5.5 \pm 0.2\%$  was the soil moisture retained at 5 cm depth at  $-1.5$  MPa ( $n = 16$ )]. These extreme soil temperatures and moisture contents must have inhibited seed germination, and seedling establishment of germinated seeds, in microenvironment 4 (Bonvissuto and Busso, 2007b). Gashaw and Michelsen (2002) reported that heating seeds of the grasses *Sorghum arundinaceum* (Desv.) Stapf and *Hyparrhenia confinis* (A. Rich.) Stapf var. *nudiglumis* (Hackl.) W.D.Clayton at 60 °C during 1 min significantly reduced germination of these species. Given the very small number of viable seeds in the soil seed bank of *L. divaricata* and *A. lampa* (this study), seedling survival of these species in the interspaces is highly unlikely as a result of the high soil summer temperatures under rainfed conditions (long-term annual precipitation = 137 mm). A related species, *Larrea tridentata* (Sessé & Moc. ex DC.) Coville, is one of the most stable members of desert communities, but because of their clonal growth habit (McAuliffe et al., 2007).

In the other microenvironments (1–3), the soil seed bank of the woody species was more abundant than that in microenvironment 4. In a parallel field study, it was observed that shrub germination in microenvironments 1–3 from sown seeds was greater than that in microenvironment 4; however, only 1 juvenile of *A. lampa* survived in microenvironment 1 (Bonvissuto, 2006). These data and those of the viable soil seed banks of *L. divaricata* and *A. lampa* at microenvironments 1–3 suggest that plant establishment of these species from the soil seed bank is also unlikely at these microenvironments. This conclusion is similar to that of Bouza and del Valle (1993) in patches of bare soil due to their low roughness. Plant establishment of these shrub species at the study site might be episodic, and limited to years of adequate soil temperatures and abundant, above-average precipitation (Bonvissuto, 2006). Peláez et al. (1996) also reported that establishment of the shrub *Condalia mycophylla* Cav. was most likely limited to a rare sequence of years of adequate soil temperatures and plenty rainfall in rangelands of central Argentina.

The small abundance of perennial grasses in the soil seed bank is due to, at least in part, the poor rangeland condition and heavy use of these rangelands by livestock (Bonvissuto et al., 2001). Grasses are found overgrazed and their density is often low (Bonvissuto et al., 2001, 2008). Smith et al. (2000) showed that *Bouteloua curtipendula* cv. *caespitosa* populations showed reduced seed production after grazing. This was attributed, at least partially, to a lower (1) tiller and inflorescence numbers per plant, (2) spikelets per inflorescence, and (3) seed production per spikelet. All this may lead to a reduced potential colonization by grass seedlings. Additionally, grass seeds can also be predated by ants and rodents (Mayor et al., 2003).

Between 50 and 80% of the perennial grass seeds were found entire. After dispersal, Blate et al. (1998) and Kollmann et al. (1998) are of the opinion that large seeds (i.e., *Larrea* spp. and *Atriplex* spp., if they are considered with their involucre) may have a smaller survival than small seeds (i.e., *Stipa* spp.). Large seeds may be more easily found by predators, and can remain on the soil surface longer

because it is more difficult for them to become incorporated into the soil profile (Moles et al., 2003). In addition, it is possible that *Stipa* spp. have a smaller proportion of their seeds damaged because of anatomical characteristics; the caryopsis of *Stipa* spp. is surrounded by a convoluted, fusiform, coriaceous lemma at maturity (Correa, 1978). In addition, *Stipa* spp. have self-burial mechanisms (hygroscopic awns) (Fitter and Hay, 1983) which assist seed incorporation into the soil; this in turn reduces the likelihood for soil surface seed predation. Spatial patterns of vegetation may have, in consequence, a direct effect on the dynamics, conservation and sustainable management of the steppe of *L. divaricata* and *Stipa* spp. The reduced seed bank of perennial dicots, mostly represented by non-palatable, long-lived shrubs, does not seem to be critical in maintaining their cover in the short term. This is because the density of standing individuals does not depend on a successful annual seed production, germination and seedling establishment. Established shrubs have a minimal dependency from the soil seed bank for its generation and protection against climate change (Kemp, 1989). Their strategy consists in producing a few seeds almost every year. Most of them do not persist in the seed bank (Boyd and Brum, 1983), probably because of animal predation (rodents, ants and fungi) (Marone et al., 1998) or due to they are short lived (Kemp, 1989). When conditions are favourable for shrub establishment, the seed source will be that of the previous reproductive season. Perennial desert plants are protected against climate change because of a long life rather than a soil seed bank (Beatley, 1980). Additionally, recruitment in this group is probably more limited by the availability of safe sites (Andersen, 1989), which are expected to increase by the death of adult plants.

