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Soil nitrogen in relation to quality and decomposability of plant litter in the Patagonian Monte, Argentina

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Abstract

In two consecutive years, we analysed the effect of litter quality, quantity and decomposability on soil N at three characteristic sites of the Patagonian Monte. We assessed (i) concentrations of N, C, lignin and total phenolics and the C/N ratio in senesced leaves as indicators of litter quality of three species of each dominant plant life form (evergreen shrubs and perennial grasses), and (ii) N, and organic-C concentrations, potential N-mineralisation and microbial-N flush in the soil beneath each species. Rate constants of potential decomposition of senesced leaves and N content in decaying leaves during the incubation period were assessed in composite samples of the three sites as indicators of litter decomposability. Further, we estimated for each species leaf-litter production, leaf-litter on soil, and the mass of standing senesced leaves during the senescence period. Senesced leaves of evergreen shrubs showed higher decomposability than those of perennial grasses. Leaf-litter production, leaf-litter on soil, and the mass of standing senesced leaves differed significantly among species. The largest variations in leaf-litter production and leaf-litter on soil were observed in evergreen shrubs. The mass of standing senesced leaves was larger in perennial grasses than in evergreen shrubs. Nitrogen, organic C and potential N-mineralisation in soil were higher underneath evergreen shrubs than beneath perennial grasses, while no significant differences were found in microbial-N flush among life forms. The initial concentrations of C, N and total phenolics of senesced leaves explained together 78% of the total variance observed in the dry mass loss of decaying leaves. Litter decomposition rates explained 98%, 98%, 73%, and 67% of the total variance of soil N, organic C, net-N mineralisation, and microbial-N flush, respectively. We concluded that leaf-litter decomposition rates along with leaf-litter production are meaningful indicators of plant local effects on soil N dynamics in shrublands of the Patagonian Monte, and probably in other similar ecosystem of the world dominated by slow growing species that accumulate a wide variety of secondary metabolites including phenolics. Indicators such as C/N or lignin concentration usually used to predict litter decomposability or local plant effects may not be adequate in the case of slow growing species that accumulate a wide range of secondary metabolites or have long leaf lifespan and low leaf-litter production.

Introduction

Litter decomposition and nutrient mineralisation are key processes in nutrient cycling, especially of N, which represents one of the main controls of plant productivity in arid ecosystems (Cross and Schlesinger 1999). Climate, litter chemistry, and soil organisms primarily control the amount of N released to the soil through litter decomposition. Plant traits such as growth habit, phenology, chemistry of secondary compounds, nutrient resorption, and tissue lifespan are directly related to both the quantity and quality of litter. In general, plants exhibiting high N-resorption efficiency produce N-poor litter with high C/N ratio (Lambers et al. 1998; Aerts and Chapin III 2000). High N-resorption efficiency is characteristic of short-lived plants such as herbs and graminoids, usually resulting in low litter decomposition rates, high N immobilisation in microbial biomass, low N mineralisation, and consequently low soil N-availability (Schlesinger 1991; Lambers et al. 1998; Aerts and Chapin III 2000; van der Krift and Berendse 2001; Hobbie and Gough 2002; Pouyat and Carreiro 2003). In contrast, N remaining in senesced leaves of plants with low N-resorption efficiency may circulate in the ecosystem through litter decomposition and subsequent mineralisation processes (Zaady et al. 1996; Hooper and Vitousek 1998; Lambers et al. 1998). The ability of microbes to decompose litter depends not only on the C/N ratio but also on the chemical form in which carbon occurs (Ehrenfeld 2001). High lignin and/or polyphenols concentration may reduce litter decomposability by either toxic effects on microorganisms or by retarding microbial breakdown of organic matter (Lambers et al. 1998; Hättenschwiler and Vitousek 2000). Mineral N can be retained in the soil through a variety of mechanisms, but probably the most significant processes involve microbial immobilisation and physicochemical reactions mediated by clay minerals (Barrett and Burke 2002). Microbial biomass is considered as an indicator of substrate quality and a regulator of N dynamics in arid and mesic environments (Mazzarino et al. 1998). Additionally, plants may control decomposition process through tissue lifespan that directly affects the quantity of litter available to decomposers. A thorough understanding of controls of plant litter decomposition and its consequences for N cycling is therefore indispensable for a good comprehension of terrestrial ecosystem functioning.

