

Patch structure dynamics and mechanisms of cyclical succession in a Patagonian steppe (Argentina)

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ABSTRACT

The plant community in the Patagonian steppe is arranged in two structural patch types: scattered grasses and shrubs, which are often surrounded by a ring of grasses. Previous studies suggested that this pattern results from a cyclical succession driven by plant interactions. Although there is a good understanding of the factors affecting the formation of the grass rings encircling the shrubs, there is little evidence testing the causes of its fragmentation when the shrub dies, and the relation between the two structural patches. We evaluated the physiological status of two *Stipa* species in different degenerative stages of the ring surrounding *Adesmia volckmannii* shrubs, measuring microclimate and soil nutrients. Results support the cyclical succession model. As long as *Adesmia* shrubs are alive, both *Stipa* species coexist under its canopy, supported by facilitation via improved microclimate and nutrients under the shrub. After shrub death, degeneration of the ring of grasses is caused by competition. The species spatial distribution suggests that *Stipa speciosa* withstands poorer soil nitrogen levels than *Stipa humilis*. We suggest that when facilitation by the shrub ceases, *S. speciosa* may have a competitive advantage over *S. humilis* that may result in the dominance of *S. speciosa* in gaps between shrubs.

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1. Introduction

The composition and structure of plant communities can be strongly influenced by interactions among its components (Roughgarden and Diamond, 1986). Plant interactions commonly comprise positive and negative effects operating simultaneous and bidirectionally (Aguilar and Sala, 1994; Bertness and Shumway, 1993; Holzapfel and Mahall, 1999). The net effect of one plant on the other is therefore the balance between all positive and negative effects (Armas and Pugnaire, 2005; Callaway and Walker, 1997; Maestre et al., 2003).

Although there is evidence of change in the net balance of an interaction between two species (Kikvidze et al., 2005; Ludwig et al., 2003; Tielbörger and Kadmon, 2000), the processes and mechanisms involved are still poorly known. Understanding these mechanisms has both theoretical and practical importance to issues of biodiversity maintenance and ecosystem productivity. This is particularly true in semi-arid ecosystems, where positive interactions play an outstanding role in determining the structure of plant communities (Aguilar and Sala, 1999; Tirado and Pugnaire, 2005).

Water availability alters the net balance of plant interactions in semi-arid environments (Kitzberger et al., 2000; Maestre and Cortina, 2004; Tielbörger and Kadmon, 2000), and it is the major factor governing the interaction between grasses and their

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spatial arrangement in this system (Aguilar and Sala, 1994; Aguilar et al., 1992; Sala et al., 1989). In dry systems, facilitation by shrubs on understory plants usually involves increased water or nutrient availability (Holzapfel and Mahall, 1999). However, shrubs may also simultaneously impair performance of understory plants through competition for water (see review in Fowler, 1986) and reduced light availability (Forseth et al., 2001; Hastwell and Facelli, 2003; Holmgren et al., 1997).

In semi-arid systems, shrubs often act as 'islands of fertility' (Garner and Steinberger, 1989; Schlesinger et al., 1996) in which establishment and performance of seedlings beneath their canopies is enhanced by an increase in soil fertility (Carrillo-García et al., 2000; Pugnaire et al., 1996; Reynolds et al., 1999; Shumway, 2000). These hubs of fertility under the shrubs have different species composition and succession dynamics than the surrounding vegetation in gaps (Maestre and Cortina, 2005; Moro et al., 1997; Pugnaire and Lázaro, 2000; Reynolds et al., 1999). However, the role of soil nutrients has rarely been addressed in the context of the facilitation–competition interplay among plant species (Corinna et al., 2005; Rebele, 2000).

Interactions among plant species clearly influence community dynamics in the semi-arid steppe of Patagonia, Argentina, where the community is mainly composed of tussock grasses around 0.3 m in height and hemispherical shrubs 1-m tall. Plant community structure consists of shrub patches often encircled by a dense ring of tussock grasses and surrounded by scattered tussocks in a bare-soil matrix (Soriano et al., 1994). Previous work suggested a model of cyclical succession (*sensu* Watt, 1947) where the interaction between shrubs and grasses drives the cycle and determines the transitions among successional stages (phases) that coincide with specific structural patches (Soriano et al., 1994, see Aguilar and Sala (1999) for a diagram of the model).

The model proposes that shrub establishment can occur in any location in the bare-soil matrix. When shrubs mature, they promote the formation of a ring of grasses beneath their canopies (building phase). The facilitative effects of shrubs on grasses occur through several mechanisms and processes. Shrubs act as traps for seeds, which accumulate beneath their canopies (Aguilar and Sala, 1997), and facilitate the establishment of grass seedlings (Aguilar and Sala, 1994; Aguilar et al., 1992). Aguilar and Sala (1994, 1999) hypothesized that the main mechanisms of facilitation occur via amelioration of microclimatic conditions and an increase in water availability under the canopy compared with bare soil. When the grass ring is complete (mature phase), facilitation by the shrub seems to be counterbalanced and even overshadowed by root competition among grasses (Aguilar et al., 1992), which prevents the establishment of new grass seedlings (Aguilar and Sala, 1994; Aguilar et al., 1992).

