



Patterns of nitrogen conservation in shrubs and grasses in the Patagonian Monte, Argentina

A.L. Carrera*, C.L. Sain and M.B. Bertiller

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

Received 15 November 1999. Accepted in revised form 20 April 2000

Key words: arid ecosystems, Monte shrublands, N-resorption efficiency, N-resorption proficiency, plant functional types

Abstract

We analysed the main plant strategies to conserve nitrogen in the Patagonian Monte. We hypothesized that the two main plant functional groups (xerophytic evergreen shrubs and mesophytic perennial grasses) display different mechanisms of nitrogen conservation related to their structural and functional characteristics. Evergreen shrubs are deep-rooted species, which develop vegetative and reproductive growth from spring to late summer coupled with high temperatures, independently from water inputs. In contrast, perennial grasses are shallow-rooted species with high leaf turnover, which display vegetative growth from autumn to spring and reproductive activity from mid-spring to early-summer, coupled with precipitation inputs. We selected three evergreen shrubs (*Larrea divaricata* Cav., *Atriplex lampa* Gill. ex Moq. and *Junellia seriphioides* (Gilles and Hook.) Moldenke) and three perennial grasses (*Stipa tenuis* Phil., *S. speciosa* Trin. and Rupr. and *Poa ligularis* Nees ex Steud.), characteristic of undisturbed and disturbed areas of the Patagonian Monte. N concentration in expanded green and senesced leaves was estimated in December 1997 (late spring) and June 1998 (late autumn). Deep-rooted evergreen shrubs displayed small differences in N concentration between green and senesced leaves (low N-resorption efficiency), having high N concentration in senesced leaves (low N-resorption proficiency). Shallow-rooted perennial grasses, conversely, showed high N-resorption efficiency and high N-resorption proficiency (large differences in N concentration between green and senesced leaves and very low N concentration in senesced leaves, respectively). The lack of a strong mechanism of N resorption in evergreen shrubs apparently does not agree with their ability to colonize N-poor soils. These results, however, may be explained by lower N requirements in evergreen shrubs resulting from lower growth rates, lower N concentrations in green leaves, and lower leaf turnover as compared with perennial grasses. Long-lasting N-poor green tissues may, therefore, be considered an efficient mechanism to conserve N in evergreen shrubs in contrast with the mechanism of strong N resorption from transient N-rich tissues displayed by perennial grasses. Evergreen shrubs with low N-resorption efficiency provide a more N-rich substrate, with probably higher capability of N mineralization than that of perennial grasses, which may eventually enhance N fertility and N availability in N-poor soils.

Abbreviations: NRP – N-resorption proficiency

Introduction

Arid ecosystems are characterized by the scarcity of water and nutrients, whose cycling is strongly associated with the erratic and discontinuous inputs of precipitation (Noy Meir, 1973; Skujins, 1981). Nitrogen is one of the most limiting nutrients in arid ecosys-

tems (Skujins, 1981), and its availability is strongly coupled with the quantity and quality of organic pools, as well as with water inputs (Aerts, 1996; Binkley, 1994; Bloemhof and Berendse, 1995; Killingbeck, 1993; Martin and Aber, 1997; Vinton and Burke, 1995; Vitousek et al., 1982; Wedin and Tilman, 1990).

N resorption from senescent leaves is an important mechanism of N conservation in plants (Eckstein et al., 1998; Killingbeck, 1996) and may be quantified

* FAX No: 2965451543. E-mail: unanalia@cenpat.edu.ar

by the proportion of N remobilization from senesced leaves (N-resorption efficiency) or by the N concentration in senesced leaves (N-resorption proficiency) (Killingbeck, 1996). Strong mechanisms of N conservation, however, would be associated with N-poor litter, low N-mineralization rates and low N availability in soil (Bloemhof and Berendse, 1995; Epstein et al., 1998; Lambers et al., 1998; Wedin and Tilman, 1990). N conservation may vary among plants with different growth habits. Mesophytic species, with high leaf area index, high growth rates and high leaf turnover, normally display high N resorption (Reich et al., 1992). In contrast, low leaf area index, low growth rates and low leaf turnover displayed by evergreen or some xerophytic species has been related to low N resorption and high persistence of N in plants (Aerts and Van der Peijl, 1993; Aerts, 1996; Mazzarino et al., 1998).

In Patagonia, vegetation displays a patchy structure dominated by two plant functional groups: Perennial grasses and shrubs (Bertiller and Bisigato, 1998; Bertiller et al., 1991; Sala et al., 1989). Grazing promotes changes in the vegetation structure such as the reduction of the grass cover and the increase of evergreen shrubs prompting the acceleration of soil degradation processes and to the disruption of ecosystem functioning (Ares et al., 1990; Bisigato and Bertiller, 1997; Soriano, 1983). As in other ecosystems, these physical processes cause losses of fine material, organic matter, nutrients, and seeds from the topsoil leading to the concentration of soil resources underneath remnant plant patches (Beeskow et al., 1995; Bertiller, 1994, 1998; Bertiller and Coronato, 1994; Bertiller and Bisigato, 1998; Ludwig and Tongway, 1995; Rostagno et al., 1991; Mazzarino et al., 1998a). The result of these processes is a two phase-mosaic structure consisting of resource-rich plant patches separated from resource-poor areas of bare soil. Under this scenario, perennial grasses are able to colonize only the resource-rich areas while shrubs may eventually increase their cover in the patches or recolonize resource-poor bare soil (Bertiller, 1994, 1996; Beeskow et al., 1995; Bisigato and Bertiller 1997, 1999). These dynamics might be partially explained by the ability of shrubs to access soil resources stored at depth (Bertiller et al., 1991; Sala et al., 1989) and/or by their ability to conserve resources in the plant. In previous reviews for Patagonia, Mazzarino et al. (1998b) and Mazzarino and Bertiller (1999) reported evidences of higher N-resorption proficiency in perennial grasses as compared with shrubs. These results are in accordance with others previously reviewed

by Aerts (1996) indicating low nutrient contents and resorption efficiency in evergreen species. We hypothesized that perennial grasses and evergreen shrubs display different N-conservation strategies related to their morphological and functional traits. Evergreen shrubs have low growth rates, growth activity concentrated during the dry period and low leaf turnover (Bertiller et al., 1991). We predicted that mechanisms of N conservation in evergreen shrubs would depend, to a greater extent, on maintaining long-lasting leaves with low N-concentration than on a high N-resorption efficiency. In contrast, perennial grasses, with high growth rates, phenological activity during the precipitation period and high leaf turnover (Bertiller et al., 1991), would display high N concentration in green tissues and high N-resorption efficiency and N-profiency (*sensu* Killingbeck, 1996).

Materials and methods

Study area

The study site is located in northeastern Patagonia (Argentina), 40 km west of Puerto Madryn (42° 39' S, 65° 23' W, 115 m a.s.l.). The mean annual temperature is 13.7° C (15 years series) and mean annual precipitation is 188 mm (Bertiller, 1998). Soils are a complex of Typic Palaeorthid - Typic Calciorthid (Soil Survey Staff, 1992).

The study was conducted in an area of about 2 ha, where large domestic herbivores were excluded for a period of 5 years. Vegetation is representative of the steppe of *Larrea divaricata* Cav. and *Stipa* spp., characteristic of the southern portion of the Monte Phytogeographic Province (Cabrera, 1976; Soriano, 1950). Plant canopy covers between 40 and 60% of the soil and presents a random patchy structure (Bertiller 1998; Bisigato and Bertiller, 1997; Mazzarino et al., 1996). Dominant plant patches consist of shrubs and grasses arranged in four layers. The upper shrub layer (1.5–2 m) is dominated by *Larrea divaricata*, *Schinus molle* F. A. Barkley, *Chuquiraga hystrix* D. Don and *Lycium chilense* Miers ex Bert.; the medium shrub layer (0.5–1.2 m) is dominated by *Atriplex lampa* Gill. ex Moq.; the low shrub layer (0.2–0.3 m) is formed by dwarf shrubs such as *Junellia seriphioides* (Gillies and Hook.) Moldenke, *Nassauvia fueguiana* (Speg.) Cabrera and *Acantholipia seriphioides* (A. Gray) Moldenke; and the grass layer (0.1–0.5 m), rich in perennial bunchgrasses, is dominated by *Stipa*

tenuis Phil., *Stipa speciosa* Trin. and Rupr. and *Poa ligularis* Nees ex Steud (Bertiller, et al., 1991).

Study species

We selected species of the two main functional groups (Bertiller et al., 1991; Sala et al., 1989), evergreen shrubs and perennial grasses, characteristic of disturbed and undisturbed patches of vegetation (Bisigato and Bertiller, 1997). The groups display different grades of xerophytism/mesophytism and phenological asynchronism (Bertiller et al., 1991; Bertiller, pers. comm.; Sala et al., 1989). In evergreen shrubs, vegetative and reproductive growth is concentrated during the warm period from spring to late summer. Perennial grasses display vegetative growth from autumn to spring and reproductive activity from mid-spring to early-summer, coupled with precipitation inputs (Bertiller et al., 1991). In perennial grasses, senescence of most aboveground-green tissues occurs from late spring to summer. In evergreen shrubs, senescence of a small portion of green leaves occurs from late spring to autumn but most of the senescence takes place at late-summer (Bertiller et al., 1991).

Among shrubs, the species selected were *Atriplex lampa*, *Larrea divaricata* and *Junellia seriphioides*. *A.lampa* is a deep-rooted shrub (more than 3.00m depth), which replaces some of its leaves during the year. This species is characteristic of non- or lightly disturbed areas. *L. divaricata* is a deep-rooted (more than 3.00 m depth) tall shrub, with very low annual foliage turnover, which increases in cover in areas disturbed by grazing. *J. seriphioides* is a shallow-rooted dwarf shrub, with low annual leaf turnover, which increases in abundance in areas severely disturbed by grazing (Bertiller et al., 1991; Bisigato and Bertiller, 1997; Morello, 1958; Passera and Borsetto, 1989).

Among perennial grasses, the species selected were: *Poa ligularis*, *Stipa tenuis* and *Stipa speciosa*. *S. tenuis* is a shallow-rooted grass (0.40–0.50m depth), sensitive to grazing, with high annual leaf turnover (most green tissues senesce during summer). *P. ligularis* is a perennial grass widely distributed in Patagonia and one of the most preferred species by native and domestic herbivores; its cover is markedly reduced in grazed areas (Ares et al., 1990; Boelcke, 1957; Correa, 1978; Soriano, 1956, 1959). This medium-rooted (0.9–1 m depth) grass exhibits a high annual leaf turnover since all green tissues senesce during summer. *S. speciosa* is a deep-rooted grass (1.0–1.2 m depth) which maintain green tissues all year round

(Bertiller et al., 1991), although some reduction occurs in summer. This grass species is less sensitive to grazing than the former. Taking into consideration leaf turnover and rooting characteristics, a gradient of xerophytism may be established among species as follows: *L. divaricata* > *J. seriphioides* > *A. lampa* > *S. speciosa* > *S. tenuis* > *P. ligularis* (Figure 1).

Sampling

Samples of each species were collected in December of 1997 and in June of 1998. Both dates covered different phenological phases in perennial grasses and evergreen shrubs. In June (late autumn), perennial grasses had fully expanded green leaves of the year as well as senesced leaves (tissues completely dry yellow without signs of deterioration, Defossé et al., 1990) produced in the previous summer. At the same date, evergreen shrubs had fully expanded green leaves and senesced leaves both produced during the previous spring and summer (Bertiller et al., 1991). In December (late spring), perennial grasses had fully expanded green leaves and senesced leaves produced during autumn and spring of the year while evergreen shrubs had fully expanded green leaves and senesced leaves produced in spring of the year. At each sampling date, five individuals of each species of similar diameter and height were randomly selected. One representative main branch with second and third order ramifications of each evergreen shrub or the complete plant of perennial grasses were harvested. After harvest, old standing dead material (tissues deteriorated, gray colored as defined in Defossé et al. (1990)) was discarded. Fully expanded totally green and senesced (completely dry yellow without signs of deterioration) leaves of each branch or individual were sorted, dried at 45 °C for 48 h and weighed. N concentration per leaf category and species was determined by the Kjeldahl acid-digestion method (Bremner and Mulvaney, 1982). N concentration in green and senesced leaves was used to calculate N-resorption efficiency (Killingbeck, 1996) as follows:

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

where: N_g is the concentration of N in green leaves, and N_s is the concentration of N in senesced leaves. Additionally, the N concentration in senesced leaves was directly employed as an indicator of N-resorption proficiency *sensu* Killingbeck (1996).

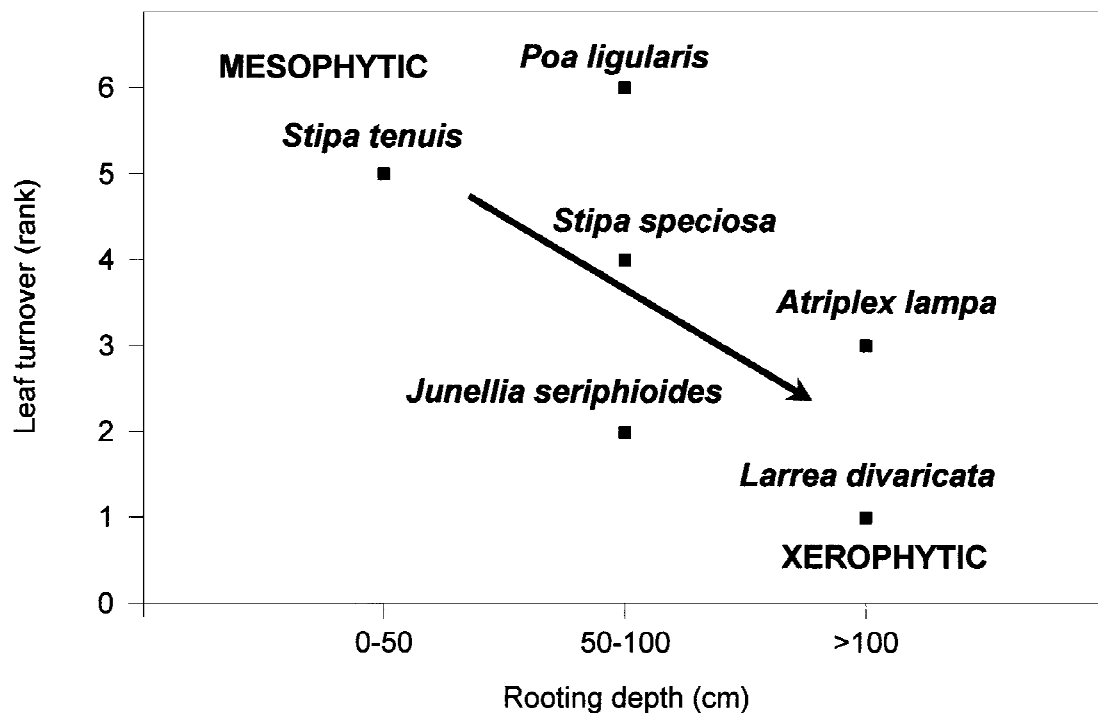


Figure 1. Gradient of xerophytism of the studied species based on annual leaf turnover and rooting-patterns (Bertiller et al., 1991; A. L. Carrera, pers. comm.). Annual leaf turnover was quantified by a six point rank scale ranging from: 1 (very low) to 6 (very high) annual leaf turnover.

The differences in N concentration in green and senesced leaves and in N-resorption efficiency between species and dates were evaluated by Tukey's test for multiple comparisons (Norusis, 1986). In those cases in which the assumptions of homocedasticity and normal distribution were not met, the data were transformed by the arcsin of the square root (Sokal and Rohlf, 1981). In all cases, the assumptions of the variance analysis were checked after transformation.

Results

The N concentration in green leaves of evergreen shrubs ranged from 14.4 to 19.2 mg g⁻¹ and did not differ significantly among species and between dates. In perennial grasses, however, the N concentration in green leaves varied markedly between dates being lower in December than in June (Figure 2). In December, it ranged from 6.1 to 9.9 mg g⁻¹ and did not differ among species, while in June, it varied between 22.3 and 33.0 mg g⁻¹, differing significantly among species (*S. tenuis* > *P. ligularis* > *S. speciosa*). At this last date, the N concentration in green leaves was significantly higher in perennial grasses than in ever-

green shrubs while the reverse occurred in December (Figure 2).

The N concentration in senesced leaves of evergreen shrubs ranged from 9.9 to 13.4 mg g⁻¹. *L. divaricata* displayed the highest values being the only species that showed significant differences between dates (December < June). In perennial grasses, the N-concentration in senesced leaves ranged from 3.6 to 5.3 mg g⁻¹, being significantly lower than in evergreen shrubs. No differences in the N concentration in senesced leaves of perennial grasses were observed between dates and among species (Figure 3). Values of N concentration in senesced leaves indicated significantly ($p < 0.05$) higher N-resorption proficiency (NRP) in perennial grasses than in evergreen shrubs.

The N-resorption efficiency in evergreen shrubs varied among species (*L. divaricata* < *J. seriphioides* ≤ *A. lampa*). *A. lampa*, was the only species which exhibited significant differences in the N-resorption efficiency between dates (June > December). In perennial grasses, N-resorption efficiencies differed between dates (June > December) and only in December significant differences in N-resorption efficiencies were observed among species: *S. speciosa* < *S. tenuis* < *P. ligularis* (Figure 4). Both in December and June,

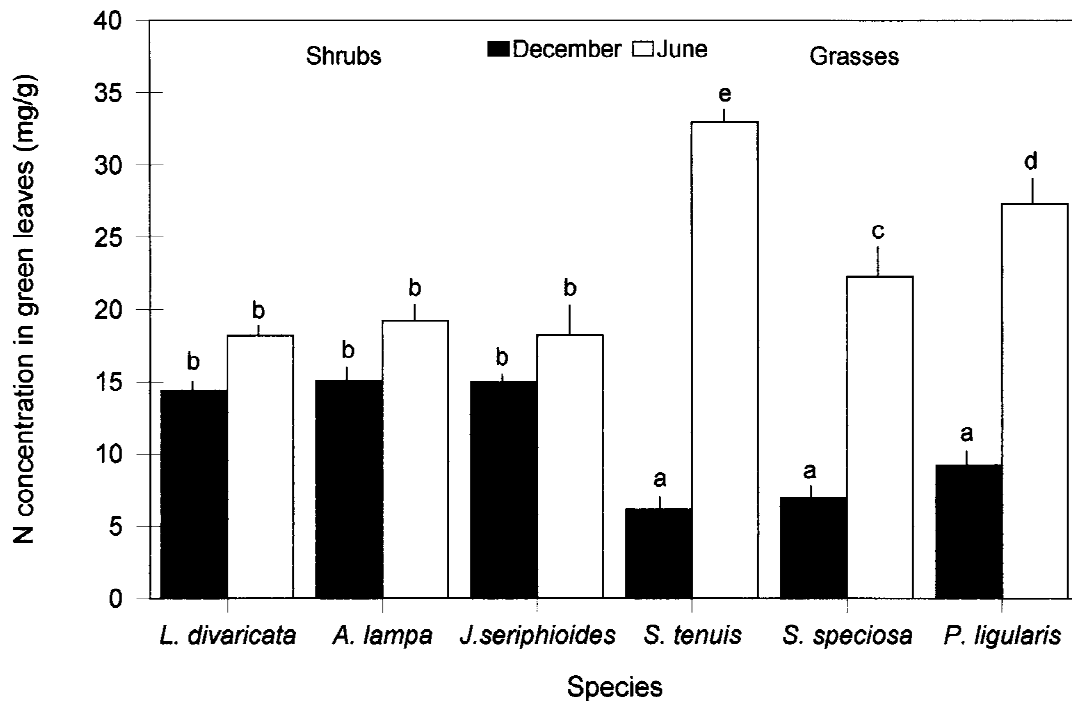


Figure 2. Mean N concentration (mg/g) in green leaves by species and dates. Different small case letters indicate significant differences among species and dates (Tukey's test for multiple comparisons). Vertical bars = 1 standard error.

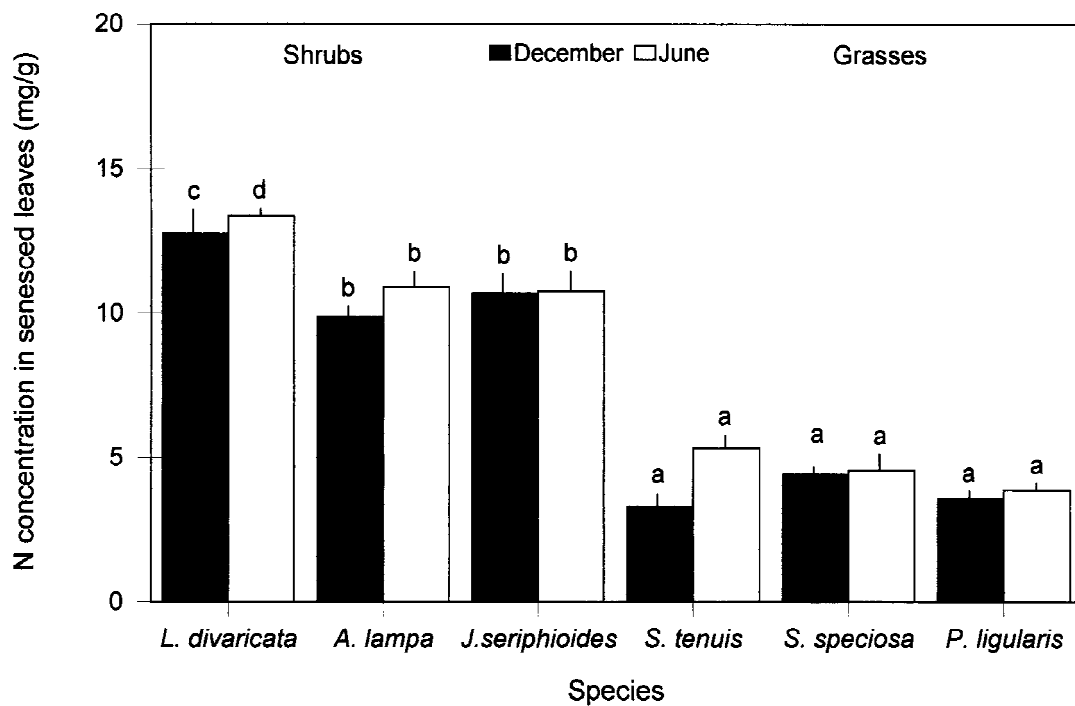


Figure 3. Mean N concentration (mg/g) in senesced leaves by species and dates. Different small case letters indicate significant differences among species and dates (Tukey's test for multiple comparisons). Vertical bars = 1 standard error.

the N-resorption efficiency was higher in perennial grasses than in evergreen shrubs, except for *S. speciosa* in December which exhibited similar values than *A. lampa* and *J. seriphioides*.

Discussion

Perennial grasses and evergreen shrubs in the shrublands of *L. divaricata* and *Stipa* spp., characteristic of the Patagonian Monte, differed in their N-conservation strategies. Perennial grasses displayed the highest N concentration in green leaves, while evergreen shrubs had the highest N concentration in senesced leaves (Figures 2 and 3). Differences in N concentration of green leaves of perennial grasses between December and June are related to the timing of growth and senescence. In December, perennial grasses had expanded green leaves produced during the previous autumn and spring, while in June they had only recent expanded leaves from the ongoing growing season. Except for *L. divaricata*, we did not find temporal fluctuations in the N concentration of senesced leaves of both perennial grasses and evergreen shrubs. The N concentration in senesced leaves of evergreen shrubs (9.9–13.4 mg g⁻¹) fell into the range from 8.7 to 22.0 mg g⁻¹ reported for other desert shrubs (Garcia-Moya and McKell, 1970; Killingbeck, 1996; Killingbeck and Whitford, 1996; Ritchie et al., 1998; Rundel, 1982). In perennial grasses, the N concentration in senesced leaves was significantly lower than that in evergreen shrubs ranging from 3.6 to 5.3 mg g⁻¹. In accordance with Killingbeck (1996), who proposed the term of N-resorption proficiency (NRP) as the level to which plants reduce nutrients in senesced leaves, these values allow us to distinguish two different resorption patterns between perennial grasses and evergreen shrubs. Evergreen shrubs with high N concentrations in senesced leaves (>7.0 mg g⁻¹) may be considered as a low N-proficient plant group while perennial grasses with low N concentrations in senesced leaves (<7.0 mg g⁻¹) may be identified as a high N-proficient plant group. As in the case of NRPs, we identified different patterns of N-resorption efficiency between both plant groups. In accordance with previous studies that have reported low N-resorption efficiency in species with gradual leaf turnover (Lambers et al., 1998), evergreen shrubs exhibited lower N-resorption efficiency than perennial grasses. N-resorption efficiency in evergreen shrubs varied between 11 and 43%, falling into the range from 10 to 64% indicated by Eckstein et

al. (1998) for evergreen shrubs in northern Sweden. Conversely, our values of N-resorption efficiency of *L. divaricata* were lower than those previously reported for the congener *L. tridentata* in the Chihuahuan desert (Lajtha, 1987; Lajtha and Whitford, 1989). We might have eventually underestimated N-resorption efficiency, due to probable seasonal changes in specific leaf mass resulting, among others, from resorption of soluble carbon compounds (Aerts, 1996; Guha and Mitchell 1966). In the case of *L. tridentata*, however, Lajtha and Whitford (1989) reported that mean N-resorption efficiencies were similar when they were expressed on a leaf area or weight basis. The differences between the two species may be probably traced back to the relation between the costs of re-absorbing/reassimilating N and those of uptake from the soil. Lajtha (1987) found a direct relation between leaf N, the ratio of labile N to structural N, and the N-resorption efficiency. Since in our study site *L. divaricata* grows in N-poor patches of soil (Bisigato and Bertiller, 1997; Mazzarino et al., 1996; 1998a) low levels of leaf N could be related to a low ratio labile N/structural N and consequently to a low N-resorption efficiency. Killingbeck (1996) found wide differences in N concentration consistent with differences in N content (micrograms per square centimetre) in senesced leaves among congeners of different woody plants. N-resorption efficiencies in perennial grasses (65.9%) were slightly higher than those reported by Aerts (1996) for the same plant group in the northern hemisphere (58.5%). N-resorption efficiencies of perennial grasses at the end of the growing period (December in Figure 4) were significantly lower than those calculated in June. This is explainable because of the onset of N remobilization from green leaves and the senescence process (although this latter was not detectable to us by external changes in leaf color). N-resorption efficiencies of both plant functional groups calculated at the end of the growing period (values from June for evergreen shrubs and from December for perennial grasses in Figure 4) varied in accordance with the grade of xerophytism of the species (Figure 1) within and between functional groups (N-resorption efficiency in *L. divaricata* < *J. seriphioides* < *A. lampa* < *S. speciosa* < *S. tenuis* < *P. ligularis*). N-resorption efficiency and NRP showed to be good estimators of N resorption in plant species in the Patagonian Monte, however, N-resorption efficiency allowed us to distinguish differences among species within each functional group that were not detected by NRP (Figure 5). It might be considered, however,

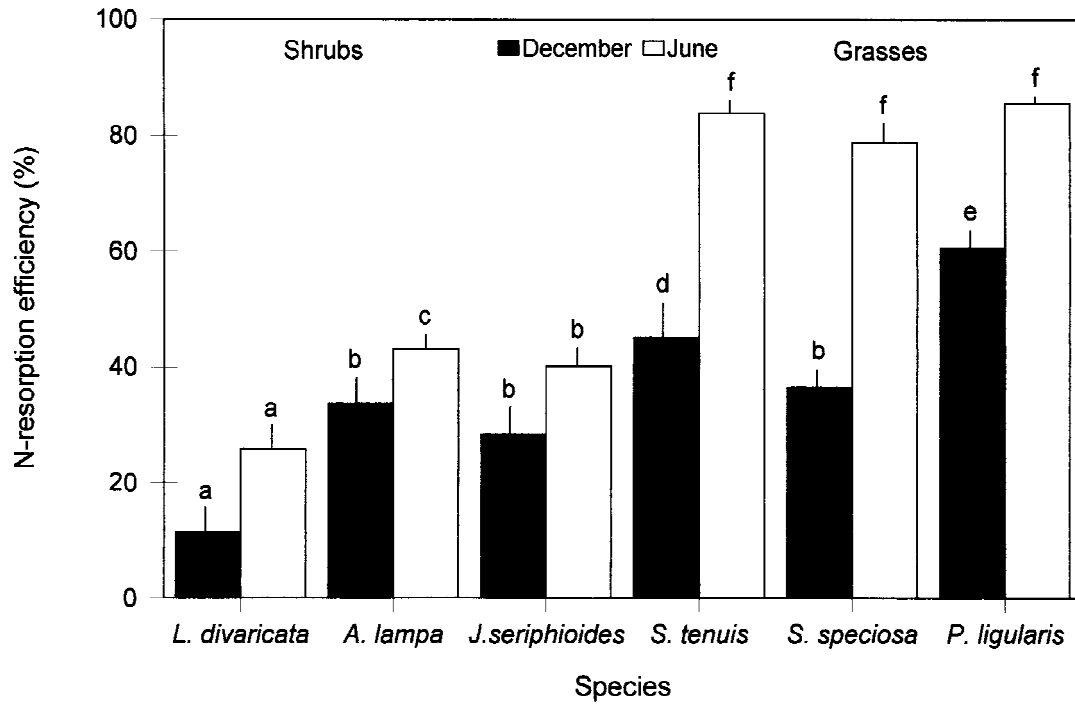


Figure 4. Mean N-resorption efficiency (%) by species and dates. Different small case letters indicate significant differences among species and dates (Tukey's test for multiple comparisons). Vertical bars = 1 standard error.

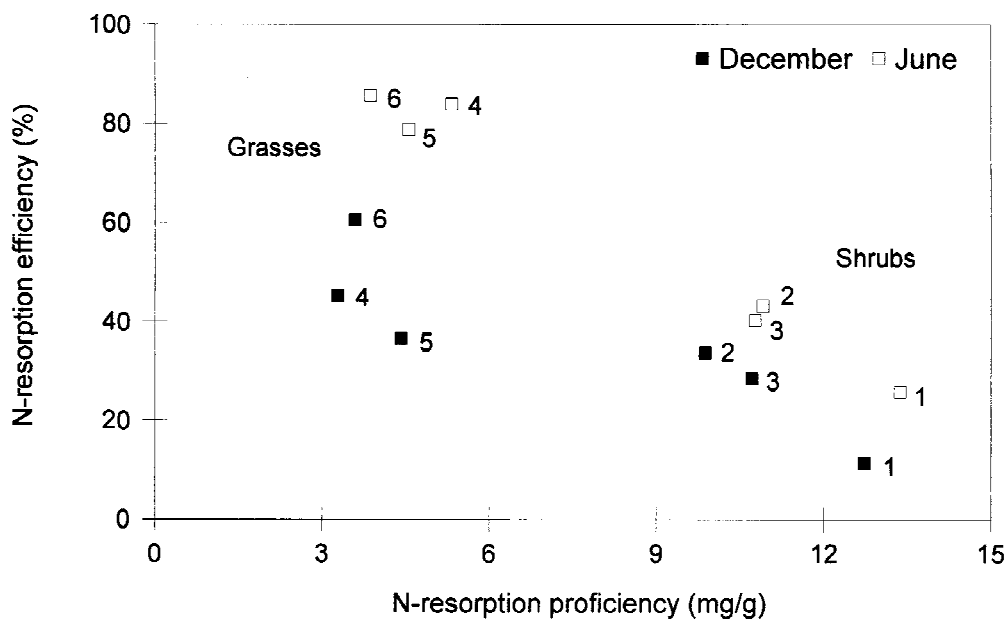


Figure 5. N-resorption efficiency (%) vs. NRP (mg/g of N concentration in senesced leaves, low values=high NRP) by species and dates. 1: *L. divaricata*, 2: *J. seriphioides*, 3: *A. lampa*, 4: *S. speciosa*, 5: *S. tenuis*, and 6: *P. ligularis*.

that N-resorption efficiency may vary between years depending on environmental factors such as water availability while NRP seems to be a less variable indicator of the inherent resorption ability of the species (Killingbeck, 1996).

The lack of a strong mechanism of N resorption in evergreen shrubs is apparently not in accordance with their ability to colonize N-poor soils (Bisigato and Bertiller, 1997; Bertiller and Bisigato, 1998). As in other ecosystems (Aerts and Van der Peijl, 1993; Bisigato and Bertiller, 1999; Heckathorn and Delucia, 1996; Killingbeck, 1996; Killingbeck and Whitford, 1996; Mazzarino et al., 1998b; Tolsma et al., 1987), these results may be explained by lower N requirements in evergreen shrubs resulting from lower growth rates, lower N concentration in green leaves and lower leaf turnover as compared with those in perennial grasses. In a study including a wide variety of sites and species, Aerts (1996) concluded that evergreen species do not reduce nutrient losses by a high resorption efficiency but rather by having long-span leaves with low nutrient concentration. Long-lasting N-poor green tissues may, therefore, be considered an efficient mechanism to conserve N in evergreen shrubs in the Patagonian Monte in contrast with the mechanism of strong N resorption from transient N-rich tissues displayed by perennial grasses.

Differential N-conservation patterns between perennial grasses and evergreen shrubs may have important implications for nutrient cycling and ecosystem functioning (Epstein et al., 1998; Facelli and Facelli, 1993; Horn and Redente, 1998; Lambers et al., 1998; Vinton and Burke, 1995). Evergreen shrubs produce N-rich litter, while perennial grasses contribute N-poor litter, due to very low and high N-resorption mechanisms, respectively. This fact may result in differences in the mineralization capability of the substrate provided by each plant group. Results from *in situ* and potential N mineralization, and N immobilization in microbial biomass in the same study area (Mazzarino et al., 1996, 1998a) showed that both N mineralization rates and microbial biomass were significantly higher in soil microsites underlying evergreen shrub patches than those beneath perennial grasses. According to this, evergreen shrubs play an important role in the conservation of the N-fertility in soils of the Patagonian Monte ecosystems.

Acknowledgements

We would like to thank M. Mazzarino for her helpful comments and manuscript revision. This research was partially funded by PIP-CONICET 4270/97. A. Carrera fellowship is supported by CONICET (National Research Council of Argentina). Recognition is also given to Mr Fermín Sarasa who allowed access to the study area in Estancia San Luis.

References

- Aerts R 1996 Nutrient resorption from senescing leaves of perennials: Are there general patterns? *J. Ecol.* 84, 597–608.
- 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.
- Ares J, Beeskov A M, Bertiller M B, Rostagno C M, Irisarri M, Anchorena J, Defossé G and Merino C 1990 Structural and dynamic characteristics of overgrazed lands of northern Patagonia, Argentina. *In* *Managed Grasslands*. Ed. A. Breymeyer. pp 149–175. Elsevier Science, Amsterdam.
- Beeskov A M, Elissalde N O and Rostagno C M 1995 Ecosystem changes associated with grazing intensity on the Punta Ninfas rangelands of Patagonia, Argentina. *J. Range Manage.* 48, 517–522.
- Bertiller M B, Beeskov 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 Coronato F 1994 Seed bank patterns of *Festuca palllescens* in semiarid Patagonia (Argentina); a possible limit to bunch re-establishment. *Biodiv. Conserv.* 3, 57–67.
- Bertiller M B 1994 Modelos ecológicos de la dinámica de la vegetación en los ecosistemas de pastizales: Un caso de estudio en la Patagonia. *Rev. Agr. Prod. Anim.* 14, 15–23.
- Bertiller M B 1996 Grazing Effects on Sustainable Semiarid Rangelands in Patagonia: The State and Dynamics of the Soil Seed Bank. *Environ. Manage.* 20, 123–132.
- Bertiller M B 1998 Spatial patterns of the germinable soil seed bank in northern Patagonia. *Seed Sci. Res.* 8, 39–45.
- Bertiller M B and Bisigato A J 1998 Vegetation dynamics under grazing disturbance. The state - and - transition model for the Patagonian steppes. *Ecología Austral* 8, 191–199.
- 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 the Patagonia - 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.
- Boelcke O 1957 Comunidades herbáceas del norte de la Patagonia y sus relaciones con la ganadería. *Revista de Investigaciones Agrícolas.* 11, 5–98.
- Bremner J M and C S Mulvaney 1982 Regular Kjeldahl method. *In* *Methods of Soil Analysis Part 2. Chemical and Microbiological*

- Properties. Second edition, Eds A.L. Page, RH Miller and DR Keeney. Serie Agronomy No. 9. Cp. 31, 595–624.
- Cabrera A L 1976 Las Regiones Fitogeográficas Argentinas. Enciclopedia Argentina de Agricultura, Jardinería y Horticultura. ACME Ed. Bs As, Arg.
- Correa Maevia N 1978 Flora Patagónica. Colección Científica. Bs. As.: Inst. de Tecnología Agropecuaria (INTA)
- 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.
- 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.
- Epstein H E, Burke I C and A R Mosier 1998 Plant effects on spatial and temporal patterns of nitrogen cycling in shortgrass steppe. *Ecosystems* 1, 374–385.
- Facelli J M and Facelli E 1993 Interaction after death: plant litter controls priority effects in a successional plant community. *Oecologia* 95, 277–282.
- García-Moya E and McKell C M 1970 Contribution of shrubs to the nitrogen economy of desert-wash plant community. *Ecology* 51, 81–88.
- Guha M M and Mitchell R L 1966 The trace and major element composition of leaves of some deciduous trees. Seasonal changes. *Plant Soil* 24, 90–112.
- Heckathorn S A and Delucia E H 1996 Retranslocation of shoot nitrogen to rhizomes and roots in prairie grasses may limit loss of N to grazing and fire during drought. *Funct. Ecol.* 10, 396–400.
- Horn B E and Redente E F 1998 Soil nitrogen and plant cover of an old-field on the shortgrass steppe in southeastern Colorado. *Arid Soil Res. Rehab.* 12, 193–206.
- Killingbeck K T 1993 Nutrient resorption in desert shrubs. *Rev. Chilena His. Nat.* 66, 345–355.
- Killingbeck K T 1996 Nutrients in senesced leaves: Keys to the search for potential resorption and resorption proficiency. *Ecology* 77, 1716–1727.
- Killingbeck K T and Whitford W G 1996 High foliar nitrogen in desert shrubs: An important ecosystem trait or defective desert doctrine?. *Ecology* 77, 1728–1737.
- Lajtha K 1987 Nutrient reabsorption efficiency and the response to phosphorus fertilization in the desert shrubs *Larrea tridentata* (DC.) Cov. *Biogeochemistry* 4, 265–276.
- Lajtha K and Whitford W 1989 The effect of water and nitrogen amendments on photosynthesis, leaf demography and resource-use efficiency in *Larrea tridentata*, a desert evergreen shrub. *Oecologia* 80, 341–348.
- Lambers H Chapin III F S and Pons T 1998 Mineral nutrition *In* Plant Physiological Ecology. Eds Lambers H, Chapin III F S and Pons T pp 239–298. Springer Verlag, New York.
- Ludwig J A and D J Tongway 1995 Spatial organization of landscapes and its function in semi-arid woodlands, Australia. *Landscape Ecology* 10, 51–63.
- 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, 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. *Ecología Austral.* 8, 167–182.
- Mazzarino M J and Bertiller M B 1999 Soil N pools and processes as indicators of desertification in semi-arid woodlands and semi-arid to arid steppes of Argentina. People and rangelands building the future. VI International Rangeland Congress. 1, 101–105.
- Morello J 1958 La Provincia Fitogeográfica del Monte. Opera Lilloana II. 155 p.
- Norusis M J 1986 SPSS/PC+ for the IBM PC/XT/AT. SPSS. Inc. Chicago, Illinois.
- Noy Meir Y 1973 Desert ecosystems: Environment and producers. *Annu. Rev. Ecol. Syst.* 4, 25–52.
- Passera C B and Borsetto O 1989 Aspectos ecológicos de *Atriplex lampra*. *Invest. Agr.: Prod. Prot. Veg.* 4, 179–197.
- Reich P B, Watson M B and Ellsworth D S 1992 Leaf life-span in relation to leaf, plant and stand characteristics among diverse ecosystems. *Ecol. Monogr.* 62, 365–392.
- Ritchie M E, Tilman D and Knops J 1998 Herbivore effect on plant and nitrogen dynamics in oak savanna. *Ecology* 79, 165–177.
- 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.
- Rundel P W 1982 Nitrogen utilization efficiencies in Mediterranean-climate shrubs of California and Chile. *Oecologia* 55, 409–413.
- 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.
- Skujins J 1981 Nitrogen cycling in arid ecosystems. *In* Terrestrial Nitrogen Cycles. Eds. F.E. Clark, and T. Rosswall, Eds Swedish Natural Science Research Council, Stockholm. *Ecol. Bull.* 33, 477–491.
- Soil Survey Staff 1992 Procedures for collecting soil samples and methods of analysis for soil survey. Soil Survey Investigation. Report 1. U. S. printing Office. Washington, DC.
- 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.
- Soriano A 1956 Los distritos florísticos de la Provincia Patagónica. *Rev. Inv. Agr.* 10, 323–347.
- Soriano A 1959 Síntesis de los resultados obtenidos en las clausuras instaladas en Patagonia en 1954 y 1955. *Rev. Agronómica del Noreste Argentino.* 3, 163–176.
- Soriano A 1983 Vegetation in deserts and semi-deserts of Patagonia. *In* Ed. N.E. West Temperate Deserts and Semi-deserts of the World. pp 423–460. Elsevier, Amsterdam.
- Tolsma D J, Ernst W H O and Verweij R A 1987 Seasonal variation of nutrient concentrations in a semiarid savanna ecosystem in Botswana. *J. Ecol.* 75, 755–770.
- Vinton M A and Burke I C 1995 Interaction between individual plant species and soil nutrient status in Shortgrass steppe. *Ecology* 76, 1116–1133.
- West 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 A D and Tilman D 1990 Species effect on nitrogen cycling: a test with perennial grasses. *Oecologia* 84, 433–441.

Section editor: H Lambers