In Patagonia, various studies reported differential patterns of N conservation among dominant plant life forms. In temperate forests, the highest N-resorption efficiency was found in broad-leaved deciduous trees and the lowest in conifer trees, but this attribute was not related to potential soil-N dynamics which was explained by soil C and N, and lignin in senesced leaves (Diehl et al. 2003; Satti et al. 2003). In the arid shrubland of the Patagonian Monte, Carrera et al. (2000, 2003) reported higher N-resorption efficiency in short lived perennial grasses than in long lived evergreen shrubs but a weak relationship between the C/N ratio of senesced leaves and some components of the soil-N cycling. This was attributed to possible differences in litter decomposability among species induced by secondary metabolites. In this work we assessed the decomposition rates of senesced leaves of dominant species of evergreen shrubs and perennial grasses and analysed the relationship among decomposability, litter quantity and quality (N, C, phenolics, and lignin concentration and the C/N ratio in senesced leaves) and soil–N related attributes in three sites of the Patagonian Monte.

Methods

Study area

We selected a study area of about 2400 km^2, located in the Patagonian Monte (Argentina). The mean annual temperature is 13.7 °C (15 years series) and mean annual precipitation is 188 mm (Barros and Rivero 1982). Soils are a complex of Typic Petrocalcids- Typic Haplocalcids (del Valle 1998; Soil Survey Staff 1998). Vegetation corresponds to the shrubland of *Larrea divaricata* Cav. and *Stipa* spp., characteristic of the southern portion of the Monte Phytogeographic Province, which shares plant species with the Patagonian Phytogeographic Province (Cabrera 1976; Soriano 1950). Plant canopy covers less than 40–60% of the soil and 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 colonising bare soil areas (Bisigato and Bertiller 1997; Mazzarino et al. 1998).

Senesced leaves and soil attributes

Sampling was carried out during two consecutive years (2000–2001). Annual precipitation amounted 209 mm, and 279 mm in 2000 and 2001, respectively. Within the study area, we selected three study sites: Estancia "San Luis" (42°39′ S, 65°23′ W), Estancia "Ranchito" (42°49′ S, 65°34′ W), and Estancia "Amparo" (42°41′ S; 65°38′ W). At each study site and at two sampling dates (June and December of 2000 and 2001), we randomly selected 5 individuals of three species of each dominant life form. Among evergreen shrubs, the species selected were *Atriplex lampa* Gill, ex Moq. (Al), *Larrea divaricata* Cav. (Ld), and *Junellia seriphioides* (Gilles and Hook) Moldenke (Js). Among perennial grasses, the species selected were *Poa ligularis* Nees ex Steud. (PI), *Stipa tenuis* Phil. (St), and *Stipa speciosa* Trin. and Rupr (Ss). We sampled the soil under each plant canopy with a metallic tube (10 cm height and 10 cm in diameter) and we harvested four branches from each evergreen shrub and all the aboveground biomass of each perennial grass.

Chemical analyses in soil

From each soil core, we separated three sub-samples. One of them was air-dried, sieved to 0.5 mm and analysed for soil–N concentration by semimicro Kjeldahl (Bremmer and Mulvaney 1982) and for soil organic-C concentration by wet combustion (Nelson and Sommers 1982). The other two sub-samples were sieved to 2 mm. One of them was incubated at 25 °C and at 15% soil moisture for 12, 42 and 112 days for the estimation of the potential N-mineralisation. After incubation, soil samples were extracted with 2 M KC1 (1:5, soil:solution ratio) and analysed for $N–NH_4^+$ and $N–NO_3^-$. We used the indophenol-blue method to determine $N–NH_4^+$ and copperised Cd reduction to assess $N–NO^{3-}$ (Keeney and Nelson 1982). We adjusted a lineal model to potential N-mineralisation data to assess mean net-N mineralisation rate (*Nr*) in the soil underneath each plant species as follows:

$$y = \mathrm{Nr}^* t$$

where y is the potential N-mineralisation (mg kg^{-1}) accumulated at the time t (days).