Although there is a good understanding of the main factors affecting the formation of the grass rings encircling the shrubs, there is much less information explaining the causes of the degeneration and thinning of the grass ring (degenerative phase) that closes the successional cycle. The model suggests that when the shrub dies and begins to collapse, aerial protection disappears and belowground competition among grasses dominates any remaining facilitative effects of the shrub. At this stage, the density of grasses becomes higher than the current carrying capacity of the grass ring, which results in the death of some tussocks (Aguilar and Sala, 1994) leading to a thinning of the grass ring. Tussock mortality slows down as grass density reaches values equivalent to that of the bare-soil matrix; the ring then loses its identity and the remnant grass individuals form the scattered-tussock patch type (Soriano et al., 1994).

This model of cyclical succession has similarities with others described in some desert systems (e.g., McAuliffe, 1988; Yeaton, 1978), savannas and woodlands (Archer et al., 1988; Olff et al., 1999; Sankaran et al., 2004; Scholes and Archer, 1997), where plant–plant interactions play an important role on vegetation dynamics, structured in cycles of different phases that alternate regularly.

In this Patagonian steppe, grass species appear in different frequencies in the two patches (sparse tussocks and shrub-ring). Two perennial *Stipa* species have disparate spatial distributions. While *Stipa speciosa* Trin and Ruprecht is less frequent under the shrubs than in gaps, *Stipa humilis* Cav. appears more often beneath shrubs than in gaps (Soriano et al., 1994). The association of *S. humilis* with shrubs is species-specific, since it is positively associated with the leguminous shrub *Adesmia volckmanni* Philippi (ex- *Adesmia campestris* Rowlee), and negatively associated to the other common shrub, *Senecio filaginoides* DC (Soriano et al., 1994).

In this study, we explored the mechanisms underlying: (i) the maintenance of the ring of grasses around the shrubs, (ii) its fragmentation during the degenerative phase, and (iii) the causes of the unequal spatial distribution of grasses. We hypothesized that (1) there is strong competition for belowground resources among individual grasses in the ring under shrubs, (2) the maintenance of the ring depends on the balance between the positive effects exerted by the shrub and the negative effects of grass competition, (3) after the shrub dies its positive effects on grasses diminish and competition among grasses prevails, leading to the degeneration of the ring of grasses around the shrub.

For this purpose, we selected *S. humilis* and *S. speciosa* tussocks and analyzed the abiotic environment in which the grasses grew, their physiological status and compared them among different phases of ring fragmentation, from beneath living *Adesmia* shrubs, to dead shrubs to gaps among shrubs (Fig. 1).

2. Materials and methods

2.1. Study site, species

This study was conducted in the Patagonian region of Argentina, in a site located near Río Mayo, Chubut (45°41'S, 70°16'W, 500 m elevation). Mean monthly temperatures ranged from 1 °C in July to 15 °C in January; mean annual rainfall