#### 4.2. Plant recruitment

There were shrub and some grass seeds in the soil bank at all four microenvironments in the vegetations patches. This was partially because shrub and grass seed rains reach these microenvironments (Bonvissuto and Busso, 2007a). However, plant recruitment from the soil seed bank was not shown for *L. divaricata*, *A. lampa* and *L. erianthus*, in disagreement with hypothesis 2. In agreement with this hypothesis, however, recruitment from the soil seed bank was measured for *S. neaei*, *P. lanuginosa* and *B. tectorum*. Although differences were not significant ( $p > 0.25$ ), biomasses of *S. neaei* and *P. lanuginosa* (both rhizomatous perennial grasses) tended to be the greatest in microenvironment 2 than in any other microenvironment. Both species did not produce biomass in microenvironment 4. Lack of emergence and subsequent shrub and grass seedling establishment in the interspaces was partially due to high soil temperature amplitudes and desiccating wind effects during the day at this location, and the very scarce precipitation in the study region (Bonvissuto, 2006). Even though, plant recruitment of perennial grass species is often low in arid regions and it may occur (as a rare event) in years when moisture and temperature conditions are favourable (Wilson and Briske, 1979; Pyke, 1990). Sexual reproduction and subsequent plant recruitment are necessary for maintenance of genetic diversity and population regeneration, after large-scale disturbances produce high plant mortality (O'Connor, 1991).

In this environment, the unique annual invader, exotic grass (Milby and Johnson, 1987) which grew in all study microenvironments was *B. tectorum*. There can be high variations among years in the dry matter production of this species because of differences in the time and quantity of fallen rainfall (Young et al., 1999). In years of poor conditions for growth, production is much less in annual than perennial grasses, while the reverse is true in years of good growth conditions (Young et al., 1987). In our study, precipitations were 221.3 mm in 2000, when *S. neaei* and *P. lanuginosa* were harvested in the plots. In 2001, when *B. tectorum* was harvested at all microenvironments, precipitation was 253.6 mm, and in 2002,

when precipitation was only 141.5 mm, no plants of *B. tectorum* were recruited.

The abundance of *B. tectorum* varied with microenvironments. Microenvironment 3 was the most abundantly colonized, followed by microenvironments 4, 2 and 1, respectively. Although weight of individual plants was similar in all microenvironments, plant density was the highest and lowest in microenvironments 3 and 1, respectively. Schenk et al. (2003) found that the density of annual species was significantly greater at the periphery of the subshrub canopies (i.e., *Ambrosia*) than in the open spaces (interspaces). *B. tectorum* rapidly develops a large root system, through an early elongation of its roots and the branching of its adventitious roots (Aguirre and Johnson, 1991). The dense, shallow root system of *B. tectorum* seedlings enables them to produce a rapid water and nutrient uptake from the soil, hindering the growth of perennial grass seedlings (Robertson and Pearse, 1945; Aguirre and Johnson, 1991). It is thus necessary to control annual grasses to achieve recruitment of perennial grasses from the soil seed bank (Young et al., 1987). This could help explain, at least in part, the lack of perennial grass seedling recruitment in the permanent plots during 2001. Although perennial grasses can extract water from deeper soil layers, seedlings may not reach enough depth before arrival of the summer drought, dying thus as a result of water stress.

#### 4.3. Management implications

What measures could be taken to foster vegetation establishment in the nude interspaces? It is evident that there is urgent need for land reclamation and range improvement in the eroded, nude areas. This has also been a concern in other rangelands of the world. For example, the Soil Conservation Service in Iceland, has been concerned primarily with protection and reclamation of denuded range areas (Thorsteinsson et al., 1971). In these areas, for example, they have re-seeded grasses for haymaking and grazing. They have also worked with livestock management. Different means for improving livestock distribution, such as increased fencing, salt distribution on the range, herding, etc. are being used in some areas. This livestock management approach should also be taken in the MAN to avoid further degradation of the ecological system.

Rupture of the superficial soil layers in the inter-patch spaces together with seeding of shrub species like *L. divaricata* and *A. lampa* could also be beneficial for vegetating interspaces in years with above-average precipitation. It is recommended to wash the seeds of *A. lampa* before seeding because of the presence of chemical inhibitors in their bracts (Bustos, unpublished data, EEA INTA Bariloche, Argentina). Germination of *L. tridentata* is also related to precipitation since a minimum of at least 25 mm appeared necessary to induce its germination (Marshall, 1995). Raven et al. (1986) also suggest that some seeds will not germinate after having some abrasion treatment such as that provided from the soil. Scarification of *L. divaricata* seeds is recommended before conducting germination trials with this species (Zappe, personal communication, EEA INTA Bariloche, Argentina). When seed germination of *L. divaricata* was evaluated under controlled moisture and temperature, and its seeds were scarified, germination percentages of up to 25% were obtained (Bonvissuto and Busso, 2007b). Norton and Bermant (1977) have demonstrated that *L. divaricata* seeds occasionally germinate in infertile, nude vegetation interspaces.

Overgrazing by cattle in certain arid and semiarid landscapes has resulted in severe soil compaction, and manipulations such as heavy discing are required to promote water infiltration and re-establishment of herbaceous vegetation in the interspaces among vegetation patches (Fulbright, 1991).

We compared the size and spatial and temporal patterns of the germinable soil seed bank of the two dominant shrubs and perennial grass species in the Monte Austral of arid Patagonia, Argentina.

These species differ in plant functional traits (Bonvissuto, 2006), seed morphology (Bonvissuto and Busso, 2007a) and preference to grazers (Cano, 1988). During two consecutive years, we sampled at different times during each season the soil seed bank at four microsites within and between (i.e., nude interspaces) vegetation patches, the spatial vegetation distribution model in the Monte Austral. Studies were conducted at two sites with similar grazing history. Plant recruitment from the soil seed bank was also investigated for the study shrub and grass species. Results indicated that despite the presence of shrub, but not native grass, seeds in the soil bank at all four microenvironments, no natural, field recruitment was determined from that soil bank for all the study native species. Several management alternatives were discussed to vegetate the nude interspaces. Plant recruitment occurred from asexual reproduction for the native, rhizomatous perennial grasses *S. neaei* and *P. ligularis* in all but the nude interspace microenvironments. The exotic, annual grass *B. tectorum* was, and most likely will be, the most abundant at all microenvironments in years of above average, long-term annual precipitation. The size and the spatial and temporal patterns of the germinable soil seed bank of the dominant perennial shrub and grass species in the arid Monte Austral were related not only to seed and plant traits but also to plant phenology, the spatial distribution of shrub and grass plants and their exposure to grazers.

This paper demonstrated that the small magnitude of the viable shrub soil seed bank, and both the high and low soil summer temperatures (50 °C) and moisture contents [1% out of the  $5.5 \pm 0.2\%$  ( $n = 16$ ) retained at  $-1.5$  MPa] at 5 cm depth, respectively (Bonvissuto, 2006), inhibited shrub seedling establishment in the bare interspaces among vegetation patches in an arid zone of Argentina. Since this is a critical step to allow new path formation, some corrective measurements were suggested to permit vegetation restoration in the degraded, open interspaces.

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