The third sub-sample was used to estimate microbial-N flush (flush of NH_4^+ due to fumigation, Horwath and Paul 1994) by a modification of the chloroform fumigation-incubation technique (Vitousek and Matson 1985). After 10 days of soil incubation at 15% soil moisture at 25 °C, 1 ml of chloroform was added directly to each soil sample, stirred, and left in sealed beakers for 20 h. Afterwards, chloroform was removed and samples were incubated at 15% soil moisture at 25 °C for 10 days. Samples were extracted with 2 M KCl (1:5, soil:solution ratio) and analysed colorimetrically for $N–NH_4^+$ (Mazzarino et al. 1998). No attempt was made to express microbial-N flush in terms of microbial biomass, since reported values of recovery factor are extremely variable (k_N = 0.41−0.68, Mazzarino et al. 1998). Both, potential N-mineralisation and microbial-N flush were expressed on the basis of oven-dried (105 °C) soil weight.

Chemical analyses in senesced leaves

Recently senesced leaves (yellow–brown leaves without signs of deterioration) were separated from each evergreen shrub branch or perennial grass individual. After separation senesced leaves were dried at 60 °C for 48 h, weighed and analysed for their N concentration by semimicro Kjeldahl, (Coombs et al. 1985) and for their C concentration by dry digestion at 550 °C (Schlesinger and Hasey 1981). We analysed lignin concentration by the Van Soest (1963) procedure and total phenolics concentration by Folin–Ciocalteu method using 50% methanol as extract solution and tannic acid as standard (Waterman and Mole 1994).

Decomposition of senesced leaves

In March 2001, we collected samples of standing and fallen senesced leaves (yellow–brown leaves without signs of deterioration) from 20 plants of each study species and topsoil from 10 inter-patch areas at the three study sites. In the laboratory, all collected senesced leaves of each species were

composed in a single sample. Soil samples were also pooled and sieved to 2 mm. We evaluated the rates of decomposition of senesced leaves of each perennial grass and evergreen shrub species in a laboratory experiment using 21 litterbags (0.3 mm mesh) per species, containing 1 g of senesced leaves each, Each litterbag was then incubated on the top of 100 g of air-dry soil placed in a flask at 15% soil moisture and at 25 °C. After 12, 42 and 84 days from the beginning of incubation, seven litterbags of each species were removed, dried at 60 °C for 48 h, and weighted to evaluate the dry weight loss of decaying leaves at each litterbag at each extraction date. We used a simple negative exponential model to assess decomposition rate constants (k) of dry mass of each species (Swift et al. 1979) as follows:

$$y = a^{*}\mathrm{e}^{-(t^{*}k)}$$

where y is the dry mass of senesced leaves remaining in litterbags at time t (days), a is the constant of the equation, and k is the decomposition rate constant. Additionally, at each extraction date, we assessed N content (mass) in decaying leaves of each species by the method mentioned above.

Litter production

Sampling to assess annual leaf-litter production was carried out at Estancia San Luis. For this purpose, we randomly selected 5 individuals of each species (*A. lampa*, *L. divaricata*, *P. ligularis*, *S. tenuis* and *S. speciosa*) and installed two baskets (10.5 cm of diameter, 15 cm height) below each evergreen shrub canopy and one basket (20 cm of diameter, 30 cm height) surrounding each perennial grass individual. We collected the material accumulated at each basket, at monthly intervals, during the period July 2004–January 2005 in coincidence with the observed rhythms of senescence and litterfall of perennial grasses and evergreen shrubs (Bertiller et al. 1991; Carrera et al. 2003). In the laboratory, we eliminated from each basket the senesced leaves of trapped non-target species and separated recently senesced leaves, which were subsequently dried at 60 °C for 48 h and weighed. We calculated leaf-litter production of each species as the total mass of recently senesced leaves accumulated during the whole senescence period expressed per m^2 of plant canopy.

In January 2004, we also harvested the recently senesced leaves of (*A. lampa*, *L. divaricata*, *J. seriphioides*, *P. ligularis*, *S. tenuis* and *S. speciosa*) accumulated on the soil in 10 randomly selected plots (0.50×0.25 m). Leaf-litter was dried at 60 °C for 48 h and weighed. Additionally, at the same date, we estimated the mass of standing recently senesced leaves in five randomly selected individuals of *A. lampa*, *L. divaricata*, *J, seriphioides*, *P. ligularis*, *S. tenuis* and *S. speciosa*. For *J. seriphioides* and all perennial grass species, we harvested the whole plant. For the other two evergreen shrubs, we harvested a modal branch and counted the total number of branches of each individual for calculation of standing senesced leaves per individual. We also assessed the area of the canopy projection of each individual (Mueller-Dombois and Ellenberg 1974) and expressed the mass of standing senesced leaves per m^2 of plant canopy.