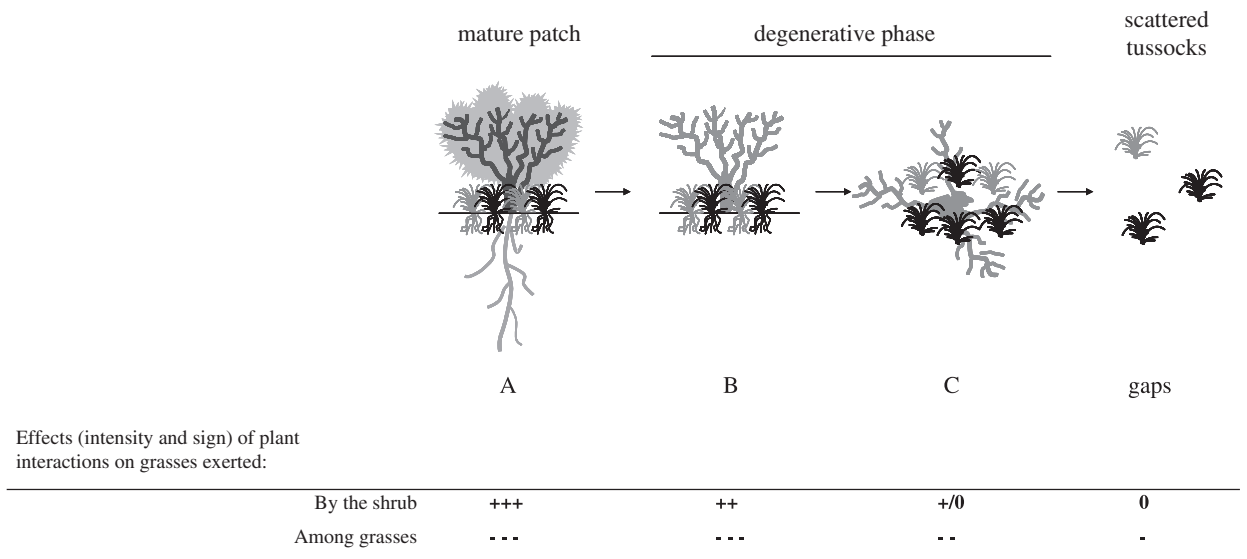


Fig. 1. Four ecological situations where the status of *Stipa speciosa* and *Stipa humilis* tussocks were measured: (A) beneath live *Adesmia* shrubs with complete ring of tussock grasses, (B) beneath recently dead *Adesmia* shrubs and the ring of grasses still complete, (C) around a dead *Adesmia* shrub with its canopy collapsed and the ring of tussock grasses beginning to fragment but it is still recognizable; and in bare ground (gaps). The figure also shows what the model of cyclical succession (Soriano et al., 1994) proposes that will be the result of the interactions of the shrub on grasses and among grasses at these different ecological situations.

recorded over 37 years was 136 mm and ranged between 47 and 230 mm. Precipitation is concentrated in autumn and winter periods (March–September). The area is subject to strong dry winds (15 km h^{-1} annual mean) mostly from the west (Aguilar and Sala, 1997). The soil is coarse textured, contains pebbles that account for 47% of its weight, and has a cemented calcareous layer at about 0.4 m depth (Paruelo et al., 1988). The plant community is mainly composed of grasses and shrubs. Tussock grasses have a basal cover of 33% while shrub cover is 12% (Golluscio et al., 1982). The three dominant shrub species are *A. volckmanni* (ex- *A. campestris*), *Mulinum spinosum* (Cav.) Pers. and *S. flaginoides* (Golluscio et al., 1982). *A. volckmanni* is a deciduous leguminous species, bearing leaves from September to February (Soriano et al., 1994). Its canopy shape is similar to an inverted cone with branches diverging from a central area at the base of the plant.

The three dominant grass species are *S. speciosa*, *S. humilis* and *Poa ligularis* Nees ex. Steud (Golluscio et al., 1982). All are bunch grasses approximately 30 cm in height with linear, plicate leaves. Tussocks of these three species keep old dead leaves as a high proportion of standing biomass. Live tillers of the three species show expanding leaves all year round (Soriano and Sala, 1983).

2.2. Experimental design

In January 2001 (Southern Hemisphere summer), we randomly selected six *Adesmia* shrubs of each life stage (Fig. 1) and marked at random six individuals of *S. humilis* and *S. speciosa* growing in the ring of grasses beneath the shrubs and in bare soil (Fig. 1). In stage A, grasses were part of the complete ring beneath living *Adesmia* shrubs. In stage B, grasses were under recently dead *Adesmia* shrubs with an intact woody canopy. In stage C, grasses were part of a fragmented ring under dead *Adesmia* shrubs with a collapsed canopy leaning on the soil. Finally, in the last stage grasses grew scattered in gaps among shrubs. All selected plants were inside long-term enclosure where large herbivores have been excluded since 1983.

2.3. Shrub-ring size, microclimatic and soil nitrogen measurements

For each *Adesmia* shrub, we measured the largest canopy diameter, its perpendicular diameter, and shrub height. We calculated the projected area and canopy volume considering its shape as an inverse cone, except for *Adesmia* shrubs at stage C where we only measured height. We also recorded the internal and external diameters of the grass ring and derived its basal area as that of a circular crown.

We recorded air temperature every 2 min at 10 cm above the surface with temperature probes connected to HOBO H8 data loggers (Onset Computers, Pocasset, MA, USA) protected with a roof (i.e., a PCV hood) for 5 consecutive days both under the geometrical centre of *Adesmia* shrubs and in the bare-soil matrix ($n = 2$ in each treatment).

To have a qualitative estimation of wind intensity and of the sheltering effect of shrubs, we placed 150 cm² paper flags 15 cm above the soil surface to the east (leeward) of the shrubs and scattered in gaps ($n = 19$ in each situation). Flags were

left in the field for a week and then the area of each flag was scanned, its area measured with image analyzer software (MideBmp, R. Ordiales, 2000) and the lost fraction expressed as percentage of the initial area.

We collected five 500 cm³ samples taken from the upper 5 cm of the soil in each ecological situation. Soils were sieved the same day through a 2-mm mesh. A subsample of 10 g was extracted for determination of inorganic N (NH₄⁺ and NO₃⁻) with 50 ml 2 N KCl. Soil extracts were filtered and analyzed using an AlpKem[®] autoanalyzer (O-I Corporation, College Station, TX, USA). A further subsample was placed in an oven at 105 °C for 48 h for determination of gravimetric soil water content. We corrected soil nitrogen concentrations for soil water content.

