

## Temporal and micro-spatial patterning of seedling establishment. Consequences for patch dynamics in the southern Monte, Argentina

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### Abstract

We compared the temporal and micro-spatial patterning of seedling emergence and establishment of two cohorts of perennial grasses and shrubs in the southern Monte, Argentina. Samplings were carried out in two contrasting areas (grazed and non-grazed) during four years. We found lower densities of emerged and established seedlings of perennial grasses in the grazed relative to the non-grazed area. Conversely, emerged seedlings of shrubs did not vary between the grazed and the non-grazed area and densities of established shrub seedlings were higher in the grazed than in the non-grazed area. We only found differences between cohorts in seedling emergence of perennial grasses. These differences could be associated with the amount of precipitation in the year previous to the emergence. Both in the grazed and non-grazed area, seedlings of perennial grasses were concentrated at the periphery of plant patches. We defined a plant patch as a discrete unit of the spatial pattern of vegetation surrounded by, at least, 20 cm of bare soil from the nearest neighbour patch. Emergence in perennial grasses was more frequent at the southern/western patch-periphery than at other patch-periphery locations. Established seedlings of perennial grasses, however, were homogeneously distributed throughout patch periphery. Emergence in shrubs was more frequent at the centre and periphery of patches than at inter-patch microsites. In contrast, established seedlings of shrubs were homogeneously distributed among microsites. Our results suggest that differential seedling establishment between life forms is the outcome of complex biotic and abiotic interactions and feedbacks at the patch level between seedlings and established plants. Both life forms appear to have a different role in the origin, dynamics, and maintenance of spotting vegetation. Because of the ability to establish both at inter-patch and patch microsites, shrubs could be identified as colonizers or initiators of small plant patches in bare soil or they may contribute to increase the cover and size of pre-existing plant patches. Both processes would be promoted in grazed areas. Due to the ability to establish at patch peripheries, perennial grasses would contribute to the isodiametric growth of pre-existing patches, preferentially in non-grazed areas.

### Introduction

In arid ecosystems, plant processes strongly depend on highly unpredictable water inputs (Noy-Meir 1973; Westoby 1979, 1980). The establishment of new plant cohorts mainly occurs after a succession of favourable climatic events (Guterman 1993). Favourable years for one particular species or life form,

however, may not eventually be favourable for others, resulting in differential temporal patterns of seedling recruitment among species or life forms (Milton 1995; Owens et al. 1995). At a fine spatial scale, seed availability and microsite quality may also limit seedling establishment and plant recruitment (Grubb 1977; Jurena and Van Auken 2003; Lamont et al. 1993; Owens et al. 1995; Schupp 1995). Graz-

ing may also affect both processes by the direct removal of seedling tissues (Clements and Young 1996) or indirectly through its effects on seed production (Bertiller and Coronato 1994; O'Connor 1991; O'Connor and Pickett 1992) and microsite quality (Dunkerley 1997; Oesterheld and Sala 1990; Rambo and Faeth 1999; Schlesinger et al. 1996).

Vegetation in arid ecosystems is mostly characterised by a two-phase mosaic (spotted or banded) formed by areas with high plant cover alternating with areas of scattered vegetation or bare soil (Aguilar and Sala 1999; Ares et al. 2003; Bisigato and Bertiller 1997; Noy-Meir 1973; Soriano et al. 1994). Concentration of resources (i.e., seeds, organic matter, soil nutrients) and suitable microclimatic conditions for plant processes (i.e., sheltering) characterise the phases of high plant cover (Bertiller 1998; Bertiller et al. 2000; Callaway 1995; Carrera et al. 2003; Guo et al. 1998; Mazzarino et al. 1998). In spotted vegetation, microclimatic and edaphic features vary from plant patch centres to inter-patch areas (Bertiller et al. 2002; Moro et al. 1997; Weltzin and Coughenour 1990) or among different locations around patch canopies (Gass and Barnes 1998; Rousset and Lepart 2000). Sheltering (i.e., low evaporative demand) and concentration of resources (i.e., nutrients, water, seeds) nearby plant patches may promote seedling establishment and plant recruitment (Belsky et al. 1989; Bertiller et al. 2002; Bisigato and Bertiller 1999; Callaway 1995). However, these processes may be affected by biotic interactions (i.e., below-ground competition) between seedlings and the established vegetation (Bisigato 2000; Jurena and Archer 2003; Valentin et al. 1999; Van Auken and Bush 1997). Thus, emergence and establishment of seedlings and plant patch dynamics result from the balance between facilitation and competition processes (Callaway and Walker, 1997).

The relative occurrence of these processes under different microenvironmental conditions has been identified for perennial grasses (Aguilar and Sala, 1999; Scholes and Archer 1997) and shrubs (Franco Pizaña et al. 1996, Jurena and Van Auken 2003) in various arid ecosystems. Both life forms differ not only in morphotype but also in functional characteristics. Shrubs exhibit marked xeromorphic traits such as deep rooting depth, long leaf lifespan, low growth rates, low specific leaf area, and low N concentration in green leaves (Carrera et al. 2000; 2003; Killingbeck 1993; Levang-Brilz and Biondini 2002; Schenk and Jackson 2002). In contrast, perennial grasses ex-

hibit traits such as shallow rooting depth, high growth rates, high leaf turnover, high specific leaf area and high N concentration in green leaves. Also, active growth in perennial grasses is usually coupled with precipitation inputs (Aerts and Chapin III 2000; Bertiller et al. 1991; Carrera et al. 2000; 2003; Fernández et al. 1991). There are also evidences that adults of shrubs and perennial grasses may differentially affect the establishment of individuals of the other life form. While shrubs may facilitate the establishment of grasses in their vicinity (Lauenroth and Aguilera 1998; Scholes and Archer 1997), grasses frequently inhibit the establishment of shrubs (Jurena and Archer 2003; Van Auken and Bush 1997). However, studies on the simultaneous spatial patterning of emergence and establishment of both life forms and their relationship with environmental patchiness are scarce. This knowledge could provide new insights on the relationships between life forms and environment, necessary to identify processes involved in vegetation dynamics and to manage shrub encroachment processes in disturbed arid ecosystems.

In the present study, (i) we compared the temporal and micro-spatial patterning of seedling emergence and establishment of two cohorts of perennial grasses and shrubs in two contrasting areas (grazed, non grazed) with spotted vegetation representative of the southern Monte Phytoecographic Province, Argentina and (ii) based on this patterning and functional traits of each life form, we discussed the probable role of shrubs and perennial grasses in the origin and maintenance of spotted vegetation. We hypothesised that emergence and establishment of shrubs and perennial grasses would be differently affected by environmental patchiness. Shrub seedlings, due to their predominantly xeromorphic traits, would be less affected by the harsh abiotic conditions in inter-patch microsites than by negative biotic interactions with established vegetation. In contrast, perennial grass seedlings, due to their predominantly mesomorphic traits, would be likely to emerge and establish in microsites with high availability of resources and sheltering rather than in inter-patch microsites. Further, higher direct and indirect grazing impact on seedlings and adults of perennial grasses relative to those of shrubs would result in reduced emergence and establishment of the former as compared to shrubs.

## Methods

### Study site

The study site is located in north-eastern Chubut Province, Argentina (42°39'S, 65°23'W, 115 m a.s.l.). Annual mean temperature is 13.7 °C and average precipitation is 188 mm with high mean interannual variation (Coronato and Bertiller 1997). Soils are a complex of Typic Petrocalcids–Typic Haplocalcids (Soil Survey Staff 1998). Field observations were conducted in a paddock of 2,500 ha representative of the community of *Larrea divaricata* Cav. and *Stipa* spp (Bisigato and Bertiller 1997). Within the paddock, we selected two areas of about 3 ha each. One of them was fenced in 1993 to exclude grazing of domestic herbivores, and the other was continuously grazed with the usual stocking rate of the paddock in the last years (0.14 sheep/ha). In both areas, vegetation has a random patchy structure covering between 40% and 60% of the soil. *Larrea divaricata*, *Chuquiraga hystrix* D. Don, *Lycium chilense* Miers ex Bert., *Schinus johnstonii* F.A. Barkley, and *Atriplex lampa* Gill. ex Moq. dominate the upper layer (1–2 m), while the lower layer (< 1 m) is composed by perennial grasses (*Stipa tenuis* Phil., *S. speciosa* Trin. and Rupr., *S. humilis* Cav. and *Poa ligularis* Nees ex Steud.) and dwarf shrubs (*Nassauvia fuegiana* (Speg.) Cabrera, *Acantholippia seriphioides* (A. Gray) Moldenke, and *Junellia seriphioides* (Gillies and Hook.) Moldenke) (Bisigato and Bertiller 1997). Throughout this study nomenclature follows Correa (1969; 1971; 1978; 1984; 1988; 1998; 1999).

As in other arid ecosystems, vegetation in the southern Monte is clumped in isodiametric (having similar diameter in all directions) patches of different size, floristic and structural complexity (Bisigato and Bertiller 1997). Plant patches create wind sheltered, and nutrient-rich soil areas with abundant seeds around and beneath them (Bertiller 1998; Bertiller et al. 2002; Mazzarino et al. 1998; Rostagno and del Valle 1988). Sheep grazing was introduced at the beginning of the last century (Ares et al. 1990), and led to the reduction of vegetation cover, soil erosion, and the lack of plant reestablishment (Ares et al. 1990). Changes induced by grazing may also be identified at the fine patch-scale through the reduction of patch size and floristic richness, the decrease in abundance of grass patches, and the increase of tall shrub patch densities (Bisigato 2000). Seeds of grasses are abundant near shrub-grass or grass patches, while seeds of

shrubs are scarce and mainly associated with shrub-dominated patches (Bertiller 1998).

### Environmental data

Daily precipitation and air temperature were registered with an automatic data recorder (21X Micrologger, Campbell Scientific) from January 1996 to June 2000. Soil moisture of the upper soil layer (0–15 cm) was computed at monthly intervals from precipitation and air temperature data (Coronato and Bertiller 1997).

### Patch and plant cover in the study areas

In March 1997, we estimated the total plant cover and patch attributes (patch cover, internal patch cover, the number of patches per 50-m transect, and patch area) along four 50-m linear transects at each area (grazed and non-grazed). Along each transect, patch cover was evaluated as the percentage of the interval length intercepted by patches. We also visually estimated the cover within each patch canopy. The internal patch cover was further calculated by the average of covers within patch canopies weighted by the respective length intercepted along each transect. The total plant cover was computed by multiplying internal patch cover and patch cover (Bisigato and Bertiller 1997). Patch area was assessed by the crown diameter method (Mueller-Dombois and Ellenberg 1974). For the purpose of this study, we defined a vegetation patch as a discrete unit of the spatial pattern of vegetation surrounded by bare soil (at least 20 cm from the nearest neighbour patch) (Bisigato and Bertiller 1997). This definition does not imply constraints on patch size, internal homogeneity, or discreteness (Pickett and White 1995).

### Seedling counts

We randomly selected 12 sampling plots of 5 m<sup>2</sup> (0.5×10 m), 6 at the grazed and 6 at the non-grazed area. At each sampling plot, we identified all plant patches. We defined three zones associated with each plant patch: “centre”, “periphery” and “inter-patch”. “Centre” corresponded to soil mounds underneath the central portion of patch canopies (Rostagno and del Valle 1988). This zone concentrates microsites rich in organic matter, nutrients and seeds. “Periphery” corresponded to the zone beneath the external crown of patch canopies with sheltered microsites, poorer in

soil resources than the “centre” zone. “Inter-patch” corresponded to the inter-patch bare soil with more exposed and nutrient-poorer microsites than “centre” and “periphery” (Bertiller et al. 2000, 2002; Mazzarino et al. 1998; Rostagno and del Valle 1988). We estimated the proportion of each patch zone along a central 10-m transect within each plot using the line intercept method (Mueller-Dombois and Ellenberg 1974). Additionally, for “periphery” and “inter-patch”, we delimited four locations with respect to cardinal points (N, E, S, W).

At each selected plot, seedling emergence was registered in October 1997 and 1998 (cohort I and II, respectively) by counting all seedlings of perennial grasses and shrubs emerged during the previous wet period (March to September). Emerged seedlings were tagged and discriminated by patch zone (centre, periphery, inter-patch), and patch location (N, E, S, W). In July 1999 for cohort I and in June 2000 for cohort II, we registered the established seedlings by counting the surviving tagged seedlings.

The total observed (O) number of emerged or established seedlings of perennial grasses or shrubs by patch zone and area (grazed, non-grazed) was compared with the expected (E) number which was computed by assuming a random spatial distribution of seedlings as follows:

$$E_z = T_a * P_z$$

where, for each life form and area (*a*), *E* is the expected number of emerged or established seedlings at each patch zone (*z*), *T* is the total (all patch zones and plots) number of emerged or established seedlings counted, and *P* is the proportion of cover of each patch zone (*z*) at the whole area. Additionally, at each area, the number of seedlings (perennial grasses or shrubs) observed at each location with respect to cardinal points was compared with the number expected by chance (25% at each N, E, S, or W location).

#### Data analysis

The significance of the differences in arcsin-transformed cover data, (patch, total plant, internal patch), and in square root-transformed patch area and number of patches per 50-m transect between areas was tested by One-Way ANOVA. The significance of the differences in the density of emerged and established seedlings between cohorts (I, II), and areas (non-

Table 1. Patch and plant cover characteristics in the grazed and non-grazed area. Different lower case letters indicate significant differences ( $p \leq 0.05$ ) between areas. To perform the data analysis cover data were arcsin-transformed and patches per 50-m transect data were square root transformed.

Plant/patch trait	Area	
	Non-grazed	Grazed
Patch cover (%)	50.8 <sup>a</sup>	47.2 <sup>a</sup>
Internal patch cover (%)	53.8 <sup>a</sup>	43.3 <sup>b</sup>
Patches per 50-m transect	35.2 <sup>a</sup>	31.5 <sup>a</sup>
Patch area (m <sup>2</sup> )	2.1 <sup>a</sup>	2.1 <sup>a</sup>
Total plant cover (%)	27.4 <sup>a</sup>	20.5 <sup>b</sup>

grazed, grazed) was evaluated by Two-Way ANOVA of square root transformed data. The significance of the differences between observed and expected (random) number of seedlings at different patch zones and locations with respect to cardinal points was inspected using  $\chi^2$  test.

## Results

### Patch and plant cover of the study areas

We found no differences in most patch traits (patch cover, number of patches per 50-m transect, and patch area) between areas while internal patch cover was higher in the non-grazed than in the grazed area. Due to reduced internal patch cover, total plant cover was lower in the grazed than in the non-grazed area (Table 1).

### Seedling emergence and establishment

Emergence of perennial grasses varied between areas and cohorts (Table 2a, Figure 1a). In the non-grazed area, it was greater in cohort II than in cohort I. In the grazed area, we did not find differences between cohorts. Emergence of shrubs did not vary between areas or cohorts (Table 2b).

The establishment of seedlings of perennial grasses was greater ( $p < 0.01$ ) in the non-grazed relative to the grazed area while the establishment of shrub seedlings was greater ( $p=0.05$ ) in the grazed than in the non-grazed area (Table 2c-d, Figure 1b). In both areas, no differences in seedling establishment between cohorts of perennial grasses or shrubs were observed (Table 2c-d; Figure 1b).

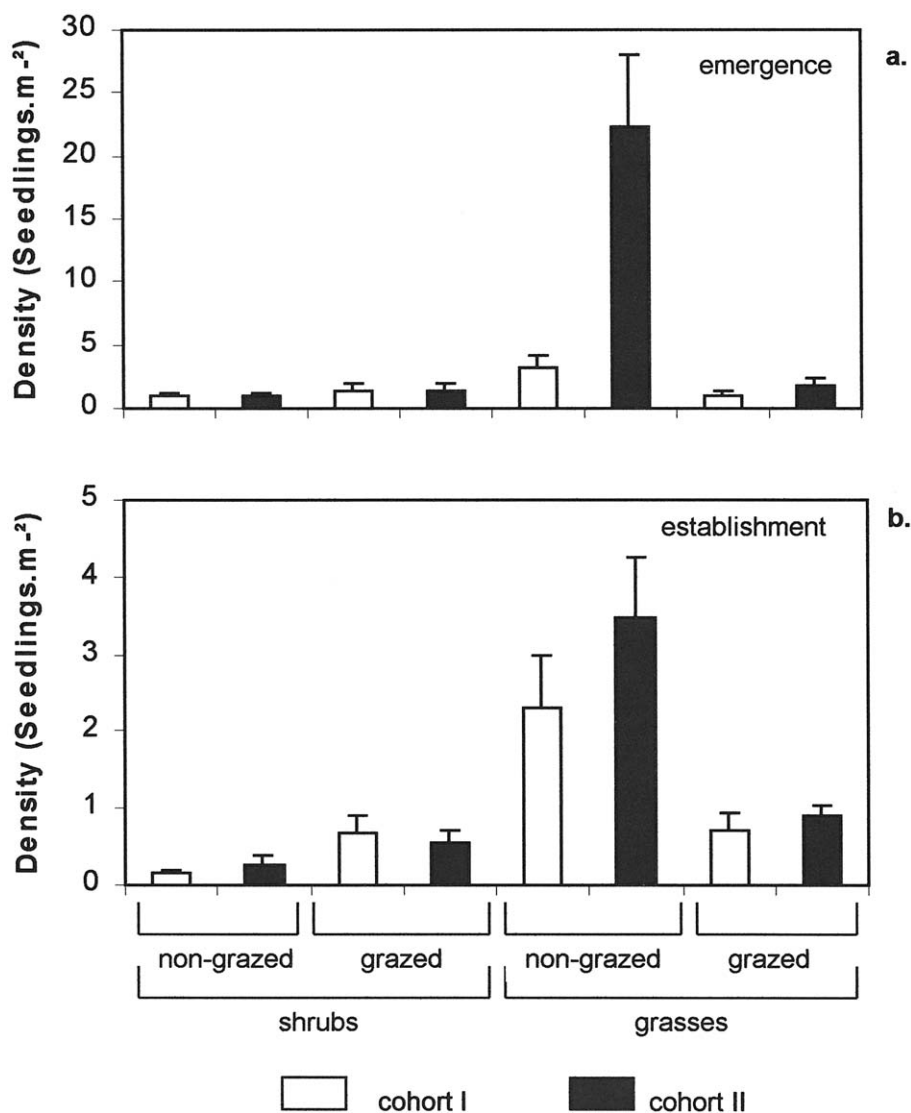


Figure 1. Emerged (a), and established (b) seedling densities of perennial grasses and scrubs of cohort I and II in the grazed and non-grazed area. Bars indicate one standard error.

#### *Spatial patterning of seedlings*

The distribution of seedlings among patch zones varied between life forms and areas. In both areas, the emergence and establishment of perennial grass seedlings of the two cohorts were more frequent at the periphery of patches than at the other patch zones (Table 3). The distribution of seedlings of shrubs among patch zones varied between areas. In the non-grazed area, the emergence of seedlings of shrubs of the cohort I was more frequent at the periphery of patches than at the other patch zones. This pattern

changed after 2 years, since no differences were observed in the established shrub seedlings among patch zones. In cohort II, seedling emergence of shrubs did not differ among patch zones but established seedlings were more frequent at the periphery of plant patches than at the other patch zones. In the grazed area, the emergence of shrub seedlings of cohort I was concentrated at centre and periphery zones and that of cohort II was concentrated at the centre zone. In

Table 2. Analysis of variance of (square root transformed) seedling densities of perennial grasses and shrubs: a. Emerged grasses, b. Emerged shrubs, c. Established grasses, d. Established shrubs.

Source	Sum of squares	df	Mean square	F	Sig.
a.					
Area	112.5	1	112.5	21.3	< 0.01
Cohort	72.1	1	72.1	13.7	< 0.01
Area * cohort	41.4	1	41.4	7.9	0.01
Error	105.5	20	5.3		
Total	850.0	24			
b.					
Area	0.2	1	0.2	0.1	0.74
Cohort	0.0	1	0.0	0.1	0.82
Area * cohort	0.4	1	0.4	0.3	0.61
Error	31.1	20	1.5		
Total	144.0	24			
c.					
Area	17.7	1	17.7	13.7	< 0.01
Cohort	2.7	1	2.7	2.1	0.16
Area * cohort	0.3	1	0.3	0.2	0.66
Error	25.8	20	1.3		
Total	221.0	24			
d.					
Area	3.0	1	3.0	4.2	0.05
Cohort	0.0	1	0.0	0.0	0.85
Area * cohort	0.0	1	0.0	0.1	0.81
Error	13.9	20	0.7		
Total	50.0	24			

both cohorts, established seedlings were homogeneously distributed among patch zones.

We only find patterns of directionality with respect to cardinal points in emerged seedlings of perennial grasses. In the non-grazed area, emerged seedlings of perennial grasses of both cohorts were concentrated at S or W locations (Table 4) while established seedlings were homogeneously distributed among locations. In the grazed area, except for the emerged seedlings of cohort II which were concentrated at S locations, perennial grass seedlings were homogeneously distributed among locations with respect to cardinal points. Emerged and established seedlings of shrubs of the two cohorts were homogeneously distributed among locations with respect to cardinal points.

#### Environmental data

During the study period (January 1996–June 2000), the driest year was 1996 and the wettest year was 1997 (Figure 2a). Precipitation in the rest of the years

exceeded the long term mean for the area (188 mm). Soil water content varied among years in accordance with the variability of precipitation. The highest values of soil water content were estimated in autumn while, in the spring-summer period, we calculated the lowest values (Figure 2b). Accordingly, the year previous to the emergence of cohort I was the driest and the emergence of this cohort occurred during the wettest year (1997). In contrast, the year previous to the emergence of cohort II was the wettest (1997), and seedling emergence occurred in a year with annual precipitation higher than the long term mean for the study site. Seedling establishment of both cohorts occurred during a period with above-mean precipitation values.

#### Discussion

Our results showed differential temporal and spatial patterning of seedling emergence and establishment between perennial grasses and shrubs that may be associated with different environmental controls, congruent with the functional traits of each life form. Furthermore, the differential patterning in seedling establishment provides new insight on the role of each life form in the origin and dynamics of spotted vegetation patterning.

#### Density and spatial patterning of perennial grass seedlings

Low emergence of seedlings of perennial grasses in the non-grazed area after a dry year (Figure 1a, Figure 2, Table 2) could be traced back to low seed availability in soil. Low precipitation in 1996 probably affected seed production, reducing the size of the soil seed bank of perennial grasses and subsequently the number of perennial grass seedlings emerging in 1997 (cohort I) in comparison with those emerging in 1998 (cohort II). Previous reports for the study area indicated that reproductive growth of perennial grasses is mainly controlled by water availability (Bertiller et al. 1991). Reduced seedling densities of grasses in or following dry years are common in arid ecosystems where plant vegetative and reproductive growth and seed production are largely affected by water availability (Gutterman 1993; Knapp 1984; Puigdefábregas 1998; Westoby 1979, 1980). In contrast, no differences in seedling emergence between cohorts in the grazed area could be associated with

Table 3. Observed and expected (in parentheses) numbers of emerged and established seedlings of perennial grasses and shrubs at each area (non-grazed, grazed) and patch zone (center, periphery, and interpatch), and  $\chi^2$  values (Significant  $\chi^2$  values at  $p < 0.05$  ( $\chi_{0.05 [2]}^2 = 5.99$ ) in bold). Italics indicate zones where observed numbers are significant greater than expected numbers.

Cohort	Date	Non-grazed				Grazed			
		center	Periphery	Interpatch	$\chi^2$	center	Periphery	Interpatch	$\chi^2$
Perennial grasses									
I	Emergence	16 (33)	36 (15)	45 (49)	<b>38.4</b>	5 (8)	14 (7)	12 (16)	<b>11.0</b>
I	Establishment	14 (24)	28 (11)	27 (34)	<b>33.5</b>	5 (6)	9 (4)	7 (11)	<b>6.3</b>
II	Emergence	233 (228)	208 (103)	222 (332)	<b>143.4</b>	16 (15)	31 (12)	8 (29)	<b>47.8</b>
II	Establishment	35 (36)	39 (16)	31 (52)	<b>40.4</b>	9 (7)	12 (6)	6 (14)	<b>12.1</b>
Shrubs									
I	emergence	4 (10)	12 (5)	13 (14)	<b>16.2</b>	19 (11)	14 (9)	9 (22)	<b>15.9</b>
I	establishment	0 (2)	2 (1)	3 (2)	3.7	9 (5)	5 (4)	6 (10)	4.5
II	emergence	12 (11)	9 (5)	10 (15)	5.8	27 (12)	8 (9)	9 (23)	<b>28.1</b>
II	establishment	0 (3)	4 (1)	4 (4)	<b>8.9</b>	7 (5)	4 (3)	6 (9)	2.3

Table 4. Observed and expected numbers of emerged and established seedlings of perennial grasses and shrubs at each area (non-grazed and grazed) and at each location with respect to cardinal points (N, S, E, W), and  $\chi^2$  values (Significant  $\chi^2$  values at  $p < 0.05$  ( $\chi_{0.05 [3]}^2 = 7.82$ ) in bold). Italics indicate locations where observed numbers are significant greater than expected numbers.

Cohort	Date	Non-grazed						Grazed					
		expected	N	S	E	W	$\chi^2$	expected	N	S	E	W	$\chi^2$
Perennial grasses													
I	emergence	20.25	18	29	10	24	<b>9.9</b>	6.5	4	9	4	9	3.8
I	establishment	13.75	13	18	7	17	5.4	4	3	8	1	4	6.5
II	emergence	107.5	58	199	68	105	<b>115.2</b>	9.75	4	21	6	8	<b>18.1</b>
II	establishment	17.5	17	22	12	19	3.0	4.5	3	9	3	3	6.0
Shrubs													
I	emergence	6.25	8	5	5	7	1.1	5.75	3	6	6	8	2.2
I	establishment	1.25	0	2	2	1	2.2	2.75	1	4	2	4	2.4
II	emergence	4.75	5	6	3	5	1.0	4.25	2	4	3	8	4.9
II	establishment	2	3	0	2	3	3.0	2.5	1	2	1	6	6.8

indirect effects of grazing on reproductive output and on the soil seed bank. Bisigato (2000) reported for the study area strong reductions of soil seed bank of grasses with increasing grazing pressure. Herbivores remove reproductive and/or vegetative tissues and this lead to a decrease in plant reproductive output, to low availability of seeds in soil and consequently to low seedling emergence (Bertiller and Coronato 1994; Clements and Young 1996; O'Connor 1991; O'Connor and Pickett 1992; Oesterheld and Sala 1990). Furthermore, grazing may indirectly affect microsite quality (i.e., sheltering, physical and chemical features of the top soil) reducing the density of safe microsites for seedling emergence (Dunkerley 1997; Rambo and Faeth 1999; Schlesinger et al. 1996). As in other ecosystems (Hunt 2001), the negative effects

of grazing on the early stages of perennial grass establishment seem to be the main cause of the strong reduction of grass cover, and eventually of the local extinction of grasses in severely grazed areas of the Patagonian Monte (Ares et al. 2003; Bisigato and Bertiller 1997). Our results also showed that the high emergence of perennial grasses in the non-grazed area after a wet year (cohort II) was not followed by a high seedling establishment. Probably, density-dependent mortality of seedlings was the main factor accounting for this outcome, even during years with high water availability (Lauenroth and Aguilera 1998; Schupp 1995).

As in other arid ecosystems (Aguilar and Sala 1999; Belsky et al. 1989), seedling emergence and establishment of perennial grasses in the southern Monte occurred with higher intensity at the periphery of plant patches than at the inter-patch microsites (Table

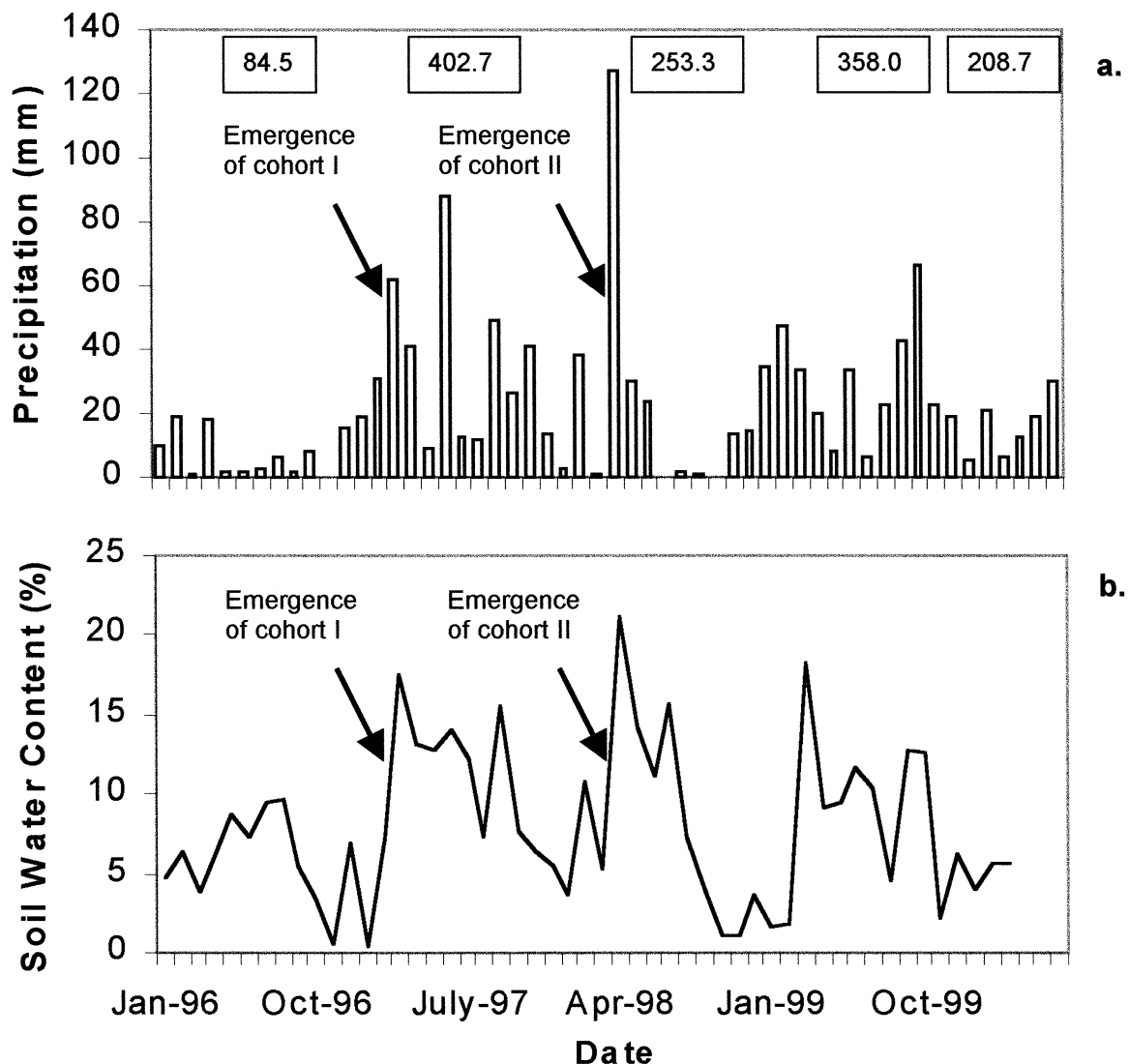


Figure 2. Annual (boxes) and monthly (bars) precipitation (a) and estimated soil water content (0–15 cm depth) (b) in the period January 1996–June 2000. Arrows indicate the onset of emergence of both cohorts.

3). Sheltering, nitrogen-rich soils (Bertiller et al. 2002; Carrera et al. 2003; Mazzarino et al. 1998; Rostagno and del Valle 1988) and high seed availability (Bertiller 1998) associated with plant patches would explain those results (Callaway 1995; Guo et al. 1998). In a greenhouse experiment under controlled climatic conditions and where seeds were not limiting, Bisigato and Bertiller (1999) found that the performance of perennial grass seedlings was greater in the nutrient-rich patch soil than in the inter-patch soil. Although in the study area canopy centres provide optimal sheltering and high resource availability (Bertiller et al. 2002), high above- and

belowground competition may cause the low establishment of perennial grass seedlings at these microsites (Aguar and Sala 1999). Conversely, lower establishment at inter-patch compared to periphery microsites may be explained by the harsh microenvironmental conditions prevailing at inter-patch microsites (Bertiller et al. 2002). In addition, lower insolation and lower soil evaporation rates at S or W locations relative to other patch locations probably favoured the observed directionality in the emergence of grass seedlings at patch peripheries (Gass and Bar-



nes 1998; Rousset and Lepart 2000). Seedling establishment of perennial grasses, however, did not vary among locations with respect to cardinal points, probably due to density-dependent seedling mortality (Lauenroth and Aguilera 1998) at S and W locations with high seedling emergence. Moreover, higher soil temperatures at N and E locations compared to S and W locations could promote root growth (Lambers et al. 2000) during the wet autumn-winter period, increasing seedling establishment at those locations.

#### *Density and spatial patterning of shrub seedlings*

The density of shrub seedlings was not affected by inter-annual variability of precipitation. Similar results were reported by Brown and Archer (1999), who found that the survival of seedlings of *Prosopis glandulosa* did not vary with different water levels. This could indicate lower functional sensitivity of shrubs than perennial grasses to inter-annual variability of precipitation. Accordingly, Bertiller et al. (1991) found that, in the southern Monte, grass phenology was coupled with water inputs while vegetative and reproductive growth of shrubs was mostly associated with the temperature, independently of water inputs. Also, Paruelo and Lauenroth (1995) found stronger relationships between annual precipitation and NDVI in grasslands than in shrublands. Grazing, however, induced an increase in the establishment of shrub seedlings (Figure 1, Table 2) consistent with our previous observations in the field (Bisigato and Bertiller 1997), and in manipulative experiments (Bisigato and Bertiller 1999), as well as with results from other ecosystems (Scholes and Archer 1997). In the grazed area with reduced grass cover, the promotion of shrub establishment could be related to lower competition between shrub seedlings and grass populations relative to the non-grazed area (Lauenroth and Aguilera 1998; Van Auken and Bush 1997). Previously, in the study area, Bisigato (2000) found that in treatments where roots of the neighbouring grasses were excluded, the early growth of shrub seedlings was higher than in treatments without root exclusion of grasses.

Seedling emergence of shrubs was associated with patch canopies indicating a positive effect of sheltering, concentration of shrub seeds or fertility on shrub seedling emergence (Bertiller 1998; Bertiller et al. 2002). This micro-spatial pattern varied, however, between the non-grazed and the grazed area. In the grazed area, as found by Van Auken and Bush (1997),

emerged shrub seedlings were concentrated at the centre of patches (Table 3). In contrast, in the non-grazed area, emergence of shrubs occurred at the periphery of patch canopies. High above- and below-ground competition by high internal patch cover in the non-grazed area is probably the cause of the shift of shrub emergence to patch peripheries where competition between emerging seedlings and established vegetation would be reduced (Bertiller et al. 2002; Bisigato 2000). Similarly, Soriano et al. (1994); Aguiar and Sala (1999) and Couteron and Lejeune (2001) identified different areas around plant patches where competition or facilitation prevails depending on the characteristics of plant patches.

Established seedlings of shrubs, in contrast to emerged shrub seedlings, were mostly uniformly distributed among patch zones (Table 3) both in the non-grazed and in the grazed area. This indicates negative effects of above-belowground competition of patch canopies on the establishment of shrub seedlings as well as a high tolerance of these to the harsh environmental conditions prevailing at inter-patch microsites. Homogeneous spatial distributions of young shrubs have also been reported for other arid ecosystems (Montaña et al. 2001) and are consistent with a combination of negative and positive interactions between seedlings and established plants (Schenk and Mahall 2002).

#### *Seedling patterning and its implications on patch dynamics*

Shrub establishment occurred both at patch and inter-patch microsites (Table 3). This indicates that established shrubs at inter-patch microsites could be loci for the generation of new plant patches. The role of shrubs in the origin of plant patches has been previously suggested and considered in spatial-explicit models of vegetation dynamics in desert ecosystems of Patagonia and the southern Monte (Aguiar and Sala 1999; Bisigato and Bertiller 1997; Bisigato et al. 2002; Soriano et al. 1994). Shrubs colonising inter-patch soil may not only create sheltered areas with abundant seeds around them (Bertiller 1998; Bertiller et al. 2002) but also may exert an important effect on soil N-fertility since they contribute with N-rich litterfall (Carrera et al. 2000; 2003; Mazzarino et al. 1998). These would facilitate the further establishment of perennial grasses or shrubs (Bertiller et al. 2002; Bisigato and Bertiller 1999). The establishment of both life forms at periphery and central patch zones

would contribute to the isodiametric patch growth and eventually to the coalescence of pre-existing plant patches.

In summary, spotted plant patterning in the southern Monte appears to be the outcome of complex biotic and abiotic interactions and feedbacks, at the patch level, between seedlings of the main life forms and established plants. Thus, established shrubs at inter-patch microsites could be loci for the generation of new plant patches while both growth forms may contribute to the isodiametric patch growth. This suggests that the origin and permanence of plant patches in the southern Monte as in other desert ecosystems could be explained by different scales of facilitation and competition around plant patches (Couteron and Lejeune 2001; Montaña et al. 2001). Under this scenario, natural or man-induced disturbances affecting the life form composition, the architecture and the spatial patterning of plant patches and soil resources (Adler et al. 2001; Bisigato and Bertiller 1997; Dunkerley 1997; Ludwig and Tongway 1995) would indirectly affect demographic processes of each life form and the capability of the system to maintain or recover the vegetation structure (Grubb 1977; Oesterheld and Sala 1990). The understanding of these complex interrelationships between vegetation and the biotic and physical environment is the focus of our ongoing research.

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