



Relationship between plant nitrogen conservation strategies and the dynamics of soil nitrogen in the arid Patagonian Monte, Argentina

Analía Lorena Carrera^{1,3}, Mónica Beatriz Bertiller¹, Claudia Leticia Sain¹ & María Julia Mazzarino²

¹*Centro Nacional Patagónico (CONICET), Boulevard Brown s/n, 9120 Puerto Madryn, Chubut, Argentina.*

²*Centro Regional Universitario Bariloche, Universidad Nacional del Comahue-CONICET.* ³*Corresponding author**

Received 29 October 2002. Accepted in revised form 31 March 2003

Key words: arid shrublands, evergreen shrubs, microbial-N, N-resorption efficiency, perennial grasses, potential N-mineralisation

Abstract

During three consecutive years with contrasting precipitation, we analysed the relationship between strategies of N conservation in the dominant plant functional groups (perennial grasses and evergreen shrubs) of the Patagonian Monte and the main components of N cycling in soil. We hypothesised that the different patterns of N conservation in perennial grasses and evergreen shrubs would have direct consequences for soil-N, inorganic-N release and microbial-N flush in soil. In autumn and late spring of 1999, 2000, and 2001, we assessed N and C concentration in green and senesced leaves, N-resorption efficiency and C/N ratio in senesced leaves of three dominant species of each plant functional group. In the soil associated with species of each plant functional group, we determined N and C concentration, potential-N mineralisation, and the associated microbial-N flush. Slow-growing evergreen shrubs exhibited low N-concentration in green leaves, high N-concentration in senesced leaves and low N-resorption from senescing leaves. In contrast, fast-growing perennial grasses showed high N-concentration in green leaves, low N-concentration in senesced leaves, and high N-resorption from senescing leaves. In evergreen shrubs, the maintenance of long-lasting green leaves with low N-concentration was the most important mechanism of N conservation. In contrast, perennial grasses conserved N through high N-resorption from senescing leaves. Soil-N concentration, potential N-mineralisation, and microbial-N flush in the soil were higher underneath evergreen shrubs than beneath perennial grasses. Observed differences, however, were lower than expected considering the quality of the organic matter supplied by each plant functional group to the soil. A possible reason for this relatively weak trend may be the capacity of evergreen shrubs to slow down N cycling through low leaf turnover and the presence of secondary compounds in leaves. Alternatively or simultaneously, the weak relationship between plant and soil N could result from shrubs being able to colonise N-poor soils while grasses may preferably occupy fertile microsites previously influenced by the decomposition pathway of evergreen shrubs. Differences between evergreen shrubs and perennial grasses in the mechanisms of plant N-conservation and in components of N cycling in the underlying soil were consistent over the three years of the study with differing precipitation. Inter-annual differences in N concentration in green leaves and in the microbial-N flush in soil indicate that during the wettest year fast-growing perennial grasses would outcompete slow-growing evergreen shrubs and microorganisms for N uptake.

Introduction

Nitrogen is one of the most limiting nutrients in arid ecosystems (Skujins, 1981) and N availability in soil

* FAX No: +54-2965-451543. E-mail: unanalía@cenpat.edu.ar

is strongly coupled with the quantity and quality of litterfall along with the decomposition/mineralisation pathway controlled by the erratic water inputs (Aerts, 1996; Binkley, 1994; Bloemhof and Berendse, 1995; Martin and Aber, 1997; Vinton and Burke, 1995; Vitousek et al., 1982). Leaf lifespan and N resorption from senescing leaves are strongly related to litter production and decomposability, respectively. Nitrogen resorption from senescing leaves is usually expressed as the proportion of N reduction in senesced leaves as compared to green leaves or by the N concentration in senesced leaves (N-resorption efficiency and N-resorption proficiency, respectively, *sensu* Killingbeck, 1996). Strong mechanisms of N resorption in plants are often associated with N-poor litter, low N-mineralisation rates, low-N availability in soil, and high-N retention in microbial biomass (Aerts, 1996, 1999; Aerts and Van der Peijl, 1993; Bloemhof and Berendse, 1995; Eckstein et al., 1998; Lambers et al., 1998; Mazzarino et al., 1998b; Schlesinger, 1991; Wedin and Tilman, 1990). In contrast N non-reabsorbed from senescing leaves may circulate in the ecosystem through litterfall and subsequent decomposition processes (Aerts, 1996; Hooper and Vitousek, 1998; Lambers et al., 1998; Wedin and Tilman, 1990). However, rapid decomposability and mineralisation of N-rich litter may not always be associated with high-N availability in soil since losses of mineralised-N by denitrification and leaching may also be high (Schlesinger, 1991). Despite such evidence, the relationship between mechanisms of N-conservation in plants (i.e. high N-resorption, long leaf lifespan, low N-concentration in green leaves) and N-fertility and related soil processes (i.e. N-concentration, N-mineralisation or N-microbial biomass) remain uncertain (Aerts, 1996; Aerts and Chapin III, 2000; Lambers et al., 1998; Vinton and Burke, 1995). Since many arid ecosystems undergo significant changes in species composition following man induced disturbance (Bertiller and Bisigato, 1998; Schlesinger, 1996), the identification of plant controls on N pools and N cycling is an essential step in understanding their functioning (Vinton and Burke, 1995).

As in other arid ecosystems, the vegetation in the Patagonian Monte presents a patchy structure that induces islands of soil fertility (Bertiller et al., 2002; Garcia-Moya and McKell, 1970; Ithori et al., 1995; Mazzarino et al., 1998a; Rostagno et al., 1991; Vinton and Burke, 1995). Patches are dominated by two plant functional groups: perennial grasses and evergreen shrubs. Previous studies have indicated that

perennial grasses and evergreen shrubs exhibit quite different mechanisms of N-conservation. Evergreen shrubs showed lower N-resorption from senescing leaves, lower N-concentration in green leaves, higher N-concentration in senesced leaves, lower C/N ratio in senesced leaves, and lower leaf turn over than perennial grasses (Carrera et al., 2000; Mazzarino and Bertiller, 1999; Mazzarino et al., 1998b).

We hypothesised that the differential patterns of N-conservation between perennial grasses and evergreen shrubs would have direct consequences in soil-N, inorganic-N release and the microbial-N flush in soil. We predicted: (1) higher soil-N concentration and potential N-mineralisation beneath shrubs than underneath perennial grasses and (2) lower microbial-N flush beneath shrubs than under grasses.

Materials and methods

Study area

The study area is located in northeastern Patagonia (Argentina), 40 km west of Puerto Madryn (42° 39' S, 65° 23' W, 115 m a.s.l.). Mean annual temperature is 13.7 °C (15 year series) and mean annual precipitation is 188 mm (Bertiller, 1998). Both Typic Petrocalcids and Typic Haplocalcids soils are present in the area (del Valle, 1998; Soil Survey Staff, 1998). Large domestic herbivores were excluded for a period of 7 years from the study area of about 2 ha. Vegetation of the study site is representative of the shrubland of *Larrea divaricata* Cav. and *Stipa* spp., characteristic of the southern portion of the Monte Phytogeographic Province (Cabrera, 1976; Soriano, 1950). Evergreen shrubs and perennial grasses dominate the plant canopy, covering between 40 and 60% of the soil. Plant cover presents a random patchy structure consisting of large patches formed by shrub clumps encircled by perennial grasses, incipient plant patches composed by one shrub encircled by perennial grasses, and isolated individuals of grasses or dwarf shrubs colonizing bare soil areas (Bisigato and Bertiller, 1997; Mazzarino et al., 1996). Sampling was carried out during three consecutive years (1999–2001) with contrasting rainfall. Precipitation was recorded by a weather station located in the study site. Annual precipitation amounts were 358 mm, 208 mm, 278 mm, in 1999, 2000, 2001, respectively.

Plant attributes

At each sampling date (June and December 1999–2001), we randomly selected five individuals of each dominant evergreen shrub (*Junellia seriphioides* (Gilles and Hook) Moldenke, *Larrea divaricata* Cav., and *Atriplex lampa* Gill. ex Moq.), and five individuals of each dominant perennial grass (*Stipa tenuis* Phil., *Stipa speciosa* Trin. and Rupr., and *Poa ligularis* Nees ex Steud.). The vegetative growing period occurs during autumn in perennial grasses and during spring in evergreen shrubs while senescence occurs in both plant groups during summer drought (Bertilier et al., 1991). Evergreen shrubs have lower leaf turnover than perennial grasses (Carrera et al., 2000) but shedding of leaves mostly occurs immediately after senescence while in perennial grasses senesced leaves may stay attached to the plant during several years (Defossé et al., 1990). We harvested four branches from each evergreen shrub and all the aboveground biomass from each perennial grass. Recently senesced leaves (yellow-brown leaves without signs of deterioration) were separated from each evergreen shrub branch or perennial grass individual at June and December. Fully expanded green leaves were only collected during the vegetative period of each plant group (June for grasses and December for shrubs). In this way, we sampled green and senesced leaves from about the same age for both plant groups thus avoiding eventual variation in N concentration of leaves between plant groups due to age. After sampling, both green and senesced leaves were dried at 60 °C for 48 h, weighed and analysed for their N-concentration by semi-micro Kjeldahl (Coombs et al., 1985). Nitrogen concentration in senesced leaves was used as an indicator of N-resorption proficiency (Killingbeck, 1996). Nitrogen-resorption efficiency (Killingbeck, 1996) was calculated as follows:

$$\text{N-resorption efficiency (\%)} = \frac{(N_g - N_s)}{N_g} * 100,$$

where N_g is the concentration of N in green leaves and N_s is the concentration of N in senesced leaves. We measured organic C-concentration in senesced leaves by dry digestion at 550 °C (Schlesinger and Hasey, 1981).

Soil attributes

At each sampling date, soils underneath each harvested plant were sampled with a metallic tube (10

cm height and 10 cm in diameter). One soil sub-sample was air-dried, sieved to 0.5 mm and analysed for soil-N concentration by semi-micro Kjeldahl (Bremmer and Mulvaney, 1982) and for soil organic C-concentration by wet combustion (Nelson and Sommers, 1982). The rest of the soil was sieved to 2 mm and a sub-sample incubated at 25 °C and at 15% soil moisture for 42 days for the estimation of the potential N-mineralisation. After incubation, soil samples were extracted with 2 M KCl (1:5 sample: solution ratio) and analysed for N-NH_4^+ and N-NO_3^- . N-NH_4^+ was determined by the indophenol-blue method using the 'Uremia kit' of Wiener Lab. and N-NO_3^- by copperised Cd reduction (Keeney and Nelson, 1982). The other sub-sample was used to estimate the potential microbial-N flush by a modification of the chloroform fumigation-incubation technique (Vitousek and Matson, 1985). Microbial-N flush (F_n) is defined as the flush of NH_4^+ due to fumigation (Horwarth and Paul, 1994). After 10 days of soil incubation at 15% soil moisture at 25 °C, 1 mL of chloroform was added directly to each soil sample. Samples were then stirred, left in sealed beakers for 20 h, and incubated for a further 10 days. Samples were extracted with 2M KCl (1:5 soil: solution ratio) and analysed colorimetrically for N-NH_4^+ (Mazzarino et al., 1991, 1996). No attempt was made to express the microbial-N flush in terms of microbial biomass, since reported values of recovery factor are extremely variable ($k_N = 0.41-0.68$) depending on the N content of soil microorganisms (Mazzarino et al., 1998a). Both, potential N-mineralisation and the microbial-N flush were expressed according to oven-dried (105 °C) soil weight.

The significance of the differences in plant and soil parameters between plant functional groups and years was evaluated by multifactorial ANOVA (Norris, 1997). Tukey's test was used for multiple comparisons (Norris, 1997). Variable transformation was performed if needed in order to meet the assumptions of the analysis of variance (Sokal and Rohlf, 1981). The relationships between plant and soil variables were described by regression analysis. We selected the best least squares fit between a linear and a non-linear saturation function depending on the shape of the variable response (Norris, 1997).

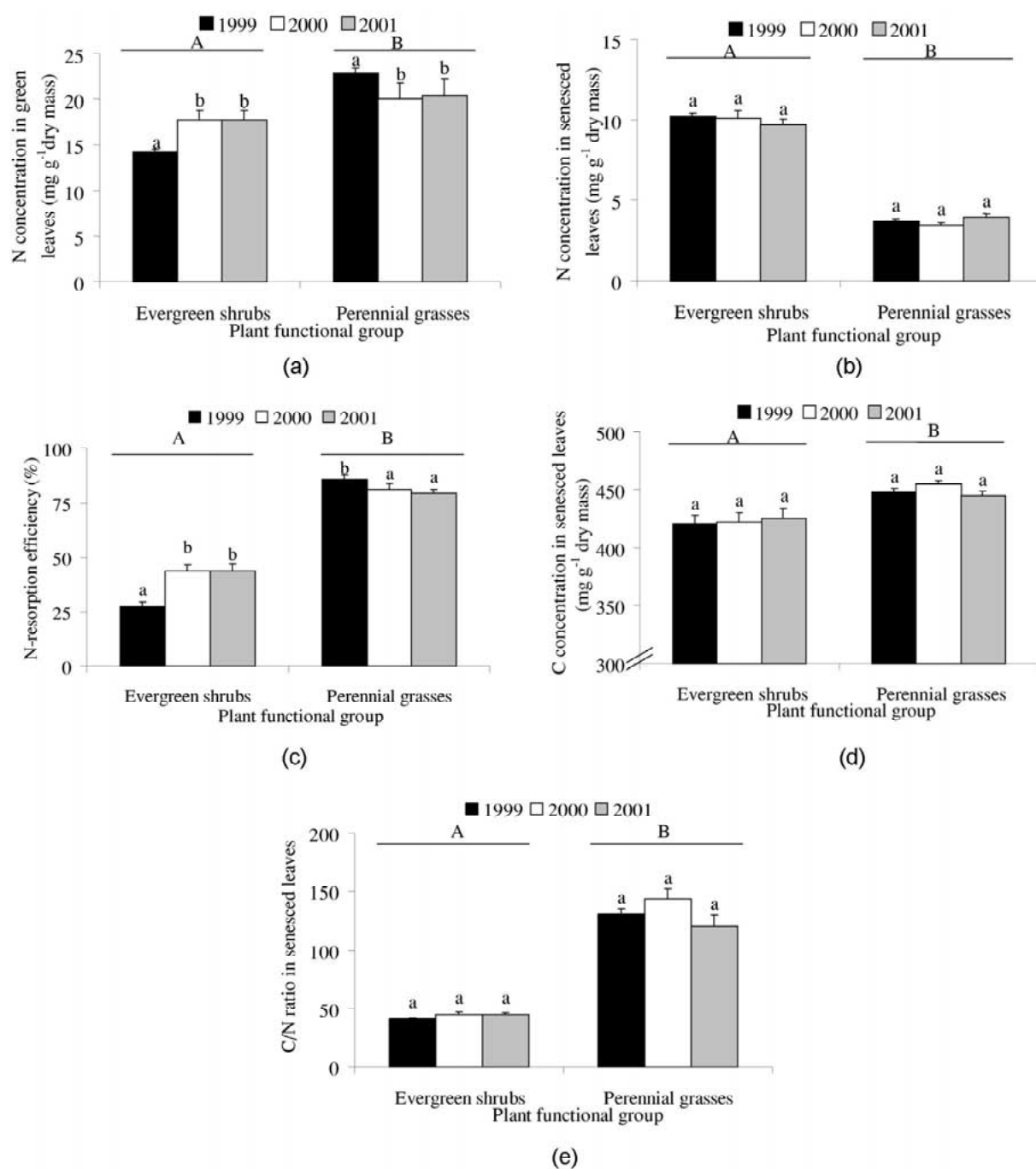


Figure 1. Mean values of: (a) N concentration in green leaves (mg g^{-1} dry mass), (b) N concentration in senesced leaves (mg g^{-1} dry mass), (c) N-resorption efficiency (%), (d) C concentration in senesced leaves (mg g^{-1} dry mass), and (e) C/N ratio in senesced leaves of evergreen shrubs and perennial grasses in different years. Different capital letters indicate significant differences among plant functional groups. Different lowercase letters indicate significant differences among years within each plant functional group. Vertical lines indicate 1 Standard error.

Results

Plant attributes

The N-concentration in green leaves (Figure 1a) was significantly lower in evergreen shrubs than in perennial grasses ($F_{1,180} = 41.94$, $P < 0.01$) and varied among years depending on the plant functional group (significant interaction between year and plant functional group, $F_{2,180} = 3.88$, $P = 0.02$). In perennial grasses, the N-concentration in green leaves was significantly higher in 1999 than in 2000 and 2001 while the reverse was observed in evergreen shrubs. The N-concentration in senesced leaves (Figure 1b) was significantly higher in evergreen shrubs than in perennial grasses ($F_{1,180} = 471.15$, $P < 0.01$) and did not vary among years ($F_{2,180} = 0.15$, $P = 0.87$). Nitrogen-resorption efficiency (Figure 1c) differed significantly between plant functional groups (evergreen shrubs < perennial grasses, $F_{1,180} = 34.68$, $P = 0.03$) and varied significantly among years depending on the plant functional group (significant interaction between plant functional group and year, $F_{2,180} = 13.51$, $P < 0.01$). Perennial grasses showed higher N-resorption efficiency in 1999 than in 2000 and 2001 while the reverse occurred in evergreen shrubs. The C-concentration and C/N ratio in senesced leaves (Figures 1d and 1e, respectively) were significantly lower in evergreen shrubs than in perennial grasses ($F_{1,180} = 53.14$, $P = 0.02$, and $F_{1,180} = 163.00$, $P < 0.01$, respectively) and did not vary among years ($F_{2,180} = 1.09$, $P = 0.48$, and $F_{2,180} = 1.21$, $P = 0.45$, respectively).

Soil attributes

Soil N (Figure 2a) and organic C (Figure 2b) concentration were higher under evergreen shrubs than beneath perennial grasses ($F_{1,180} = 21.57$, $P = 0.04$ and $F_{1,180} = 11.93$, $P < 0.01$, respectively), however there were no differences in soil-N and organic-C concentration among years ($F_{2,180} = 0.66$, $P = 0.60$ and $F_{1,180} = 4.70$, $P = 0.18$, respectively). Potential N-mineralisation in soil (Figure 2c) was higher underneath evergreen shrubs than under perennial grasses ($F_{1,178} = 56.36$, $P = 0.02$) and did not vary among years ($F_{2,178} = 7.69$, $P = 0.12$). The microbial-N flush (Figure 2d) was higher under evergreen shrubs than beneath perennial grasses ($F_{1,180} = 130.47$, $P < 0.01$) and varied significantly among years ($F_{2,180} = 330.58$, $P < 0.01$), being lower in 1999 than in the other two years.

Relationship among plant and soil attributes

The C/N ratio in senesced leaves explained only 12% of the variation in soil-N concentration ($F_{180} = 24.82$, $P < 0.01$, Table 1a). Nitrogen concentration in senesced leaves and N-resorption efficiency explained 5% (positively linear correlated) and 6% (negatively linear correlated) of the total soil N variance, respectively ($F_{180} = 10.5$, $P < 0.01$, and $F_{90} = 6.2$, $P = 0.02$, respectively, Table 1b and 1c). Nitrogen and C concentration in senesced leaves were related to the potential N-mineralisation, explaining 17% of the total variance (Table 2). The microbial-N flush was not significantly ($P > 0.05$) related to C/N ratio in senesced leaves. Nitrogen concentration in soil was positively correlated to the microbial-N flush, explaining 16% of the total variance (Table 3). Soil-N concentration and microbial-N flush accounted for 83% of the total variation of potential N-mineralisation (Table 4).

Discussion

Our results indicate that evergreen shrubs in the Patagonian Monte reduce their nutrient losses mainly by long lifespan of leaves and low nutrient concentration in green tissues rather than by a high nutrient resorption from senescing leaves. Low N-resorption in evergreen shrubs leads to the production of N-rich litter that contributes to increase N concentration in the underlying soil. This contrasts with results of other studies reporting that slow-growing species tend to depress nitrogen cycling through the production of N-poor litter (Aerts and Chapin III, 2000; Crawley, 1998). Since evergreen shrubs usually colonize nutrient-poorer habitats than those of perennial grasses (Bertiller and Bisigato, 1998; Bisigato and Bertiller, 1997, 1999), our findings would support the hypothesis that high nutrient retention rather than high nitrogen use efficiency would be selected in nutrient-poor habitats (Aerts and Chapin III, 2000).

We also found that differences in mechanisms of N conservation between evergreen shrubs and perennial grasses persisted over several years with different annual precipitation. Moreover, differences in N-concentration in green leaves between perennial grasses and evergreen shrubs increased in the wettest year (358 mm) in comparison with the other years (208 mm and 278 mm). A possible explanation for this inter-annual variation is that fast-growing perennial grasses are more sensitive than slow-growing

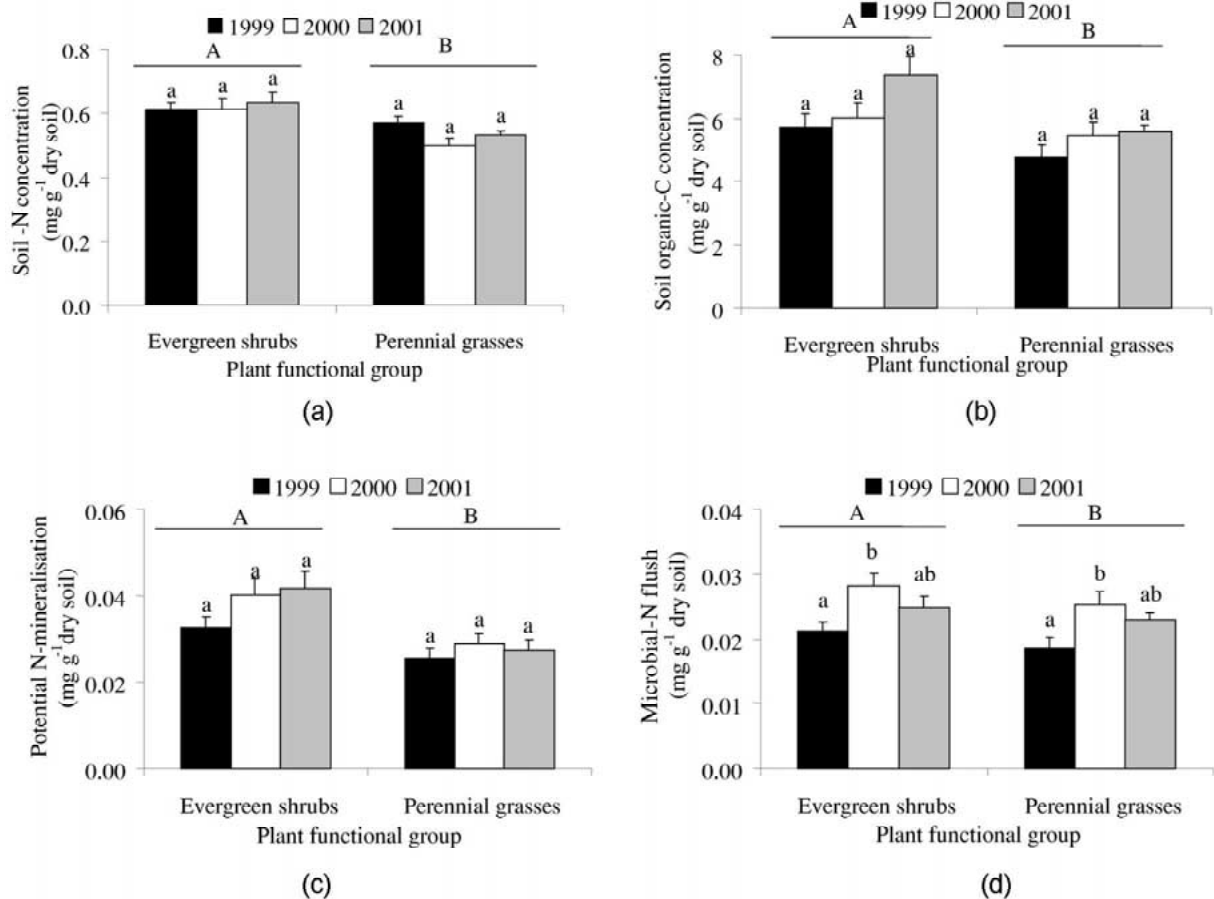


Figure 2. Mean values of: (a) N concentration (mg g^{-1} dry soil), (b) organic-C concentration (mg g^{-1} dry soil), (c) potential N-mineralisation (mg g^{-1} dry soil), and (d) microbial-N flush (mg g^{-1} dry soil) in the soil associated with evergreen shrubs and perennial grasses in different years. Different capital letters indicate significant differences among plant functional groups. Different lowercase letters indicate significant differences among years within each plant functional group. Vertical lines indicate 1 Standard error.

evergreen shrubs to changing water inputs and N availability (Bertiller et al., 1991) and can respond more quickly. Mazzarino et al. (1998a) found that soil-N availability increases during wet years. This may result in fast growth of perennial grasses that would out-compete evergreen shrubs for capture of N from soil (Bertiller et al., 1991; Sala et al., 1989). Such negative interaction of perennial grasses with evergreen shrubs would be reflected in the reduction of N-concentration in green leaves of evergreen shrubs and in the lack of 'luxury uptake' in this plant group, contrasting with results reported for other slow-growing species (Crawley, 1998; Garnier, 1998).

In accordance with Killingbeck (1996), our results indicate that N-resorption proficiency (N-concentration in senesced leaves) seems to be an adequate indicator of the inherent resorption ability of

species since it did not depend on climatic variation. In contrast, the variation of N-resorption efficiency was coupled with the variation in N concentration in green leaves induced by water and N availability. Thus, in evergreen shrubs, N-resorption efficiency was lower in the wettest year than in the two other years and the reverse occurred with perennial grasses. In other species with low nutrient resorption, it has been reported that N resorption was reduced with decreasing water availability (Lambers et al., 1998). This might have passed unnoticed in our three-year study during which the annual precipitation was higher than the long-term annual average for the area (188 mm).

According to prediction 1, soil-N concentration, and potential N-mineralisation in the soil were higher underneath evergreen shrubs than beneath perennial grasses. Observed differences, however, were lower

Table 1. Simple regression analysis between soil N-concentration (dependent variable) and (a) C/N ratio in senesced leaves, (b) N concentration in senesced leaves and (c) N-resorption efficiency (independent variables). (i) ANOVA of simple regression and (ii) fitted parameter values

(i) Analysis of variance							(ii) Parameter estimates				
Source	df	MS	F	P	R ²	Curve fitted	Variable entered	Regression coefficient	t	P	
(a) Dependent variable: Soil-N concentration vs. C/N ratio in senesced leaves (independent variable)											
Regression	1	0.49	24.60	<0.01	0.12	Inverse	Constant	0.47	20.16	<0.01	
Residual	178	0.02					C/N ratio in senesced leaves	6.11	4.96	<0.01	
Total	179										
(b) Dependent variable: Soil-N concentration vs. N concentration in senesced leaves (independent variable)											
Regression	1	0.22	10.16	<0.01	0.05	Linear	Constant	0.50	3.19	<0.01	
Residual	178	0.02					N in senesced leaves	0.01	20.89	<0.01	
Total	179										
(c) Dependent variable: Soil-N concentration vs. N-resorption efficiency (independent variable)											
Regression	1	0.13	6.19	=0.02	0.06	Linear	Constant	0.65	17.89	<0.01	
Residual	88	2.1 × 10 ⁻²					N-resorption efficiency	-1.4 × 10 ⁻³	-2.49	=0.02	
Total	89										

Table 2. Multiple regression analysis between potential N-mineralisation (dependent variable) and N and C concentration in senesced leaves (independent variables). (i) ANOVA of multiple regression and (ii) fitted parameter values

Dependent variable: Potential N-mineralisation											
(i) Analysis of variance							(ii) Parameter estimates				
	Variable entered	Source	df	MS	F	P	R ²	Variable entered	Regression coefficient	t	P
Step 1	C in senesced leaves	Regression	1	6.7 × 10 ⁻³	23.95	<0.01	0.13	Constant	0.11	6.99	<0.01
		Residual	178	2.8 × 10 ⁻⁴				C in senesced leaves	-1.7 × 10 ⁻⁴	-4.89	<0.01
		Total	179								
Step 2	N in senesced leaves	Regression	2	4.5 × 10 ⁻³	16.88	<0.01	0.17	Constant	8.9 × 10 ⁻²	5.52	<0.01
		Residual	177	2.7 × 10 ⁻⁴				C in senesced leaves	-1.5 × 10 ⁻⁴	-4.20	<0.01
		Total	179					N in senesced leaves	1.1 × 10 ⁻³	2.95	<0.01

Table 3. Simple regression analysis between microbial-N flush (dependent variable) and soil N-concentration (independent variable). (i) ANOVA of simple regression and (ii) fitted parameter values

Dependent variable: microbial N-flush vs. soil-N concentration										
(i) Analysis of variance							(ii) Parameter estimates			
Source	df	MS	F	P	R ²	Curve fitted	Variable entered	Regression coefficient	t	P
Regression	1	2.5 × 10 ⁻³	32.87	<0.01	0.16	Linear	Constant	9.7 × 10 ⁻³	3.83	<0.01
Residual	178	7.5 × 10 ⁻⁵					Soil-N	2.5 × 10 ⁻²	5.73	<0.01
Total	179									

than expected considering the quality of the organic matter supplied by each plant functional group to the soil. A possible reason for this weak trend may

consist in the eventual capacity of evergreen shrubs to slow down N-cycling through low leaf turnover (Carrera et al., 2000) and the presence of second-

Table 4. Multiple regression analysis between potential N-mineralisation (dependent variable) and soil-N concentration and microbial-N flush (independent variables). (i) ANOVA of multiple regression and (ii) fitted parameter values

Dependent variable: Potential N-mineralisation										
(i) Analysis of variance							(ii) Parameter estimates			
Variable entered	Source	df	MS	F	P	R ²	Variable entered	Regression coefficient	t	P
Step 1 Soil-N	Regression	1	0.18	656.2	<0.01	0.81	Constant	not significant		
	Residual	176	2.7×10 ⁻⁴				Soil-N	5.7×10 ⁻²	25.6	<0.01
	Total	177								
Step 2 Microbial-N flush	Regression	2	0.09	373.8	<0.01	0.83	Constant	not significant		
	Residual	175	2.5×10 ⁻⁴				Soil-N	3.3×10 ⁻²	5.5	<0.01
	Total	177					Microbial-N flush	0.6	4.3	<0.01

ary compounds in leaves such as lignin, terpenoids or phenolics (Aerts and Chapin III, 2000; Harborne, 1998; Mazzarino et al., 1998b). Low leaf turnover in evergreen shrubs, however, may eventually be compensated with a rapid shedding of senesced leaves relative to perennial grasses in which senesced leaves may stay attached to the plant during several years (Defossé et al., 1990). Secondary compounds in leaves may lead to low litter decomposability but also to precipitation of proteins reducing N-resorption and N-use efficiency (Aerts and Chapin III, 2000; Chapin III and Kedrowski, 1983; del Valle and Rosell, 1999). High concentration of secondary compounds in plant tissues has been directly related to low productive species (Aerts and Chapin III, 2000) and has been reported for evergreen shrubs of Patagonia and the Patagonian Monte (Correa, 1971; Mazzarino et al., 1998b). Alternatively or simultaneously, the lack of strong differences in N-concentration between soils underneath perennial grasses and evergreen shrubs could be also related to the past history of the soil that each plant group is able to colonise. Perennial grasses, due to their inherent mesophytic traits (i.e. high N concentration in green leaves, and high growth rates), would be more dependent on decomposition pathway and soil N-availability and would be more restricted to colonising nutrient-rich microhabitats than evergreen shrubs. Preliminary results in the Patagonian Monte indicate that perennial grasses establish more successfully in fertile micro-habitats neighbouring shrub patches than in unfertile inter-patch soil (Bisigato and Bertiller, 1999, pers. comm.).

In contrast with prediction 2, the microbial-N flush in soil was higher underneath evergreen shrubs than

beneath perennial grasses and was strongly positively correlated to potential N-mineralisation. This implies an important mechanism to avoid N-losses by leaching or denitrification and to conserve N in a labile and readily mineralisable form in the soil underneath evergreen shrubs. In arid and semiarid environments, microbial mortality during dry periods may account for 40% or more of the gross N-mineralisation produced during subsequent wet periods (Bernhard-Reversat, 1982; Mazzarino et al., 1991). The microbial-N flush, however, was reduced in wet years in the current study. Microorganisms and roots of established plants would compete for the mineralised N in the upper soil, while perennial grasses would outcompete both microorganisms and evergreen shrubs for the capture of mineralised N (Aerts and Chapin III, 2000; Lambers et al., 1998).

Conclusions

As in other systems, N cycling in the Patagonian Monte appears to result from complex interactions among evergreen shrubs, perennial grasses, and biotic and abiotic components of soils. Evergreen shrubs display characteristics of plants from N-poor habitats such as long lifespan of leaves, low growth rates, and low N-concentration in mature green leaves. However, they also produce N-rich litter that decomposes and mineralises faster than that of perennial grasses, a feature that contributes to increase N concentration in the underlying soil. Despite this, evergreen shrubs appear to have mechanisms to slow down N-cycling and to conserve soil-N since N concentration and N mineralisation in the soil underneath this plant group are lower

than expected by the quality of the organic matter that they supply to the soil. Perennial grasses, in contrast, exhibit high rates of growth, high N-concentration in green leaves, and high N-resorption from senescing leaves leading to low soil-N and low rates of N-mineralisation. Consequently, perennial grasses would depend on the decomposition pathway of evergreen shrubs for their N supply. The ability of evergreen shrubs to slow down N-cycling could be important in preventing or reducing the establishment of the highly competitive perennial grasses around them.

Acknowledgements

This research was funded by PICT 98 08-03944 BID 1201/OC-AR and PICT-99 08-06027 BID 1201/OC-AR of the National Agency for Scientific and Technological Promotion. A. Carrera fellowship is supported by CONICET (National Research Council of Argentina). We thank Jorge Ares for the critical revision of the manuscript. Recognition is also given to Mr Fermín Sarasa who allowed access to the study area in Estancia San Luis. Silvia Osman, Gustavo Pagnoni and Américo Torres helped in the laboratory work.

References

- Aerts R 1996 Nutrient resorption from senescing leaves of perennials: are there general patterns? *J. Ecol.* 84, 597–608.
- Aerts R 1999 Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. *J. Exp. Bot.* 330, 29–37.
- Aerts R and F S Chapin III 2000 The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv. Ecol. Res.* 30, 1–67.
- Aerts R and Van der Peijl M J 1993 A simple model to explain the dominance of low-productive perennials in nutrient-poor habitats. *Oikos* 66, 144–147.
- Bernhard-Reversat F 1982 Biochemical cycle of nitrogen in a semiarid savanna. *Oikos* 38, 321–332.
- Bertiller M B 1998 Spatial patterns of the germinable soil seed bank in northern Patagonia. *Seed Sci. Res.* 8, 39–45.
- Bertiller M B, Beeskow A M and Coronato F 1991 Seasonal environmental and plant phenology in arid Patagonia (Argentina). *J. Arid Environ.* 21, 1–11.
- Bertiller M B and Bisigato A J 1998 Vegetation dynamics under grazing disturbance. The state - and - transition model for the Patagonian steppes. *Ecol. Aust.* 8, 191–199.
- Bertiller M B, Sain C L, Bisigato A J, Coronato F R, Ares J O and Graff P 2002. Spatial sex segregation in the dioecious grass *Poa ligularis* in northern Patagonia: the role of environmental patchiness. *Biodivers. Conserv.* 11, 69–84.
- Binkley D 1994 The influence of tree species on forest soils. Processes and Patterns. *In* Trees and Soil Workshop Proceedings. Eds. D Mead and G Will. pp. 1–24. Lincoln Univ., New Zealand.
- Bisigato A J and Bertiller M B 1997 Grazing effects on patchy dryland vegetation in northern Patagonia. *J. Arid Environ.* 36, 639–653.
- Bisigato A J and Bertiller M B 1999 Seedling emergence and survival in contrasting soil microsites in Patagonian Monte shrubland. *J. Veg. Sci.* 10, 335–342.
- Bloemhof H S and Berendse F 1995 Simulation of the decomposition and nitrogen mineralization of aboveground plant material in two unfertilized grassland ecosystems. *Plant Soil* 177, 157–173.
- Bremner J M and C S Mulvaney 1982 Regular Kjeldahl method. *In* Methods of Soil Analysis – Chemical and Microbiological Properties. Serie Agronomy No. 9. Eds. A L Page, R H Miller and D R Keeney. pp. 595–624. Wisconsin, USA.
- Cabrera A L 1976 Las Regiones Fitogeográficas Argentinas. Enciclopedia Argentina de Agricultura, Jardinería y Horticultura. ACME. Bs As, Arg.
- Carrera A L, Sain C L and Bertiller M B 2000 Patterns of nitrogen conservation in shrubs and grasses in the Patagonian Monte, Argentina. *Plant Soil* 224, 185–193.
- Chapin III F S and Kedrowski R A 1983 Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. *Ecology* 64, 376–391.
- Coombs J, Hind G, Leegood R C, Tieszen L and Vonshsk A 1985 Analytical techniques. *In* Techniques in Bioproductivity and Photosynthesis. Eds. J Coombs, D O Hall, S Long and J M Scurlock. pp. 219–228. Pergamon Press, Oxford.
- Correa M N 1971 Flora patagónica, parte VII. Colección Científica tomo VIII. Instituto Nacional de Tecnología Agropecuaria (INTA), Buenos Aires. 451 pp.
- Crawley M J 1998 Life history and environments. *In* Plant Ecology. Ed. M J Crawley. pp. 73–131. Blackwell Science, Oxford.
- Defossé G E, Bertiller M B and Ares J O 1990 Above-ground phytomass dynamics in grassland steppe of Patagonia, Argentina. *J. Range Manage.* 43, 157–160.
- del Valle H F 1998 Patagonian soils: a regional synthesis. *Ecol. Aust.* 8, 103–123.
- del Valle H F and Rosell R A 1999 Mineral composition of perennial vegetation of shrubs patches in northeastern Patagonia. *Arid Soil Res. Rehab.* 13, 24–35.
- Eckstein R L, Karlsson P S and Weih M 1998 The significance of sorption of leaf resources for shoot growth in evergreen and deciduous woody plants from a subarctic environment. *Oikos* 81, 567–575.
- García-Moya E and McKell C M 1970 Contribution of shrubs to the nitrogen economy of desert-wash plant community. *Ecology* 51, 81–88.
- Garnier E 1998 Interspecific variation in plasticity of grasses in response to nitrogen supply. *In* Population Biology of Grasses. Ed. G P Garnier. pp. 155–182. Cambridge University Press, New York.
- Harbone J B 1998 Plant Secondary Metabolism. *In* Plant Ecology. Ed. M J Crawley. pp. 132–155. Blackwell Science, Oxford.
- Hooper D U and Vitousek P M 1998 Effects of plant composition and diversity on nutrient cycling. *Ecol. Monogr.* 68, 121–149.
- Horwarth W R and Paul E A 1994 Microbial biomass. *In* Methods of Soil Analysis 2. Microbiological and Biochemical Properties. Eds. R A Weaver, S Angle, P Bottomley, D Bezdicek, S Smith, A Tabatab and A Wollum. pp. 753–773. Soil Science Society of America, Madison, Wis.
- Ihori T, Burke I C and Hook P B 1995 Nitrogen mineralization in native cultivated and abandoned fields in shortgrass steppe. *Plant Soil.* 171, 203–208.
- Keeney D R and Nelson D W 1982 Nitrogen-Inorganic forms. *In* Methods of Soil Analysis – Chemical and Microbiological

- Properties. Serie Agronomy No. 9. Eds. A L Page, R H Miller and D R Keeney. pp. 643–698. Wisconsin, USA.
- Killingbeck K T 1996 Nutrients in senescent leaves: keys to the search for potential resorption and resorption proficiency. *Ecology* 77, 1716–1727.
- Lambers H, Chapin III F S and Pons T 1998 Mineral nutrition *In* Plant Physiological Ecology. Eds. H Lambers, F S Chapin III and T Pons. pp 239–298. Springer Verlag, New York.
- Martin M E and Aber J D 1997 High spectral resolution remote sensing of forest canopy lignin, nitrogen, and ecosystem processes. *J. Ecol. Appl.* 7, 431–443.
- Mazzarino M J and Bertiller M B 1999 Soil N pool and processes as indicators of desertification in semi-arid woodlands and semi-arid to arid steppes of Argentina. VIth Int. Rangeland Congr. Proc. 1, 101–105.
- Mazzarino M J, Bertiller M B, Sain C L, Laos F and Coronato F R 1996 Spatial patterns of nitrogen availability, mineralization, and immobilization in northern Patagonia, Argentina. *Arid Soil Res. Rehab.* 10, 295–309.
- Mazzarino M J, Bertiller M B, Sain C L, Satti P and Coronato F R 1998a Soil nitrogen dynamics in northeastern Patagonia steppe under different precipitation regimes. *Plant Soil* 202, 125–131.
- Mazzarino M J, Bertiller M B, Schlichter T and Gobbi M 1998b Nutrient cycling in Patagonian ecosystems. *Ecol. Aust.* 8, 167–182.
- Mazzarino M J, Oliva L, Núñez A, Núñez G and Bufa E 1991 Factors affecting N dynamics in semiarid woodland (Dry Chaco, Argentina). *Plant Soil* 138, 85–98.
- Nelson D W and Sommers L E 1982 Total carbon, organic carbon, and organic matter. *In* Methods of Soil Analysis – Chemical and Microbiological Properties. Serie Agronomy No. 9. Eds. A L Page, R H Miller and D R Keeney. pp. 539–579. Wisconsin, USA.
- Norusis M J 1997 SPSS Advanced statistics 7.5. SPSS, Chicago. 579 pp.
- Rostagno C M, del Valle H F and Videla L S 1991 The influence of shrubs on some chemical and physical properties of an arid soil in north-eastern Patagonia, Argentina. *J. Arid Environ.* 20, 179–188.
- Sala O E, Golluscio R A, Lauenroth W K and Soriano A 1989 Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* 81, 501–505.
- Schlesinger W H 1991 Biogeochemistry: An Analysis of Global Change. Academic Press, San Diego, CA.
- Schlesinger W H and Hasey M M 1981 Decomposition of chaparral shrubs foliage: losses of organic and inorganic constituents from deciduous and evergreen leaves. *Ecology* 62, 762–774.
- Skujins J 1981 Nitrogen cycling in arid ecosystems. *In* Terrestrial Nitrogen Cycles. Eds. F E Clark and T Rosswall. Swedish Natural Science Research Council, Stockholm. *Ecol. Bull.* 33, 477–491.
- Soil Survey Staff 1998 Keys to Soil Taxonomy. USDA, Washington, DC. 326 pp.
- Sokal R R and Rohlf F J 1981 Biometry. Freeman, San Francisco, C A.
- Soriano A 1950 La vegetación del Chubut. *Rev. Arg. Agr.* 17, 30–66.
- Vinton M A and Burke I C 1995 Interaction between individual plant species and soil nutrient status in Shortgrass steppe. *Ecology* 76, 1116–1133.
- Vitousek P M and Matson P A 1985 Disturbance, N availability and N losses: an experimental study in an intensively managed loblolly pine plantation. *Ecology* 66, 1360–1376.
- Vitousek P M, Gosz J R, Grier C C, Melillo J M and Reiners W A 1982 A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. *Ecol. Monogr.* 52, 155–177.
- Wedin D A and Tilman D 1990 Species effect on nitrogen cycling: a test with perennial grasses. *Oecologia* 84, 433–441.

Section editor: H. Lambers