2.4. Morphology and physiological measurements on *Stipa* grasses

We harvested three mature, green leaves from different tillers of five individuals of each *Stipa* species living beneath *Adesmia* shrubs and in gaps. Leaves were dried at 70 °C for 72 h and leaf length, width 1 cm above the base, and dry mass were recorded. As leaves of both species are linear and plicate, and wider at the proximal than at the distal end, we calculated the specific leaf area (SLA) and leaf density (*D*) assuming a triangular shape and the volume as that of a cone. These leaf samples were grounded with a mill (5100 Mixer Mill, SPEX CertiPrep, Metuchen, NJ) and analyzed for total N content using the dry combustion method with a CE Instruments NC 2100 elemental analyzer (ThermoQuest, Milan, Italy).

Pre-dawn water potentials (ψ_{pd}) were determined on mature, attached leaves using a pressure chamber (Scholander et al., 1965) on four individuals of each species and treatment.

We measured leaf conductance to water vapor (g_s) of six plants per species and situation on 10 mature, fully developed leaves early in the morning (7:00–8:30 solar time) at full sunlight with a portable infrared gas analyzer (LCi; Analytical Development Company Ltd., Hoddesdon, UK). Leaf temperature during the measurements was within a 5 °C range. We expressed g_s on a projected leaf area, calculated by measuring the width of the group of leaves included in the cuvette. We used Clegg's correction (1992) for cylindrical leaves.

2.5. Data analysis

We analyzed data with the STATISTICA 6.0 software (StatSoft Inc., Tulsa, OK, USA). We log-transformed leaf biomass data to normalize its distribution. Differences between species (*S. humilis* and *S. speciosa*) and among stages (plants growing in gaps and beneath three different shrub stages: alive, recently dead with standing canopy, and dead with canopy spread in the ground; Fig. 1) were tested using two-way ANOVA with a significance level of 5%, after testing the homogeneity of variances using Levene's test. Post-hoc differences were tested using Scheffé's test. Results are presented as mean value \pm 1 S.E.

3. Results

Living (stage A) and recently dead (stage B) *Adesmia* shrubs did not differ significantly in size (Table 1). In stage C, however, branches had fallen and spread on the ground so that height was shorter than in the other stages (Table 1). The ring of grasses growing beneath shrubs had a projected mean area of 0.44 ± 0.06 m², regardless of shrub stage (Table 1).

3.1. Microclimate and soil nitrogen content

Air temperature was lower under *Adesmia* shrubs than in gaps and it was similar beneath live and dead shrubs (Table 2). At the center of the canopy, daily temperature fluctuations were approximately 29 °C, while in gaps between shrubs it was 37.5 °C (Table 2).

Table 1
Size of *Adesmia* shrubs of different life stages and the ring of grasses beneath them

	<i>Adesmia</i> shrub stage		
	A	B	C
Ring of grasses projected area (m ²)	0.370 \pm 0.114a	0.481 \pm 0.124a	0.463 \pm 0.085a
Shrub height (m)	0.852 \pm 0.092a	0.754 \pm 0.054a	0.306 \pm 0.040b
Shrub projected area (m ²)	0.804 \pm 0.091a	0.766 \pm 0.246a	NA
Shrub volume (m ³)	0.232 \pm 0.047a	0.187 \pm 0.064a	NA

Data are mean values \pm 1 S.E. ($n = 6$). Different letters in the same row indicate significant differences at $P < 0.001$. Legend for *Adesmia* shrub stages as in Fig. 1.

The area of paper flags damaged by wind was three to four times greater in gaps and near stage C shrubs than around living or recently dead *Adesmia* shrubs (Table 2, $F_{3,72} = 16.12$, $P < 0.001$), showing that canopies provided an effective protection from wind.

Total inorganic soil N differed under shrubs and in gaps. Soil N was six times greater under live *Adesmia* shrubs than in gaps, and also greater than under dead shrubs (Table 3). Concentrations of ammonium (N–NH₄) in soil showed the same pattern (Table 3), while soil nitrate (N–NO₃) differed only between living shrubs and gaps (Table 3). The ammonium:nitrate ratios were similar in all cases (Table 3).

3.2. Physiological status of grasses

The two *Stipa* species had very different leaf characteristics. Compared to *S. speciosa*, leaves of *S. humilis* were shorter (9.48 ± 0.36 cm vs. 12.65 ± 0.76 cm, $P < 0.001$, Table 4) and narrower (382 ± 12 μ m vs. 481 ± 15 μ m, $P < 0.001$), with lower biomass (5.49 ± 0.24 mg vs. 15.85 ± 1.76 mg, $P < 0.001$) and greater SLA (3.13 ± 0.12 m² kg^{−1} vs. 2.24 ± 0.10 m² kg^{−1}, $P < 0.001$), although leaf density was similar for both species (Table 4).

Within species, neither leaf length nor dry mass differed between plants growing alone or under live shrubs (Tables 4 and 5), but leaf diameter and density did. Plants growing under the shrubs had thinner leaf diameter (409.0 ± 23.1 μ m vs. 454.6 ± 16.5 μ m, $P < 0.05$, Table 4) but higher leaf density (1942.7 ± 474.5 kg m^{−3} vs. 1547.6 ± 224.5 kg m^{−3}, $P < 0.05$) than those in gaps. These differences tended to be slightly more pronounced for *S. humilis* than for *S. speciosa* although they were not statistically significant (Tables 4 and 5).

Table 2

Air temperature beneath *Adesmia* canopies and in bare soil ($n = 2$) and percentage of damaged flag area by the wind ($n = 5$)

		<i>Adesmia</i> shrub stage			In gaps
		A	B	C	
Temperature	Mean	$15.44 \pm 0.09a$	$15.95 \pm 0.09a$	–	$18.45 \pm 0.14b$
	Maximum	34.85	34.01	–	42.46
	Minimum	5.40	5.40	–	4.99
Wind effect	Damaged area (%)	$3.12 \pm 1.02a$	$5.21 \pm 1.22a$	$14.26 \pm 2.04b$	$14.42 \pm 1.43b$

Different letters in the same row indicate significant differences at $P < 0.001$. Legend for *Adesmia* shrub stages as in Fig. 1.

Table 3

Inorganic N content [NH₄–N, NO₃–N and (NH₄–N+NO₃–N)] and NH₄/NO₃ ratios of soils under *Adesmia* shrubs and in gaps

		<i>Adesmia</i> shrub stage			In gaps
		A	B	C	
NH ₄ –N (μ g g ^{−1})		$27.51 \pm 2.06a$	$15.75 \pm 3.33b$	$13.44 \pm 2.26bc$	$4.38 \pm 0.84c$
NO ₃ –N (μ g g ^{−1})		$1.51 \pm 0.42a$	$0.85 \pm 0.17ab$	$0.95 \pm 0.20ab$	$0.30 \pm 0.03b$
N (NH ₄ –N+NO ₃ –N) (μ g g ^{−1})		$29.02 \pm 2.43a$	$16.60 \pm 3.37b$	$14.39 \pm 2.34bc$	$4.69 \pm 0.62c$
NH ₄ /NO ₃		$22.4 \pm 4.0a$	$22.5 \pm 5.9a$	$15.7 \pm 3.2a$	$16.0 \pm 4.5a$

Data are mean values ± 1 S.E. ($n = 5$). Different letters in the same row indicate significant differences at $P < 0.05$. Legend for *Adesmia* shrub stages as in Fig. 1.

Table 4

Results of two-way ANOVA of differences between species and stages for leaf morphology and physiology variables

Variable	Species (Sp)		Stages (St)		Sp \times St	
	F	P	F	P	F	P
Longitude	14.778	0.001	0.145	0.866	3.018	0.069
Diameter	33.889	0.000	7.184	0.016	0.329	0.574
Biomass	33.143	0.000	0.817	0.453	0.560	0.578
SLA	34.697	0.000	3.157	0.095	1.212	0.287
Density	1.131	0.303	5.561	0.031	0.540	0.473
N content	0.034	0.857	6.936	0.006	0.889	0.428
g_s	1.355	0.251	8.694	0.000	0.777	0.514
ψ_{pd}	3.962	0.058	12.950	0.000	1.026	0.399

Bold numbers show significant differences.

Plants of both species had similar leaf N content ($6.89 \pm 0.17 \text{ mg g}^{-1}$ in *S. speciosa* vs. $6.85 \pm 0.23 \text{ mg g}^{-1}$ in *S. humilis*, $P = 0.85$, Fig. 2), but differed under different situations (Table 4, Fig. 2). Both species had greater leaf N content under live or dead *Adesmia* shrubs than in gaps (Fig. 2).

Plants of both species had similar pre-dawn water potentials ($-2.8 \pm 0.2 \text{ MPa}$ in *S. speciosa* vs. $-3.2 \pm 0.2 \text{ MPa}$ in *S. humilis*, Table 4, Fig. 3), but differed under different situations (Table 4, Fig. 3). Both species displayed the most negative water potential under recently dead *Adesmia* shrubs (stage B), significantly lower than in plants growing alone or beneath live shrubs (Fig. 3), while in treatment C (long-dead shrubs) they had intermediate values (Fig. 3).

Both species had similar leaf conductance to water vapor ($0.20 \pm 0.01 \text{ mol m}^{-2} \text{ s}^{-1}$ in *S. speciosa* vs. $0.21 \pm 0.01 \text{ mol m}^{-2} \text{ s}^{-1}$ in *S. humilis*, Table 4, Fig. 4), which varied among treatments (Table 4, Fig. 4). *Stipa* plants in gaps had g_s values significantly higher than plants growing under dead shrubs (stages B and C), while those under live *Adesmia* shrubs had intermediate values (Fig. 4).

Table 5

Average length, width, and leaf dry mass, SLA, and leaf density of *Stipa speciosa* and *Stipa humilis* beneath the canopies of shrubs and in gaps

	<i>Stipa speciosa</i>			<i>Stipa humilis</i>		
	Beneath <i>Adesmia</i>		In gaps	Beneath <i>Adesmia</i>		In gaps
	A	B		A	B	
Length (cm)	$12.97 \pm 0.98a$	$11.07 \pm 1.35a$	$13.91 \pm 1.35a$	$9.03 \pm 0.38a$	$10.76 \pm 0.56a$	$8.91 \pm 0.60a$
Diameter (μm)	$463 \pm 27a$	–	$499 \pm 13a$	$354 \pm 13a$	–	$410 \pm 13b$
Biomass (mg)	$13.74 \pm 1.02a$	$18.65 \pm 4.95a$	$15.17 \pm 1.30a$	$5.60 \pm 0.49a$	$5.42 \pm 0.48a$	$5.45 \pm 0.31a$
SLA ($\text{m}^2 \text{ kg}^{-1}$)	$2.19 \pm 0.15a$	–	$2.29 \pm 0.15a$	$2.91 \pm 0.20a$	–	$3.34 \pm 0.08a$
Density (kg m^{-3})	$1970.3 \pm 233.2a$	–	$1698.3 \pm 102.0a$	$1915.2 \pm 215.8a$	–	$1397.0 \pm 30.55b$

Data are mean values ± 1 S.E. ($n = 5$). Different letters in a variable within each species indicate significant differences between plants growing in the different situations at $P < 0.05$.

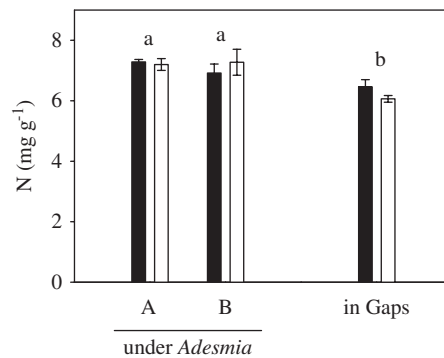


Fig. 2. Leaf N contents of *Stipa speciosa* (solid bars) and *Stipa humilis* (clear bars) growing under *Adesmia* shrubs and in gaps (legend as in Fig. 1). Data are mean values ± 1 S.E. ($n = 4$). Bars with different letters are significantly different at $P < 0.05$.

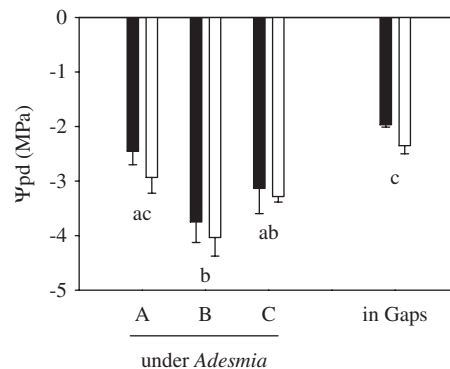


Fig. 3. Pre-dawn water potential of *Stipa speciosa* (solid bars) and *Stipa humilis* (clear bars) leaves under *Adesmia* shrubs and in gaps (legend as in Fig. 1). Data are mean values ± 1 S.E. ($n = 4$). Bars with different letters are significantly different at $P < 0.05$.

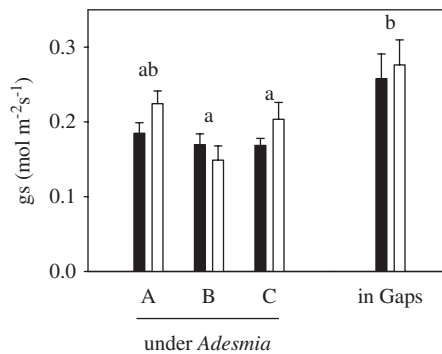


Fig. 4. Leaf conductance to water vapor of *Stipa speciosa* (solid bars) and *Stipa humilis* (clear bars) growing under *Adesmia* shrubs and in gaps (legend as in Fig. 1). Data are mean values \pm 1 S.E. ($n = 6$). Bars with different letters are significantly different at $P < 0.05$.

4. Discussion

Our results highlight some of the mechanisms that maintain the community structure in this Patagonian steppe and suggest which may be a main processes triggering degeneration of the ring of grasses after shrub death. The system is governed by the balance of interactions between shrub and grasses, and is intimately linked to shrub development and senescence. In addition, the contrasting spatial distribution of the two species of *Stipa* may be determined by differences in requirements.

4.1. Effect of the shrub

The physical effects of the shrub were clear; the canopy generated a microclimate, which lowered daily thermal fluctuations and it was an effective shelter against wind (Table 2). The shadow of the shrub may also reduce the evaporative demand of plants in the understory (Fuentes et al., 1984; Moro et al., 1997; Vetaas, 1992) and may decrease evaporation from the soil surface (Domingo et al., 1999), overall improving the water relations of plants under the shrub. This effect can be further increased by sheltering from desiccating winds. Our results agree with (Soriano and Sala, 1986), who showed that wind speed leeward of the shrub was approximately 15% that in open areas, and with Aguiar and Sala (1994), who showed that under shrubs, daily evaporation was 70% lower than in open areas.

In a study in the same community, Aguiar et al. (1992) clearly showed that shrubs facilitate grass recruitment and survival under their canopies, but only when root competition among grasses was avoided. Here we show that, as well as improving the microclimatic conditions, the presence of the shrub increased six fold the amount of inorganic nitrogen in the soil under their canopies in comparison to gaps, significantly improving soil N availability, which translated into improved N status of grasses in the ring. Leaf N content of both species was around 15% higher in grasses growing beneath the shrubs than in gaps.

In arid and semi-arid conditions, facilitation between plant species usually implies an increase in water and nutrient availability (Holzapfel and Mahall, 1999). Shrubs may often act as nurses for other species, promoting seedling establishment through seed trapping and shelter from high temperatures and low soil moisture under their canopies (Flores and Jurado, 2003; Padilla and Pugnaire, 2006). Nurse plants may also increase soil nutrient availability or protect seedlings from browsing and trampling (Flores and Jurado, 2003).

Overall, our results support the hypothesis of the facilitative effect of shrub individuals through changes in soil fertility and probably water demand. While under living *Adesmia* shrubs soil fertility was higher and microclimatic conditions more mesic, gaps represented the opposite conditions, being the other situations in between. Thus, the nurse effect of shrubs on grasses may have important implications on the productivity and resource use patterns in this system. Shrub cover is about half that of grasses (Fernández et al., 1991), but both have similar aboveground net primary production (ANPP; Jobbágy and Sala, 2000), leading to a high concentration of ANPP in shrub-ring patches, which contribute to as much as 44% of the total primary productivity of this steppe community (Soriano et al., 1994).

4.2. Interaction between grasses

The positive effects of *Adesmia* on its understory soil did not translate into improved water status of grasses. Regardless of the particular grass species, plants under living *Adesmia* shrubs had similar water potential and conductance to water vapor than those in gaps. It may be caused by the intense competition for water among grasses within the ring (Aguiar et al., 1992; Soriano and Sala, 1986) counterbalancing the positive effects of the shrub on the grasses. Sala et al. (1989) showed that there was little root competition between shrubs and grasses as their root systems were spatially segregated (Fernández and Paruelo, 1988). However, Aguiar et al. (1992) and Aguiar and Sala (1994) showed that root competition

among grasses did occur in mature rings beneath living shrubs, and that it was more intense than in gaps. At this successional stage (mature phase; stage A in Fig. 1), the ring of grasses is at its maximum plant density and complete (*sensu* Soriano et al. 1994), and belowground competition overshadows the facilitative effects of the shrub, negatively affecting growth and survival of new grass seedlings (Aguilar and Sala, 1994; Aguilar et al., 1992). However, when root competition is experimentally avoided, the positive effects of the shrub on the establishment of new grass seedling were evident (Aguilar et al., 1992).

Our results show that in the degenerative phase of the ring (stages B and C), leaf conductance to water vapor and water potential of grasses decreased by around 40% (stage B) and by 20–30% (stage C) relative to values displayed by plants living in gaps. When the shrub dies, amelioration of microclimatic conditions underneath the canopy decreases, the positive effects of the shrub start to vanish (stage B) and finally disappear (stage C), but grass competition for water remains. On the other hand, competition intensity among grass individuals likely tends to decrease as the ring disaggregated until it reaches cover values similar to that in gaps. This is the first experimental support for this process, already predicted by Soriano et al. (1994).

The pattern of soil inorganic N in this system is linked to the shrub life history, micrometeorological conditions, and N uptake by grasses. While the shrub is alive, litter decomposition provides an input of N into the soil. But when the shrub dies, litter production ceases and nutrients come from the slowly decomposing woody tissues, much more recalcitrant than leaves (Gallardo and Merino, 1993). In addition, higher wind speed may lead to higher N losses via wind erosion (Buschiazzo et al., 2007; Neff et al., 2005). We did not find significant differences in leaf N content of grasses under living or recently dead shrubs. In the long term, however, continuous grass nutrient uptake may lead to the depletion of available soil N affecting grass nutrient status.

Our results suggest interesting time lags in the response of grass individuals after the death of the nurse shrubs. The loss of the shrub canopy may result in an immediate increase in wind speed and loss of protection, along with a gradual decrease in soil fertility. The loss of facilitation may not result in an immediate reduction of grass density. After the shrub death, we observed a decrease in the performance of individual grasses shown by decreased water status and stomatal conductance. This change could translate, later on, in demographic changes that would result in the thinning of the grass ring, the loss of its integrity, and the merging into the scattered-tussock patch type (Aguilar and Sala, 1999).

4.3. Spatial distribution of *Stipa* species and soil nitrogen

These two *Stipa* species have different spatial distribution in this system; while *S. humilis* was positively associated with *A. volckmanni*, *S. speciosa* is negatively associated (Soriano et al., 1994). Water availability may not be the factor determining this differential spatial distribution, since both species have similar water status in the different ecological phases studied here (Figs. 3 and 4). However, *S. speciosa* may be more resistant than *S. humilis* to stressful conditions since it is more abundant in gaps than beneath shrubs (Soriano et al., 1994). On the other hand, the reason explaining the association of *S. humilis* with leguminous *Adesmia* shrubs may be the higher N availability. *S. speciosa* is usually more abundant than *S. humilis* in bare soils except in one particular situation, those areas surrounding drinking troughs for sheep. Here, there is a buildup of soil nitrogen because of animal droppings and urine, and in these areas, *S. humilis* is more abundant than *S. speciosa* in gaps (O.E. Sala, personal observation). Therefore, its positive association with N-rich soils suggests that may be a key factor for *S. humilis*. It may also explain the differences found in the spatial association of this grass to different shrub species. *A. volckmanni* is a leguminous species able to fix nitrogen (Golluscio et al., 2006), which may lead to a higher soil N content than under other shrubs species to which *S. humilis* is negatively associated, like *S. flaginoides* (Soriano et al., 1994). Future studies should analyze the spatial association of *S. humilis* with nitrogen rich soils, and more importantly, should analyze the likely strong effect of large herbivores on the outcome of the interaction among grass species in these Patagonian pastures.

In semi-arid environments, many nurse plants are nitrogen-fixing species (Flores and Jurado, 2003). Legumes enhance rates of colonization and growth of other species, alter species composition and drive succession dynamics on nutrient-poor soils (Chapin et al., 1994; Moro et al., 1997; Shumway, 2000; Vitousek and Walker, 1989). However, these facilitation effects may be offset by competition for resources such as light or water (Chapin et al., 1994; Morris and Wood, 1989).

The differential spatial distribution of the two *Stipa* species and our results point to slightly different effects of nitrogen-fixing *Adesmia* shrubs on the two grass species, suggesting that it may be species-specific and would depend on their dissimilar requirements. While *S. speciosa* may be a better competitor than *S. humilis* in poor soils—i.e., gaps between shrubs—*S. humilis* could be better in more fertile soils—i.e., under the N-fixing shrub. Further research on the different competitive abilities of both *Stipa* species and its relation to their spatial pattern across nitrogen gradients is, however, needed.

Finally, this study enhances the importance of indirect plant–plant interactions (i.e., the effect of shrubs on changing the outcome of the interaction between grasses) in semi-arid environments. It also provides some insight for future studies on herbivore mediated indirect interactions in the Patagonian steppe. While the latter aspect has been widely analyzed in many ecosystems (see review in Hambäck and Beckerman, 2003; van der Wal and Brooker, 2004), plant–plant indirect interactions has been overlooked in semi-arid communities, as they are considered effective mainly in mesic environments (Brooker et al., 2008). Our results support the idea that facilitative effects of the shrub on the grasses alleviate the

competition among grasses, creating non-transitive networks of interactions that promote coexistence of species with different competitive abilities (Callaway, 2007).

In conclusion, our results in the Patagonian steppe support the model of cyclical succession, and suggest that the fragmentation of the ring of grasses may be caused by competition, while the maintenance of the ring beneath live shrubs is caused by the positive effects of the shrubs on the grasses. The two *Stipa* species may have different resource requirements. The different spatial distribution of *Stipa* species in this system suggest that *S. speciosa* may withstand relatively poorer soils and adverse conditions than *S. humilis* which performs better with higher levels of soil N. We suggest that as long as *Adesmia* shrubs are alive, both *Stipa* species can coexist under the canopy in close spatial arrangement and maintain equilibrium. When the facilitative effects of the shrub decrease after the shrub death, *S. speciosa* may have a competitive advantage over *S. humilis* that results in a new equilibrium with the dominance of *S. speciosa*.

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