Statistical analysis

The significance of the differences in soil and senesced leaves variables (C and N concentration, C/N ratio) between life forms, and among sites was evaluated by two-way ANOVA (Norusis 1997). Sites and months were included as random blocks in the analysis. We did not include years as a random block since, for all variables, we did not find significant differences among them. The significance of the differences in lignin, and leaf-litter on soil and standing senesced leaves between life forms and species were evaluated by Mann Whitney test (Sokal & Rohlf 1981). The significance of the differences in net N mineralisation rates, the N content of decaying leaves and leaf-litter production between life forms and species were evaluated by ANOVA (Sokal and Rohlf 1981). Tukey's test was used for multiple comparisons among species (Norusis 1997). The significance of the differences in decomposition rate constants of senesced leaves among species was evaluated by Student t test. The relationships between plant and soil attributes were described by regression analysis (Norusis 1997). Unless otherwise noted, the level of significance throughout this study is $p \leq 0.05$.

Results

Soil attributes: N and C concentration, microbial-N flush and potential N-mineralisation

Mean values of soil-N and C concentrations differed significantly between evergreen shrubs and perennial grasses ($F_{1,360}$ = 24.28, p = 0.04; $F_{1,360}$ = 87.96, p = 0.01, respectively, Figure 1a, b). We found, however, some overlap between species of both life forms. Thus, the highest N and C concentrations corresponded to the soil under the evergreen shrub *A. lampa* (Al) and the lowest to the soil of the perennial grasses *S. tenuis* (St) and *S. speciosa* (Ss) and the evergreen shrub *J. seriphioides* (Js). The perennial grass *P. ligularis* (Pl) and the evergreen shrub *L. divaricata* (Ld) exhibited intermediate values. Organic-C concentration differed between months (June < December).

The microbial-N flush did not significantly differ between life forms, but significant differences were found among plant species. The highest value corresponded to the soil beneath Al and the lowest to St (Figure 2). The other species exhibited intermediate values. The microbial-N flush represented 3.9–4.2% of the total soil N and it was significantly higher in the soil beneath Ss than under Ld, the other species displayed intermediate values, which did not differ among them. Both N concentration and microbial N flush in soil did no vary between months.

Potential N-mineralisation was higher in the soil associated with evergreen shrubs than in the soil

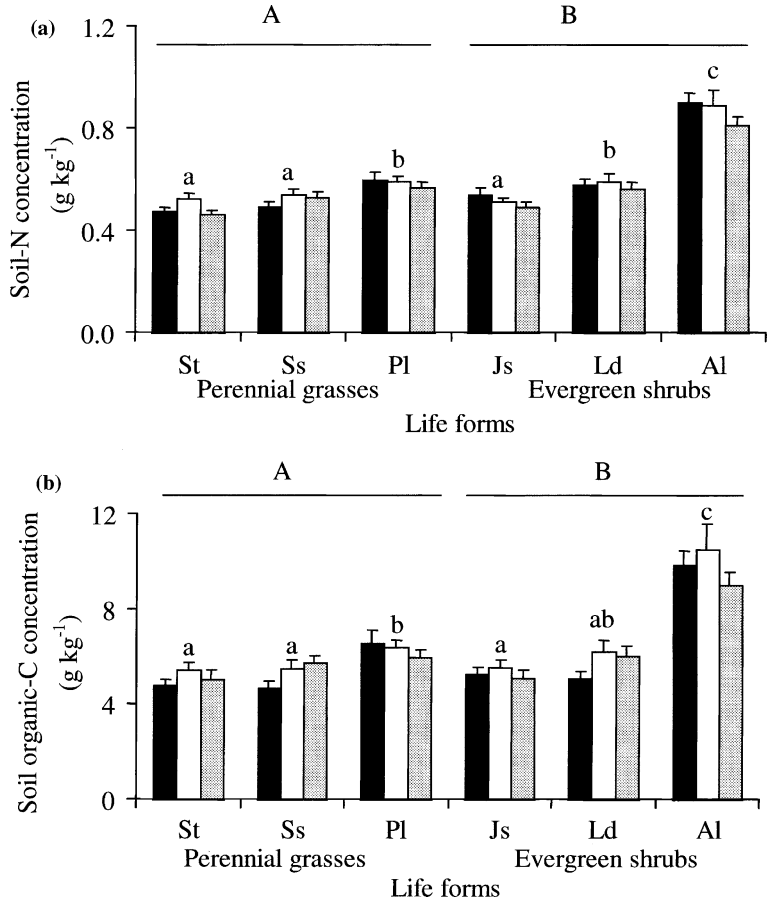

Figure 1. Mean values of: (a) N concentration (g kg^{-1}), and (b) organic -C concentration (g kg^{-1}) in the soil associated with evergreen shrubs and perennial grasses in the three study sites (black bars, Amparo; empty bars, Ranchito; grey bars, San Luis). Different capital letters indicate significant differences among life forms. Different lowercase letters indicate significant differences among species (St: *Stipa tenuis*, Ss: *Stipa speciosa*, Pl: *Poa ligularis*, Js: *Junellia seriphioides*, Ld: *Larrea divaricata*, Al: *Atriplex lampa*). Vertical lines indicate one standard error.

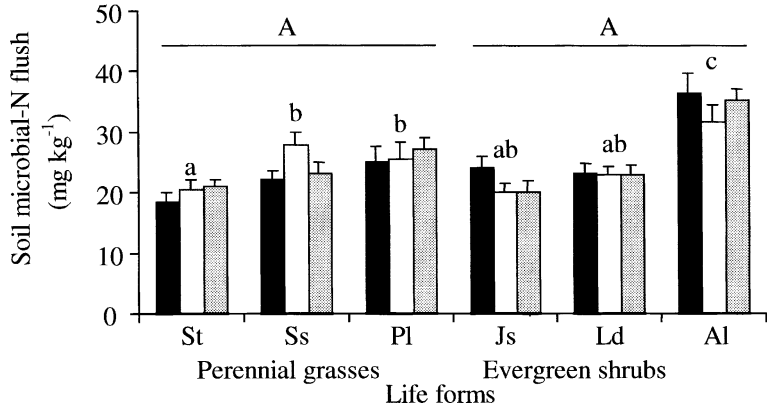

Figure 2. Mean values of microbial-N flush (mg kg^{-1}) in the soil associated with evergreen shrubs and perennial grasses in the three study sites (black bars, Amparo; empty bars, Ranchito; gray bars, San Luis). Different capital letters indicate significant differences among life forms. Different lowercase letters indicate significant differences among species. Acronyms of species as in Figure 1. Vertical lines indicate one standard error.

beneath perennial grasses at all incubation dates ($F_{1,360} = 97.18$, $p = 0.01$; $F_{1,360} = 21.69$, $p < 0.01$; $F_{1,360} = 39.73$, $p < 0.01$ at 12, 42 and 112 days of incubation, respectively). At the end of the incubation period (112 days of incubation), Al and St showed the highest and the lowest values of potential N mineralisation in soil, respectively. The other species did not differ among them (Table 1a). We found significant differences in potential N mineralisation between months (June < December) at 42 and 112 days of incubation. During the whole incubation period, the inorganic-N mineralisation proceeded mainly to nitrification ($p < 0.01$) and at the end of incubation, inorganic N represented between 10.7% and 12.7% of the total soil–N. The highest net-N mineralisation rate corresponded to the soil associated with Al and the lowest to the soil under St, the other species showed intermediate values (Table 1b). We did not find significant differences in soil N and organic-C concentrations, microbial-N flush and potential N mineralisation among sites nor significant interactions among factors (life form × site, life form × month, or life form × site × month).

Senesced leaves attributes: concentrations of N, C, lignin, and total phenolics and C/N ratio

Evergreen shrubs showed significant higher N concentration in senesced leaves ($F_{1,360} = 418.02$,

Table 1. Mean values of (a) potential N-mineralisation (mg kg^{-1}) in the soil underneath plant species at 12, 42 and 112 days of incubation, and (b) Estimated (simple lineal model) net-N mineralisation rates (Nr, day^{-1}) for the soil associated with each species.

	(a) Potential N-mineralisation (mg kg^{-1})									(b) Parameters estimated from the simple linear model		
	12 days			42 days			112 days					
	Amparo	Ranchito	San Luis	Amparo	Ranchito	San Luis	Amparo	Ranchito	San Luis	Nr (day^{-1})	R^2	p
Perennial grasses		A			A			A			A	
St	1.82	4.19	0.72ab	23.64	24.83	19.06a	61.42	54.95	49.59a	0.472a	0.87	<0.01
Ss	2.20	4.96	3.21bc	30.86	27.97	30.89ab	58.19	59.06	69.70b	0.613b	0.82	<0.01
PI	4.38	3.76	5.96bc	26.26	26.49	29.24ab	56.77	61.48	63.46b	0.619b	0.88	<0.01
Evergreen shrubs		B			B			B			B	
Js	6.60	5.10	6.29c	35.29	31.63	28.67b	73.11	66.20	53.13ab	0.567b	0.84	<0.01
Ld	8.21	4.35	5.62c	37.58	26.22	33.05b	60.87	61.01	70.26b	0.601b	0.85	<0.01
Al	−5.85	2.90	0.96a	41.87	38.07	44.28c	91.03	98.42	91.81c	0.883c	0.83	<0.01

Different capital letters indicate significant differences among life forms. Different lowercase letters indicate significant differences among species. Acronyms of species as in Figure 1.

$p < 0.01$) than perennial grasses (Table 2). We also found significant differences in N concentration in senesced leaves among evergreen shrubs, while N concentration in senesced leaves of perennial grasses did not differ among species. Carbon concentration in senesced leaves did not differ between life forms, however, significant differences were found among species of each life form (Table 2). The C/N ratio in senesced leaves was more than two fold higher in perennial grasses than in evergreen shrubs ($F_{1,360} = 140.62$, $p < 0.01$). We also found significant differences in C/N ratio in senesced leaves among species of each life form (Table 2). We did not observe significant differences in N and C concentrations and in the C/N ratio in senesced leaves among sites or months nor significant interactions among factors (life form × site, life form × month, life form × month × site).

Lignin concentration in senesced leaves was significantly lower in perennial grasses than in evergreen shrubs (Mann–Whitney $U = 115$, $p < 0.01$). We found a large range of variation in lignin concentration among evergreen shrubs, while no differences were observed in lignin concentration among perennial grasses. Lignin concentration in Ld did not differ from those found in perennial grasses (Table 2). Concentration of total phenolics in senesced leaves was significantly lower in perennial grasses than in evergreen shrubs (Mann–Whitney $U = 0$, $p < 0.01$) and varied among species of both life forms. In Ld, the value was more than six fold greater than in the other evergreen shrubs. In perennial grasses the lowest concentration of total phenolics was found in Pl and the highest value in Ss (Table 2).

Dry mass loss, decomposition rate constants and N content in decaying leaves of evergreen shrubs and perennial grasses

During the whole incubation period, mean values of dry mass loss of senesced leaves were significantly lower in perennial grasses than in evergreen shrubs (Mann–Whitney $U = 61$, $p < 0.01$; Mann–Whitney $U = 79$, $p < 0.01$; Mann–Whitney $U = 28$, $p < 0.01$; for 12, 42, and 84 days, respectively; Table 3a). However, we found a large range of variation in this trait among species of each life form and some overlapping in values of dry mass loss of senesced leaves between species of both life forms. After 12 days of incubation, mass loss of senesced leaves contained in litterbags was significantly higher in Al and Ld than in the rest of the species ($F_{5,42} = 149.87$, $p < 0.01$), After 42 days of incubation, the rate of mass loss of senesced leaves of Ld and Pl was strongly decelerated, Js and P did not differed between them, and Ld exhibited lower mass loss of senesced leaves than Al ($F_{5,42} = 46.57$, $p < 0.01$). After 84 days of incubation, we found the lowest dry mass loss in senesced leaves of Ss and St and the highest in Al. The other evergreen shrubs (Ld and Js) exhibited intermediate values. Dry mass loss in senesced leaves of P did not significantly differ from those of the other perennial grasses and from those the evergreen shrubs Ld and Js ($F_{5,42} = 41.46$, $p < 0.01$). For each species, dry mass decay was significantly described by a simple negative exponential curve (Table 3b). Evergreen shrubs showed decomposition rate constants (k) highly variable, but significantly higher than those of perennial grasses

Table 2. Mean values ± one standard error of N and C concentration (g kg^{-1}), C/N ratio, lignin concentration (g kg^{-1}) and total phenolics concentration (g Tanic acid kg^{-1}) in senesced leaves of perennial grasses and evergreen shrubs.

	N concentration	C concentration	C/N ratio	Lignin concentration	Total phenolics concentration
Perennial grasses	A	A	B	A	A
St	4.17 ± 0.12a	429.64 ± 2.75b	108.11 ± 3.41c	70.70 ± 4.85a	6.12 ± 0.11b
Ss	3.88 ± 0.13a	461.19 ± 1.61d	128.15 ± 4.70d	65.30 ± 3.04a	9.90 ± 0.08c
Pl	4.01 ± 0.10a	433.37 ± 3.05b	112.85 ± 3.25c	53.60 ± 2.44a	4.49 ± 0.14a
Evergreen shrubs	B	A	A	B	B
Js	8.77 ± 0.25b	457.94 ± 2.02d	54.58 ± 1.68b	157.40 ± 6.72c	12.48 ± 0.23d
Ld	10.86 ± 0.24c	449.48 ± 1.53c	42.60 ± 0.86a	66.20 ± 5.93a	80.52 ± 0.35e
Al	8.85 ± 0.21b	358.70 ± 2.49a	41.93 ± 1.15a	117.00 ± 8.00b	12.76 ± 0.17d

Different capital letters indicate significant differences among life forms. Different lowercase letters indicate significant differences among species. Acronyms of species as in Figure 1.

Table 3. Mean values ± one standard error of (a) dry mass loss (mg) by species at 12, 42, and 84 days and (b) estimated decomposition rate constants (k, day^{-1}) and equation parameters of the simple negative exponential model used for estimations for senesced leaves of each species.

(a) Dry mass loss (mg)				(b) Parameters estimates from the simple negative exponential model				
	12 days	42 days	84 days	n	k values (day^{-1})	a values	R^2	p
Perennial grasses	A	A	A		A			
St	100.89 ± 5.32a	240.06 ± 8.76a	312.71 ± 12.62a	28	$4.4\times10^{-3}\pm2.8\times10^{-4}$a	0.962 ± 0.013	0.91	<0.001
Ss	90.26 ± 4.79a	218.57 ± 28.66a	285.14 ± 18.82a	28	$3.9\times10^{-3}\pm4.1\times10^{-4}$a	0.965 ± 0.019	0.77	<0.001
Pl	141.03 ± 4.09b	255.97 ± 7.76a	329.83 ± 10.58ab	28	$4.4\times10^{-3}\pm3.2\times10^{-4}$a	0.942 ± 0.014	0.88	<0.001
Evergreen shrubs	B	B	B		B			
Js	113.66 ± 3.35a	235.87 ± 10.62a	383.17 ± 23.77b	28	$5.6\times10^{-3}\pm3.3\times10^{-4}$ b	0.974 ± 0.015	0.92	<0.001
Ld	236.41 ± 4.12c	320.36 ± 5.13b	371.43 ± 8.00b	28	$4.7\times10^{-3}\pm5.4\times10^{-4}$ab	0.889 ± 0.023	0.75	<0.001
Al	246.04 ± 9.01c	472.86 ± 9.44c	553.29 ± 8.49c	28	$9.1\times10^{-3}\pm6.6\times10^{-4}$c	0.888 ± 0.028	0.88	<0.001

Different capital letters indicate significant differences among life forms. Different lowercase letters indicate significant differences among species. Acronyms of species as in Figure 1.

(Table 3b). In Ld, however, k did not differ from those of perennial grasses.

The N content in decaying leaves at different incubation dates varied among plant species (Table 4). Decaying leaves of Al showed a net N-release ($F_{3,28} = 52.25$, $p < 0.01$) during the incubation period. In contrast, those of Ld, St and P exhibited increased N content along the incubation period ($F_{3,28} = 8.22$, $p < 0.01$; $F_{3,28} = 4.56$, $p < 0.05$; $F_{3,28} = 38.19$, $p < 0,01$, respectively) and decaying leaves of Ss did not show significant differences in N content among incubation dates ($F_{3,28} = 0.56$, $p = 0.64$). Decomposing leaves of Js differed from the latter since they exhibited a net N-release in the first two incubation dates and increased N content at the end of the incubation period ($F_{3,28} = 11.18$, $p < 0.01$).

Litter production

The studied species showed significant differences in leaf-litter production, leaf-litter on soil, and mass of standing senesced leaves (Table 5). Leaf-litter producction and leaf-litter on soil varied among species but we did not find significant differences between life forms. We found the highest value of leaf-litter production in Al and the lowest values in Ld and P. The other species (Ss and St) showed intermediate values. Both, Ld and St exhibited the highest values of leaf-litter on soil and Js the lowest. The mass of standing senesced leaves was significantly higher in perennial grasses than in evergreen shrubs (Mann–Whitney $U = 0$, $p < 0.01$). Among perennial grasses, the highest values of standing senesced leaves were observed in Ss. Among evergreen shrubs, both Js and Al

Table 4. Mean values ± one standard error of N content (mg) in decaying leaves of each species at 12, 42, and 84 days. Different capital letters indicate significant differences among life forms.

	Initial values	12 days	42 days	84 days
Perennial grasses	A	A	A	A
St	4.98 ± 0.13a	5.05 ± 0.08a	5.18 ± 0.43a	6.15 ± 0.22b
Ss	4.82 ± 0.30a	4.68 ± 0.16a	4.63 ± 0.16a	4.97 ± 0.15a
Pl	4.90 ± 0.17a	5.35 ± 0.09a	5.43 ± 0.08a	6.95 ± 0.21b
Evergreen shrubs	B	B	B	B
Js	9.73 ± 0.4b	7.51 ± 0.24a	8.17 ± 0.33a	9.60 ± 0.30b
Ld	15.98 ± 0.36a	15.61 ± 0.19a	16.05 ± 0.28a	17.38 ± 0.21b
Al	8.76 ± 0.17d	7.81 ± 0.14c	7.09 ± 0.17b	6.19 ± 0.12a

Different lowercase letters indicate significant differences among extraction dates for each species. Acronyms of species as in Figure 1.

Table 5. Mean values ± one standard error of leaf-litter production (g m^{-2} canopy), leaf-litter on soil (g m^{-2} soil) and standing senesced leaves (g m^{-2} canopy) by species.

	Leaf-litter production	Leaf-litter on soil	Standing senesced leaves
Perennial grasses	A	A	A
St	4.01 ± 0.64ab	1.35 ± 0.29c	19.01 ± 2.41c
Ss	13.28 ± 1.66bc	0.43 ± 0.18b	35.43 ± 4.65d
Pl	3.05 ± 1.15a	0.24 ± 0.09b	28.45 ± 10.41cd
Evergreen shrubs	A	A	B
Js	no data	$6.9\times10^{-3}\pm 5.4\times10^{-3}$a	4.01 ± 0.75b
Ld	2.70 ± 1.03a	1.18 ± 0.38c	1.29 ± 0.40a
Al	34.32 ± 15.74c	1.05 ± 0.79b	3.85 ± 0.66b

Different capital letters indicate significant differences among life forms. Different lowercase letters indicate significant differences among species. Acronyms of species as in Figure 1.

accounted for the highest and the lowest value of standing senesced leaves, respectively.

Relationship among soil attributes, senesced leaves traits, and decomposition rate constants

The initial-C, N and total phenolics concentrations of senesced leaves explained together 78% of the total variance observed in the dry mass loss in decaying leaves (Table 6). Decomposition rate constant (k) of senesced leaves was the variable best (positively) correlated to all soil variables (Table 7), explaining 98%, 98%, 73%, and 67% of the total variance of N concentration, organic-C concentration, net-N mineralisation rate and microbial-N flush in soil, respectively.

Discussion

As reported for other arid ecosystems (Garcia-Moya and McKell 1970; Cross and Schlesinger 1999; Facelli and Brock 2000), dominant evergreen shrubs of the Patagonian Monte tended to concentrate more soil N and C and to mineralise more N than perennial grasses. These differences, however, may be mostly attributed to *A. lampa*. This species exerted a stronger local effect on soil N and C than the other two shrubs (*L. divaricata* and *J. seriphioides*). This could be directly attributed to higher leaf-litter production, N concentration in senesced leaves, decomposability and net N-release from decaying leaves along with lower C and phenolics concentrations in senesced leaves of *A. lampa* relative to the two

Table 6. Multiple regression between dry mass loss in decaying leaves (mg) at the end of the incubation period (84 days, dependent variable) and the initial C (g kg^{-1}), N (g kg^{-1}), and total phenolics concentration (g Tanic acid kg^{-1}) in senesced leaves, (i) ANOVA of regression and (ii) fitted parameter values. $^{**}p \leq 0.01$.

Dependent variable: Dry mass loss

(i) Analysis of variance						(ii) