

SEEDLING RECRUITMENT AND SURVIVAL OF TWO DESERT GRASSES IN THE MONTE OF ARGENTINA

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ABSTRACT

In the Monte Austral Neuquino, Argentina, vegetation is arranged in patches. Understanding the mechanisms involved in their distribution is critical for preventing desertification. The working hypothesis was that vegetation patches reduce environmental stress on the plants. Plant patches were classified into four microenvironments: windward; below the dominant shrubs (subcanopy); vegetation at the patch periphery (canopy edge) and bare patch interspaces (open). We determined seedling survival of the dominant species in each microenvironment, using a marking method of seedlings established from sown seeds. In addition, we measured the environmental characteristics in the four microenvironments, and associated them with seedling survival. Study species were the perennial grasses *Leymus erianthus* (Phil.) Dubcovsky, *Stipa neaei* Nees ex Steudel and *Poa ligularis* Nees ex Steudel, and the shrubs *Larrea divaricata* Cav. and *Atriplex lampa* Gill ex Moquin. Results supported the hypothesis only for *L. erianthus* and *S. neaei* (but not for the other three species that showed higher seedling survival in the subcanopy than in the patch interspaces after 1 year from sowing). This study determined that (1) reduced environmental stress does not guarantee seed germination and seedling survival of a given species in the plant community and (2) seedling establishment will not be possible for any species of the plant community in the patch interspaces under the study conditions in the region. This is mostly because soil temperatures can reach up to 50°C in the patch interspaces in years of scanty precipitation during late spring and summer. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS: seeding efficiency; shrubs; soil physicochemical characteristics; temperate rangelands; vegetation patches; Argentina

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 (Erickson *et al.*, 2005). Knowledge of ecological processes influencing these vegetation patches and their associated patch interspaces is essential, since similar systems cover nearly 30 per cent of the Earth's land surface (FAO, 2005). Plant patches modify the local microenvironment and resource availability. The soils beneath plant canopies accumulate biomass, organic matter and nutrients (N, P, K); have a greater decomposer activity and the majority of seeds either settles in the neighbourhood of the mother plants or is re-deposited by winds (Aguilera *et al.*, 1999). Also, seed germination and seedling establishment may be greater under the protection of shrubs because of more favourable soil temperatures, and soil physical and chemical conditions (Fulbright *et al.*, 1995). Variations in microenvironment characteristics are caused by

differences in plant cover, litter quantity, microhabitat and soil structure among others (Harper, 1977). In bare areas among vegetation patches, superficial erosion occurs (Rostagno, 1989). Bare spaces among dominant shrubs are more sensitive than vegetated patches to degradation (Beskow *et al.*, 1987). Probability of seedling establishment in the patch interspaces is predicted to be low (Defossé *et al.*, 1997).

In the Monte Austral of the Neuquén Province, Argentina, vegetation is arranged in patches, leaving bare, eroded areas among them. This area evolved with few native herbivores, which exerted a very low pressure on native vegetation (Soriano, 1983). Since the introduction of sheep around the final decades of the 1800s, these ecosystems have been subjected to disturbances caused mainly by sheep grazing (Soriano, 1983). The effects of continued grazing and trampling have resulted in substantial changes in the structure of pristine Patagonian vegetation (Ares *et al.*, 1990). In many areas, grazing has reduced the vegetation cover and facilitated the development of bare soil patches where wind and water remove litter, plant disseminules and in some instances the upper soil layer (Ares *et al.*, 1990). This is similar to that reported by Eckert *et al.* (1986) in the US Great Basin, who found four soil-surface types on

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sampling sites in northern Nevada. Patchiness in their systems, like in ours, appeared to be the result of rangeland degradation.

Characteristics of soil surface microenvironments in our study region appear to perpetuate the existence of shrubs, *Bromus tectorum* L. and annual herbs (see Eckert *et al.*, 1978). In the vegetation patches, two shrubs (*Atriplex lampa* Gill. ex Moquin and *Larrea divaricata* Cav.) and three perennial grass species [*Leymus erianthus* (Phil.) Dubcovsky (syn.: *Elymus erianthus* Philippi); *Stipa neaei* Nees ex Steudel and *Poa ligularis* Nees ap. Steudel] are dominant.

In the present study, two predictions were derived from the hypothesis that vegetation patches reduce environmental stress: (1) microenvironmental characteristics under the vegetation patches are different from those in the interspaces among plant patches and (2) seedling establishment is higher under the vegetation patches than in the patch interspaces among them. Objectives of this study were as follows: (1) to compare the microenvironmental soil and wind characteristics in and between vegetation patches and (2) to evaluate seed germination and seedling establishment of the two dominant shrub (*L. tridentata* and *A. lampa*), and three dominant perennial grass species (*L. erianthus*, *S. neaei* and *P. ligularis*), in these plant patches. In addition to demonstrate that plant patches reduce environmental stress on *L. erianthus* and *S. neaei*, this work determined that (1) such reduced stress does not guarantee successful seed germination and subsequent seedling establishment of a given species in the plant community. This is because three out of the five species were unsuccessful in establishing seedlings in the study vegetation patches; and (2) seedling establishment of all investigated species will always be possible in the patch interspaces under the study environmental conditions in the region. This is the result of the extreme high temperatures (up to 50°C) that can be reached in those microenvironments during the summer, partially a result of the very scarce precipitations in that period (which is often the case).

MATERIALS AND METHODS

Study Area

Two sites, where the most typical vegetation patch was represented (see Figure 1), were used for this study in Picún Leufú districts (39°30'S, 69°09'W, 383 m a.s.l.; Monte Austral of the Neuquén Province, Argentina). Precipitation during the study years (1999 and 2000) tended to be higher than the long-term average precipitation (Figure 2).

Two sites were used to determine if plant patch structure was either similar or different between them. Busso and Bonvissuto (2009b) reported that plant community structure was similar among these two sites, using transects within a

15 × 15 km study area. Structural characteristics of vegetation patches were also similar at a plant patch scale (Table I). This allowed pooling of the data obtained at a plant patch scale from both sites. They were 1.5 km apart from each other, and have similar physicochemical soil properties at a plant patch scale (all microsites combined: Table II). A preliminary study demonstrated that vegetation patches in the study region had a greatest and smallest diameter of 3.15 ± 0.25 m and 2.07 ± 0.16 m, respectively (Busso and Bonvissuto, 2009b).

Four representative, similar diameter vegetation patches (see Busso and Bonvissuto, 2009b) were excluded from domestic herbivory using iron fences (made of 10 × 10 cm quadrates) at each site (grazing exclosures) from early-March 1999 to late-May 2000. These patches included the kinds of edaphic stability described by Bouza (1995).

Sampling

Litter and stone cover in the patch interspaces

They were determined using four 0.20 × 0.50 m quadrats at each study site.

Microclimatic Conditions

Determinations of soil temperature and wind speed were made at dawn and mid-afternoon every 15 days during 15 months (from early-March 1999 to late-May 2000): (a) soil temperature at 2 cm depth using thermocouples ($n = 8$) for each microenvironment connected to an HR 33T micro-voltmeter[®] (Wescor Inc.), and (b) wind speed ($n = 100$) within each site (behind the shrub protection in the patch, in the patch interspaces at the soil surface level or at 1.5 m height from the soil surface) and sampling date using a portable anemometer. Gravimetric soil moisture content ($n = 100$) was determined up to 5 cm depth.

Daily soil temperature amplitudes were calculated for each microenvironment on each patch as the difference between the daily soil minimum and maximum temperatures. Data were grouped for two periods within the year: April–September (cold period) and September–March (warm period). For each of these periods, values from the four microenvironments were compared, and it was established on a daily basis which microenvironments had either the soil minimum or maximum temperature amplitude. Relative frequencies were calculated as follows:

$$\frac{\#T}{Nd} \times 100$$

where #*T* is the number of times a given microenvironment showed either the minimum or maximum temperature amplitude, and *Nd* is the time interval (days) within the study period. When more than one microenvironment had either the minimum or maximum temperature at any date, all

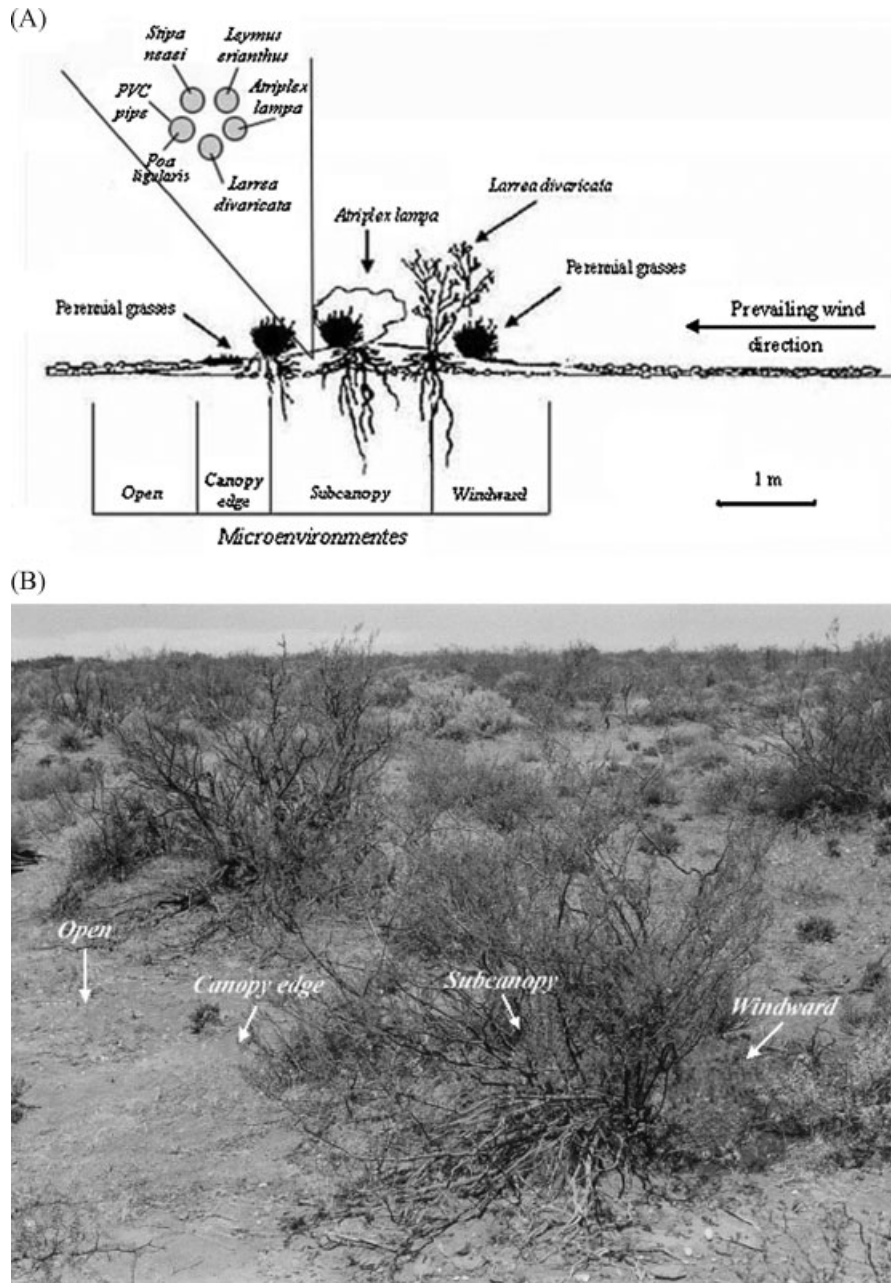


Figure 1. (A) Diagram of a vegetation patch showing the four study microenvironments (windward, subcanopy, canopy edge, open). Microplots where seeding of each species was conducted are shown in the inset for the microenvironment 'subcanopy'; (B) Microenvironments within each vegetation patch: windward, subcanopy, canopy edge and open. Infiltrimeters are shown in white above the name of each microenvironment.

of them were counted. These calculations were made separately for either the cold or warm period.

Physicochemical Attributes

At each of the two study sites, a plant patch was selected. Size, shape and floristic composition of these plant patches were representative of those most common in the region (Busso and Bonvissuto, 2009b). The soil profile up to 70 cm

soil depth was described throughout the greatest diameter of a representative plant patch at both sites. Grant constraints precluded us from increasing the number of plant patches used to determine soil profile characteristics at both sites. The following determinations were included in the soil profile description: pH (SSSA, 1996), electrical conductivity (evaluated using a conductimeter Schott Gerate[®]), organic matter (Walkley and Black, 1934), total nitrogen (Carter,

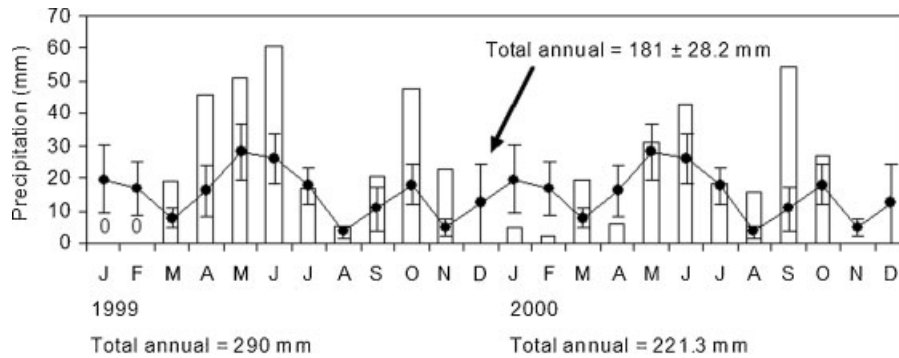


Figure 2. Precipitation during the study years (1999 and 2000), and long-term precipitation (8-year-mean \pm 1 E.E.) at the study site. There was no precipitation in November and December in 2000.

1993), C/N ratio [organic carbon was determined using an automatic C analyser (LECO, model CR-12) by dry combustion (Gasparoni, 2008)], exchangeable sodium percentage (USDA, 1954) and texture (INTA EEA Pergamino, 1998) (Table II).

In addition, physicochemical soil characteristics up to 5 cm depth were determined only in the most contrasting microenvironments: underneath the shrubs and in the interspaces among patches; grant constraints precluded us from determining soil analysis in all four study microenvironments. With that purpose, 10 vegetation patches were sampled (five at one site and five at the other, distant site). Results from both sites were pooled ($n = 10$) since they did not show to be significantly different ($p > 0.05$; Tables I and II). Extractable K and soluble P in sodium bicarbonate were determined following Carter (1993) and Olsen and Sommers (1982), respectively. Soil bulk density was determined using the cylinder method (INTA EEA Pergamino, 1998) within the first 5 cm soil depth in the four microenvironments within each of six vegetation patches.

Seed Germination and Seedling Survival

In each of the two sites, vegetation patches were used to determine percentage germination and seedling establishment after seeding the study species under rainfed conditions. Seeds of *L. divaricata*, *A. lampa*, *S. neaei*, *L. erianthus* and *P. ligularis* were randomly collected at the respective site from 50 plants of each species. Seeded seeds of each species were randomly chosen from that pool.

Abiotic variables mentioned above were measured simultaneously in those plant patches. Within each plant patch, four places (microenvironments) were chosen for study: (1) windward, (2) right below the shrubs (subcanopy), (3) at the vegetation patch periphery (canopy edge) and (4) in the patch interspaces (open) (Figure 1). Since we did not find significant differences in various soil parameters and vegetation structural characteristics at a patch scale between

the two sites (Tables I and II; Busso and Bonvissuto, 2009b), we pooled the data collected from both of them. Thus, the total observation places were 32 (2 sites \times 4 patches/site \times 4 microenvironments/patch). The species most characteristic in the study community were the shrubs *L. divaricata* and *A. lampa*, and the perennial grasses *S. neaei*, *L. erianthus* and *P. ligularis* (Bonvissuto *et al.*, 2001).

Previous to seeding, average seed weights were determined for each species. Five subsamples of 100 seeds each were weighed using a precision Mettler scale (model H10w). Mean weights (g) \pm 1 S.E. of 100 seeds were as follows: 0.55 ± 0.003 in *L. divaricata* (seeds included its hairy involucre), 0.37 ± 0.001 in *A. lampa* (seeds included bracts), 0.20 ± 0.001 in *S. neaei* (awns, but no glumes, were separated from anthesis), 0.64 ± 0.001 in *L. erianthus* (seeds were separated from their spikelets) and 0.04 ± 0.0001 in *P. ligularis* (seeds received no treatment). Seeds were placed in polyethylene gauze, buried at 0.5 cm soil depth and then covered with the same soil at the study site until seeding time. From dispersal (spring–summer: September to March) to germination (fall: April to June) time, they were thus exposed to a similar environmental stress than naturally dispersed seeds. However, germination and seedling establishment after seeding at the field occurred mainly for *L. erianthus* and *S. neaei*. This is why we focused on these two species; however, results are presented for all five plant study species. Before seeding at the field, growth chambers were used to determine germination percentages in all study species under various temperature and water availability conditions (Bonvissuto and Busso, 2007a).

In each vegetation patch, field seeding was conducted using microplots in the different microenvironments during early March 1999 (Figure 1). We acknowledge that this methodology of sowing departs from natural conditions in arid regions, where seeds are subjected to strong limitations to successfully establish a seedling due to, for example, physical soil crusts. It allowed us, however, to have a control on the (1) number of replicates in the study microenviron-

Table 1. Physicochemical soil properties at both study sites (S1, S2) at a plant patch scale. Values are the mean \pm 1 E.E. of $n = 2$; lack of dispersion measures indicate that they come from $n = 1$. Values to the left of the hyphen correspond to site 1 (S1) and those to the right of it correspond to site 2 (S2).

Horizon	Soil depth (cm)	pH	EC ^a (m Ω^{-1} cm ⁻¹)	Ω^b (per cent)	N (per cent)	C/N	ES ^c (per cent)	Texture coarse/fine fractions (per cent)
	S1-S2	S1-S2	S1-S2	S1-S2	S1-S2	S1-S2	S1-S2	Both sites
Eolian accumulation	4-10	7.8 ^d -7.7	0.30 \pm 0.10-0.25 \pm 0.05	1.0-1.2	0.05-0.06	14-11.5 \pm 0.5	3-3	82 \pm 2.5/18 \pm 2.5
A ₁ /AC	25-30	8.3-8.9		0.8-1.0			e _e	
Calcic	30-35	7.5-7.8	4.1 ^e				e _e	
Consolidated material	35-70						44-39	

^aElectric conductivity.

^bOrganic matter.

^cExchangeable sodium.

^dEach value comes from a pooled soil sample at a plant patch scale. This pooled sample of the soil profile up to 70 cm depth was taken from one plant patch at each of two sites.

^eNot determined.

ments and (2) competitive background for the study seeds. Microplots were established using PVC pipes (11 cm diameter, 3 cm height), which were placed at the soil surface (see insert in Figure 1). Empty PVC pipes were completely filled with soil obtained at the field study site. This soil was first treated by soil steaming (120°C during 15 min.). In each of five microplots per microenvironment (one per each of five species: *E. erianthus*; *S. neaei*, *P. ligularis*, *L. divaricata* and *A. lampa*), 16 seeds were individually seeded in a matrix of 4 \times 4 seeds. Thus, there was a total of 160 microplots (5 microplots/microenvironment \times 4 microenvironments/vegetation patch \times 4 vegetation patches/site \times 2 sites). Percentage germination and seedling survival were determined every 15 days during 436 days (i.e. the number of surviving seedlings were counted at each sampling time). Other studies on shoot, and root growth and development of seedlings in perennial grass species have also been conducted using soil treated by steam sterilization (Johnson and Aguirre, 1991).

Emergence and seedling establishment were followed from seeding time (March 1999) until early-June 2000, when harvest of surviving plants was conducted. Three indexes were calculated: (1) germination index: amount of germinated seeds/amount of seeded seeds, (2) survival of emerged plumules: amount of surviving juveniles/amount of germinated seeds and (3) survival efficiency: surviving juvenile amount/amount of seeded seeds. Juvenile height was measured from the soil surface to the most distal portion of the longest leaf while holding the leaf straight and in a vertical position (Busso and Richards, 1995). Afterwards, juveniles were harvested, oven-dried at 60°C until constant weight and weighed.

Statistical Analysis

A split-plot design for analysis of variance was conducted for the following variables: (a) soil physicochemical parameters for microenvironments 2 and 4 of the vegetation patches, (b) for each sampling date, morning and afternoon soil temperatures, and gravimetric soil moisture content in the four studied microenvironments. Germination indexes, survival of emerged plumules and survival efficiency data were analysed following a block design where blocks were the plant patches, and treatments were the microenvironments. As a result of the large number of zeros in the data set, survival of both emerged plumules and efficiency data were transformed to $\sqrt{x + 0.5}$ (Sokal and Rohlf, 1984) before statistical analysis. Data of information on seed germination and seedling survival through time were analysed using repeated measures analysis of variance (ANOVA) using a block design (vegetation patches), where the factor (treatments) were the microenvironments. When we treated sampling date as a repeated measure, the interaction of time of measurement with the four microenvironments was found

Table II. Analysis of variance comparing various structural plant parameters at a patch scale from two research sites distant 1.5 km one from another.

Parameter	Source of variation	Sum of squares	d.f.	F value	p
Biomass ^a (g/patch)	Between groups	98203.89	1	0.03035	0.8642 ns ^b
	Error	45304637.57	14		
	Total	45402841.46	15		
Greatest patch diameter ^a (m)	Between groups	0.17015625	1	0.72496	0.4088 ns
	Error	3.2859375	14		
	Total	3.45609375	15		
Smallest patch diameter ^a (m)	Between groups	0.34515625	1	2.88327	0.1116 ns
	Error	1.6759375	14		
	Total	2.02109375	15		
Patch surface area (m ²)	Between groups	0.09	1	0.05366	0.8202 ns
	Error	23.4812	14		
	Total	23.5712	15		
Biomass ^a (gm ⁻²)	Between groups	26132.33903	1	0.29307	0.5968 ns
	Error	1248365.07	14		
	Total	1274497.409	15		
Species diversity ^a	Between groups	0.006476628	1	0.02969	0.8656 ns
	Error	3.053691732	14		
	Total	3.06016836	15		

Values coming from eight vegetation patches (four patches from each site) were compared.

^aBusso and Bonvissuto (2009b).

^bns: not significant at $p < 0.05$.

to be significant ($p < 0.05$). Consequently, we examined seedling survival for each time interval separately with a randomized complete block design. Site was not considered as factor in the analysis after sites were similar (Tables I and II); this is why the data analysis was conducted using eight vegetation patches (four from each site). Data on plant height and dry weight of the survivors at the end of the study were analysed using ONEWAY ANOVA after data transformation to $\sqrt{x + 0.5}$ (Sokal and Rohlf, 1984). After testing for homocedasticity and normality of variances, data analysis was performed using INFostat (2008). A multivariate analysis was not used because it was not our goal. Our objective was to analyse species separately, and not a linear combination among them.

RESULTS

Soil Profile Description

Physicochemical soil characteristics appeared similar at both study sites (Table I).

Litter and Stone Cover in the Patch Interspaces

Litter (7.2 ± 1.9 per cent, site 1; 7.0 ± 2.7 per cent, site 2) and stone cover (48 ± 9.4 per cent, site 1; 52.5 ± 8.5 per cent, site 2) were similar ($p > 0.05$) at both study sites. Thereafter, values coming from both of them were pooled. Cover (mean ± 1 s.e., $n = 8$) of litter was 7.1 ± 1.5 per cent, and that of stone was 50.3 ± 5.9 per cent.

Microclimatic Conditions

Soil temperature and temperature amplitude

During the cold season (April–September 1999), morning temperatures were similar ($p > 0.05$) 50 per cent of the times in the four microenvironments (Figure 3). Between November and June of the following year, however, these temperatures were on average 2°C greater ($p < 0.05$) below the shrubs than in the patch interspaces in eight out of 12 measurements. During the afternoon, soil temperatures were greater ($p < 0.05$) in the patch interspaces than under the shrubs in 20 out of 28 measurements between March 1999 and June 2000 (Figure 3); in some cases, these temperature differences between these two microenvironments reached 12°C.

Morning temperatures were quite similar among microenvironments when this variable was averaged for 27 sampling dates from March 1999 to June 2000 (Table III). During the afternoon, soil temperatures averaged for 28 sampling dates were at least 5°C greater windward and in the open than in the patch interspaces (Table III). Data variance for monthly average soil afternoon temperatures increased substantially from the subcanopy to the open indicating that greater temperature changes took place in the open (Table III). Variances for monthly average soil temperature data were high, specially those for afternoon temperatures (Table III). This is the result of averaging temperatures throughout various months (from fall 1999 to winter 2000), which showed monthly average soil temperatures between (1) 0.63 (subcanopy and canopy edge by late-autumn/fall

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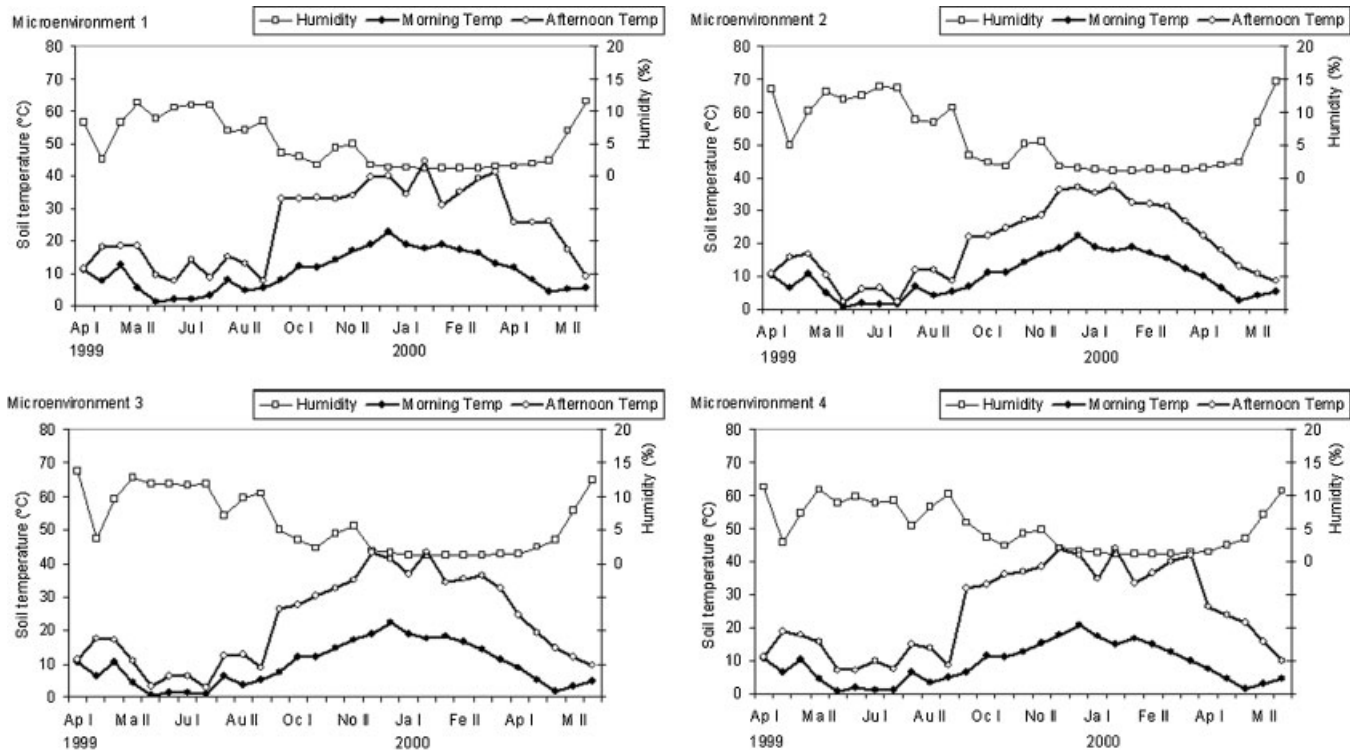


Figure 3. Monthly average soil temperatures ($^{\circ}\text{C}$, $n = 8$) at 2 cm soil depth during the morning (open symbols) and the afternoon (closed symbols), and gravimetric soil moisture content up to 5 cm soil depth (per cent, $n = 8$) for each study microsite, from March 1999 to June 2000.

1999) to 22.50°C (windward and subcanopy by early summer 1999) for morning temperatures and (2) 2.15 (subcanopy by mid-winter 1999) to 44.56°C (windward by mid-summer 2000) for afternoon temperatures.

During April–September and September–March, the maximum temperature amplitudes were in general greater in the patch interspaces (microenvironment 4) than in the subcanopy (microenvironment 2) (Figure 4). Minimum temperature amplitudes were greater in the subcanopy than in the patch interspaces (Figure 4).

Gravimetric soil moisture content

After monthly average soil moisture content data were averaged from fall 1999 to winter 2000, greatest and lowest

values were found at the subcanopy, and windward and open, respectively (Table III); it is noticeable that variances were high (Table III). This was again the result of averaging months with very different monthly average soil moisture contents. These ranged from 0.8 (windward, canopy edge, open; late summer 1999) to 14.6 per cent (subcanopy; late fall 2000).

From 3 March (late summer) to 9 April (early fall) 1999, and from 8 September (late winter) 1999 to 5 May (mid-fall) 2000, all microenvironments showed a similar ($p > 0.05$) monthly average soil moisture content [range = 0.8 ± 0.1 (windward, canopy edge, open)– 13 ± 0.6 per cent (canopy edge; see Figure 3)].

However, monthly average soil moisture contents were greater ($p < 0.05$) at the subcanopy than in the patch

Table III. Soil moisture, and morning and afternoon temperatures at each of the study microsites. Each value is the average ± 1 E.E.; variance of the corresponding parameter from samplings made every 15 days from March 1999 to June 2000.

Soil	Microenvironment			
	Windward	Subcanopy	Canopy edge	Open
Moisture (per cent)	4.97 \pm 0.73; 15.04	6.09 \pm 0.97; 26.32	5.90 \pm 0.88; 21.90	5.10 \pm 0.70; 13.83
Morning Temperature ($^{\circ}\text{C}$)	10.65 \pm 1.20; 38.84	10.04 \pm 1.24; 41.29	9.92 \pm 1.26; 42.86	9.14 \pm 1.14; 34.97
Afternoon Temperature ($^{\circ}\text{C}$)	24.97 \pm 2.36; 150.92	19.91 \pm 2.18; 128.57	22.58 \pm 2.54; 174.74	25.33 \pm 2.59; 180.56

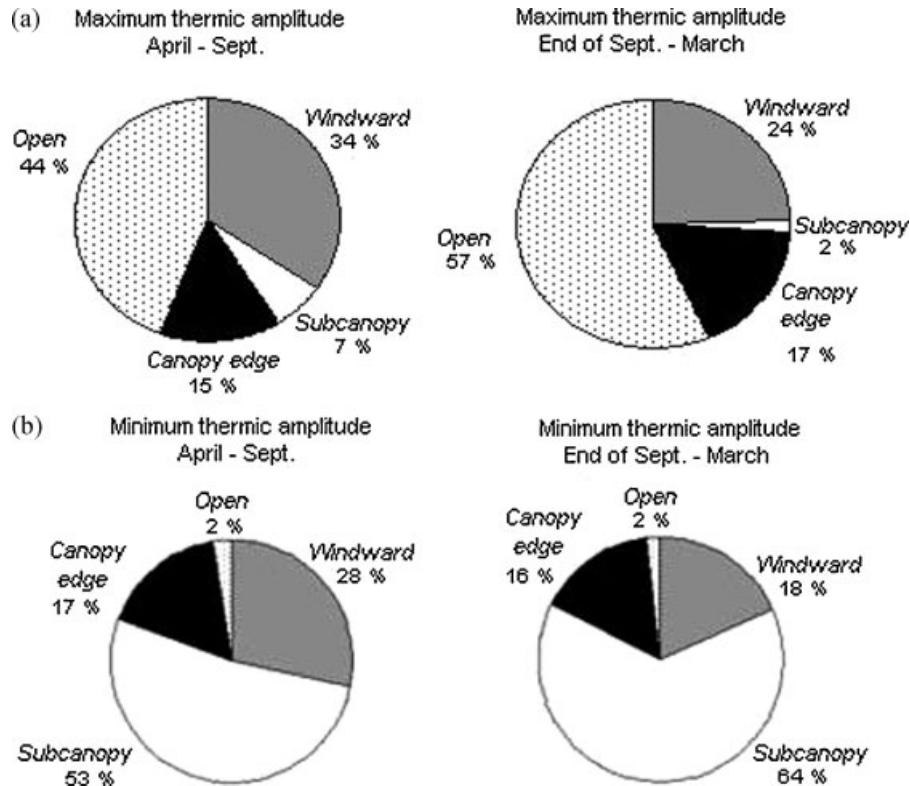


Figure 4. (a) Maximum thermic amplitude in each microenvironment. Percentage values represent the percentage of time that each microenvironment showed the maximum thermic amplitude, during both the coldest (April–September) and the warmest (end of September–March) periods. Information is based on 8 vegetation patches throughout different sampling dates. (b) Minimum thermic amplitude in each microenvironment. Percentage values represent the percentage of time that each microenvironment showed the minimum thermic amplitude, during both the coldest (April–September) and the warmest (end of September–March) periods. Information is based on eight vegetation patches throughout different sampling dates.

interspaces from 23 April (early fall) to 24 August (mid-winter) 1999, and on 1 June (late winter) 2000 [range = 2.9 ± 0.3 (open)– 14.6 ± 0.3 (subcanopy); see Figure 3]. Shrub interspaces (open) showed a greater ($p < 0.05$) monthly average soil moisture content than at the subcanopy only in two [15 October 1999 (mid-spring; 3.8 ± 0.4 vs. 2.4 ± 0.2 per cent) and 5 May 2000 (mid-autumn/fall; 3.6 ± 0.1 vs. 2.3 ± 0.1 per cent; see Figure 3)] out of 27 sampling periods.

Wind speed

There were times when wind speed was greater than 30 km h^{-1} at 1.5 m height from the soil surface, and it reached values close to 25 km h^{-1} at the soil surface in the interspaces between vegetation patches (Figure 5). Under the shrubs, values were from 0 to 5 km h^{-1} throughout the year.

Physicochemical Characterization

Physico-chemical soil characteristics

Levels of coarse texture (sand), total nitrogen and available phosphorus and potassium were significantly greater

($p < 0.05$), and those of fine texture (clay and loam), organic matter, C:N ratio, pH and soil bulk density were significantly lower ($p < 0.05$) under the shrubs than in the patch interspaces between vegetation patches (Table IV). Electrical conductivity was similar ($p > 0.05$) in both microenvironments.

Seed Essay

Seed germination indexes

Germination index was similar ($p > 0.05$) in all microenvironments and it ranged from 0.6 to 0.8 (Figure 6). However, the number of surviving seedlings/number of germinated seeds and the number of surviving seedlings/number of seeded seeds were greater ($p < 0.05$) under the shrubs than at the remaining microenvironments in *S. neaei* and *L. erianthus* (Figure 6). Height and dry weight of the survivors were greater ($p < 0.05$) under the shrubs than in the open, patch interspaces in *L. erianthus*, but not ($p > 0.05$) in *S. neaei* (Table V).

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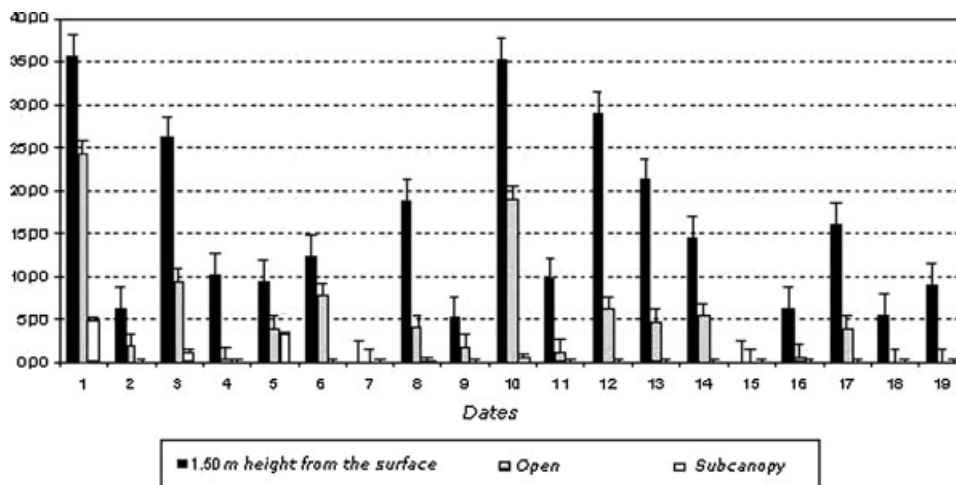


Figure 5. Wind speed (km h^{-1}) at 1.50 m height from the soil surface, in the interspaces among vegetation patches (open), and right below the shrubs in the vegetation patches (subcanopy). Measurements were taken with a hand anemometer. Dates: (1) 5 August 1999, (2) 29 September, (3) 15 October, (4) 27 October, (5) 12 November, (6) 23 November, (7) 13 December, (8) 23 December, (9) 7 January 2000, (10) 20 January, (11) 21 January, (12) 3 February, (13) 4 February, (14) 3 March, (15) 24 March, (16) 7 April, (17) 14 May, (18) 2 June, (19) 7 November. Each histogram is the mean of 100 measurements. Vertical bars represent 1 s.e. of the mean. Where there is no histograms, wind speed was 0 km h^{-1} .

Seed germination and seedling survival under field conditions

Seedling survival of *L. erianthus* and *S. neaei* was often similar ($p > 0.05$) among all four microsites from April (fall) to December (late-spring) 1999. From early-summer to mid-fall, however, seedling survival in both species was more than 53 per cent lower ($p < 0.05$) at the canopy edges and patch interspaces than under the shrubs.

There was a small number of seedlings surviving for the other three species: only (1) two for *P. ligularis*, which emerged between 23 April and 7 May 1999. These seedlings survived until mid-June 2000, were in two different vegetation patches and came one from underneath the shrubs and the other from the denuded interspaces among

vegetation patches; (2) five for *L. divaricata*, which died on 8 July 1999. These seedlings came from three different vegetation patches. One seedling died windward in one vegetation patch, another seedling died under the shrubs in another vegetation patch and three seedlings died in the open interspaces among patches and (3) 17 for *A. lampa*. These seedlings came from 14 vegetation patches. Only one of these 17 seedlings survived until mid-June 2000, while the others died mostly between 8 July and 24 August 1999. Dead seedlings came (a) seven from microenvironment 1 (windward), (b) four from microenvironment 2 (underneath the shrubs), (c) four from microenvironment 3 (plant patch periphery) and (d) one from microenvironment 4 (the patch interspaces among patches).

Table IV. Soil physicochemical parameter values at the subcanopy and open microenvironments of the vegetation patches.

	Subcanopy	Open
Texture (per cent)		
Total fine fraction (clay + fine loam + coarse loam)	16.3 ± 0.9 a	21.9 ± 2.1 b
Total coarse fraction (sand)	83.7 ± 0.9 a	78.1 ± 2.1 b
Soil bulk density (g cm^{-3})	1.16 ± 0.04 a	1.36 ± 0.02 b
Physicochemical parameters	7.99 ± 0.13 a	8.44 ± 0.08 b
Electric conductivity ($\text{m}\Omega^{-1} \text{cm}^{-1}$)	0.132 ± 0.01 a	0.174 ± 0.08 a
Organic matter (per cent)	1.25 ± 0.11 a	0.45 ± 0.03 b
Total N (per cent)	0.0595 ± 0.01 a	0.0306 ± 0.00 b
C/N	9.77 ± 0.85 a	6.63 ± 0.52 b
Available K (ppm)	389.7 ± 17.5 a	259.8 ± 21.7 b
P (ppm)	10.82 ± 1.33 a	5.50 ± 0.94 b

Each value is the mean \pm 1 s.e. of $n = 10$. Sampling were made at two sites ($n = 5$ at each site) which showed to be similar ($p > 0.05$); this is because values coming from both sites were averaged and $n = 10$. Within any row, values followed by different letters are different ($p < 0.05$) from each other.

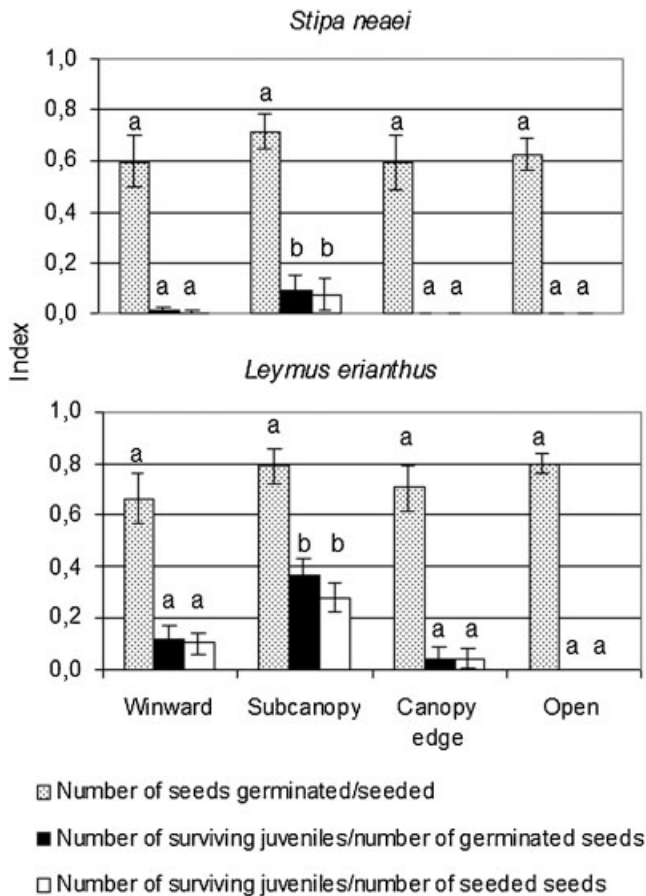


Figure 6. Germination and juvenile survival of *Stipa neaei* and *Leymus erianthus* in different microenvironments of vegetation patches. Each histogram represent: (a) number of germinated seeds/number of seeded seeds, (b) number of surviving juveniles/number of germinated seeds, and (c) number of surviving juveniles/number of seeded seeds. Each histogram is the mean \pm 1 standard error of eight vegetation patches. Within each index, different letters indicate significant differences at $p < 0.05$.

DISCUSSION

We recognize that there was an uneven sampling effort in this study, which undoubtedly caused great variation in sample variance among the data sets. However, this was the result of time, labour and grant availability constraints.

Anyhow, we were able to provide an ample set of abiotic variables, some of which helped to explain the seedling recruitment and subsequent establishment that we obtained at the research site for the study species. Also, we have to acknowledge the lack of replication in time in this study. This implies that inferences drawn from our results are valid only within the study area (Dutilleul, 1993). Generalizations could only be made after comparing our results with similar studies conducted in other areas of the same floristic district.

Microenvironments within and between Patches

Soils underneath the shrubs have lower soil (1) temperatures, (2) minimum and maximum temperature amplitudes, (3) pHs and (4) bulk densities than in the patch interspaces. At the same time, sub-canopy sites have greater soil (5) moisture contents during germination time of the study species (autumn/fall and winter), (6) N, P, and K contents, (7) soil organic matter and (8) C/N ratios than those in the open. These results are similar to those found in soils of xeric environments by Callaway and Pugnaire (1999) for temperature; del Valle (1996) for pH; Tate *et al.* (2004) for bulk density; Bertiller *et al.* (1996) for soil moisture; Castelli *et al.* (1995) for N, P and K contents; Cecchi (2000) for electrical conductivity; de Soyza *et al.* (1997) for organic matter and Distel *et al.* (2000) for the C/N ratios.

Relationship between Microenvironmental Conditions and Seedling Survival

Although we expected a certain degree of seedling mortality during winter as a result of seedling uprooting, because of periodic freezing and thawing of the soil surface, it did not occur. Minimal soil temperatures close to 0°C during several, consecutive winter months did not cause plant mortality in *L. erianthus* and *S. neaei*. During the cold season, soil freezing can cause death of fine roots and root damage (Campbell and Rochefort, 2003), and seedlings can be exposed to ice needles which form at the soil surface (Fashu-Kanu and Driscoll, 2005).

At the time when the greatest seedling mortality was determined in *L. erianthus* and *S. neaei*, maximum soil temperatures did not reach 40°C under the shrubs, while they

Table V. Morphological characteristics of juveniles of *Stipa neaei* and *Leymus erianthus* in the different microenvironments of the vegetation patches. Different letters in the same row indicate significant differences at $p < 0.05$.

Parameter	Species	Microenvironment			
		Windward	Subcanopy	Canopy edge	Open
Height (cm)	<i>Stipa neaei</i>	17.0 * a	17.7 \pm 1.3 a	0 a	0 a
	<i>Leymus erianthus</i>	13.5 \pm 1.2 ab	18.3 \pm 0.8 a	14.6 \pm 1.0 bc	0 c
Weight (mg/plant)	<i>Stipa neaei</i>	76 * a	30.3 \pm 5.3 a	0 a	0 a
	<i>Leymus erianthus</i>	176.5 \pm 40.0 ab	179.2 \pm 20.7 a	83.1 \pm 22.9 bc	0 c

For juvenile height and weight, each value is the mean \pm 1 E.E. of $n = 6-36$; * $n = 1$.

were up to 50°C in the patch interspaces among vegetation patches. Peláez *et al.* (1992) reported that grazed sites, with lower plant cover, showed significantly higher temperatures than ungrazed ones, with a higher plant cover, only in a few occasions. Exposure to temperatures over 45°C during at least 30 min can cause severe damage to plants from a wide range of climatic regions (Fitter and Hay, 1983). Ludlow (1976) reported that C₃ plants close their stomata when temperatures reached 35–45°C. If temperatures remain so high several hours per day during several weeks, it is likely that seedling death will occur. Heat causes death of plant tissue damaging membranes, and particularly denaturalizing proteins (Larcher, 2003). Hubbard (1957) also showed that *Eurotia lanata* seedlings developed best in full sunlight, but not on bare soil because the late spring-early summer high soil surface temperatures were very likely lethal to the young, tender plants.

Seedling emergence and survival, however, also depended on several other factors. Soil moisture contents underneath the shrubs were greatest at the germination time of the study species. At this time, precipitation during the study years was greater than the long-term average precipitation. Despite soil moisture was not limiting underneath the shrubs, germination and subsequent seedling establishment only occurred for *L. erianthus* and *S. neaei*. This indicates that even though vegetation patches reduce environmental stress (e.g. underneath the shrubs), it does not guarantee a successful seed germination and seedling establishment for most species in the community in that microenvironment. The two shrub species and *P. ligularis* showed an extremely low (an uneven) seed germination and seedling establishment in all microenvironments during the study period. The availability of moisture in the first 0–5 cm of the soil was reported as the most important factor in determining a successful emergence and survival of young seedlings in the grass *Festuca* spp (Defossé *et al.*, 1997). The importance of top-soil moisture for the emergence and survival of young seedlings was also determined in other arid and semi-arid grasslands (Soriano and Sala, 1986). Most values similar in all microenvironments were at the permanent wilting point (≤ 5 per cent soil moisture content in these soils: Bonvissuto, 2006).

Raven *et al.* (1986) reported that seeds of some desert species germinate only after a certain amount of rainfall wash out some chemical inhibitors present in the seed tegument. This rainfall level is directly related to the amount of soil moisture that desert plants need to establish as seedlings. This could be one of the reasons to explain the lack of emergence of the shrub *A. lampa* in the field seedlings. For this species, it is recommended to wash the fruits during at least 96 h previous to initiate a germination study because of the presence of salts in its bracts (Bustos, unpublished data, INTA EEA Bariloche). Raven *et al.*

(1986) also suggested that some seeds will not germinate after having some abrasion treatment such as that provided by the soil. This will affect the seed tegument, allowing water and oxygen entrance into the seed, in some cases removing the inhibitor sources. It is possible that this phenomenon occurred in *L. divaricata*: seedling emergence was less than 1 per cent in the patch interspaces when field seedlings were conducted without scarifying the seeds, which remained covered with its hairy involucre. Scarification of *L. divaricata* seeds was recommended by Zappe (unpublished data, pers. com., INTA EEA Bariloche) before conducting germination trials. When seed germination of *L. divaricata* was conducted under controlled moisture and temperature, and seeds were scarified, germination percentages of up to 25 per cent were obtained (Bonvissuto and Busso, 2007a).

Under conditions of severe stress, where establishment of an independent propagule can be a long and risky process, vegetative reproduction presents advantages which derives of its capacity to sustain the offspring (Grime, 1981). Vegetation establishment in the patch interspaces at the study site could be determined by colonization of rhizomatous perennial grass species such as *P. ligularis* and *S. neaei*. Colonization of these bare sites might also be dependent on the existence of shrubs highly resistant to severe stress like *Gutierrezia*, a common gender in the study vegetation patches (Busso and Bonvissuto, 2009b). It appears that its ability to colonize a site depends mainly of its reproductive potential and possible early establishment. This was reported by Osman and Pieper (1988) in New Mexico where vegetation was dominated by *Gutierrezia sarothrae* (Pursh.) Britt. & Rusby, and annual precipitation was 220 mm. This species produces a large seed amount and present a rapid seedling establishment, which makes it an increasing species in degraded plant communities (Osman and Pieper, 1988).

Advance of *Gutierrezia* sp., possibly through seedling establishment from a large seed pool [i.e. Ladyman (2003) for *G. Sarothrae*], and of *P. lanuginosa* and *S. neaei* to bare, unvegetated sites, was observed by Bonvissuto (pers. com., INTA EEA Bariloche) after 3 years (1999–2001) with precipitations 50 per cent above the historical mean. These observations were made in enclosures to domestic livestock in the Monte Austral Neuquino.

We supposed at the beginning of this work that formation of new vegetation patches would start from germination and subsequent establishment of *L. divaricata* and *A. lampa*. Shrubs like *L. tridentata* are plants which present clonal subdivisions which can facilitate (1) dispersion of the plant canopy and (2) formation of large clonal patches (Schenk, 1999). Lateral branches of *Larrea* can be covered by sand and then root close to where they show up from the mound (Barbour, 1969). Thus, shrub groups do not necessarily

develop from seedlings which grow in close association. Nevertheless, it has to be recognized that formation of vegetation patches could also start from shrub seeds colonizing empty areas. Such is the case for *Gutierrezia spp.* This species will later generate an adequate environment for establishment of other species.

In our study environment, the unique annual invader, exotic grass (Milby and Johnson, 1987) which grew in all study microenvironments was *B. tectorum* (Busso and Bonvissuto, 2009b). 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 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 (Busso and Bonvissuto, 2009a, 2009b).

Wind can influence vegetation structure through mechanical effects, influencing propagule dispersal, and affecting plant physiology (Fitter and Hay, 1983). We found that wind speed was lower under the vegetation patches than in the interspaces. In windy environments (such as ours), differences in topography and soil surface characteristics, and physiological effects can affect seed germination and seedling survival (Ennos, 1997). Seedlings grown up in windy environments can be particularly vulnerable to (1) desiccating effects on the top soil and (2) abrasive damage caused by wind-driven particles (Fryrear *et al.*, 1973; Defossé *et al.*, 1997).

The lower seedling emergence and survival found in the patch interspaces might also be attributed to the previous effects of grazing and trampling, which increased soil bulk density. These results are similar to those reported for other arid and semi-arid ecosystems (Balph and Malecheck, 1985; Bertiller, 1992).

Litter and stone covers were high (about 50 per cent) in the patch interspaces. However, Defossé *et al.* (1997) demonstrated in the steppe zone of Patagonia that litter cover was not a good indicator of seedling success, and the correlation between litter cover and seedling emergence was very poor; high winds redistributed litter within the environment during the spring and summer months (Defossé *et al.*, 1990).

It can be thought that recuperation of these environments might partially be based in improving the structure and diversity of the already existent vegetation patches. This could be achieved by implementing strategic resting periods (which prevent grazing of vegetation), such that plants can recuperate its vigour. This would be highly favoured if these periods are coincident with precipitation years above the

historical mean. Reseeding of grass and shrub species, improving livestock distribution (e.g. increased fencing), distribution of salt on the range and herding (Thorsteinsson *et al.*, 1971); heavy discing in the interspaces among vegetation patches (Fulbright, 1991); managing the timing and intensity of paddock use (Ludwig *et al.*, 1999); runoff obstruction and water collection from rainfall and air-borne particulate matter from wind (Ludwig *et al.*, 2004); understanding the natural vegetation patterning and nutrient cycling at a landscape scale (Nelson, 1999) and treatment of bare soil areas with branches (Tongway and Ludwig, 1996) have been used in some areas to reduce land degradation. We have to recognize, however, that the extensivity of livestock operations in the study area, and related restoration costs, may constraint application of these suggested management approaches to avoid further degradation in the Monte Austral Neuquino.

Our results on *L. erianthus* and *S. neaei* agreed with the hypothesis that vegetation patches reduce environmental stress. However, this was not the case for the two shrubs and *P. ligularis*. This suggests that reduction of environmental stress under the shrub canopies does not imply successful seed germination and seedling establishment of most species in the community. There is seed rain into (Bonvissuto and Busso, 2007b) and seed bank in (Busso and Bonvissuto, 2009a) the patch interspaces for all the study species. Despite this, the extreme high temperatures (up to 50°C) in this microenvironment during the summer will prevent seedling recruitment for most species in the community. Future research must address livestock utilization at the study area, simultaneously conserving the renewable natural resources, and outline proper management guidelines conducive to a sustainable use of this ecological system.

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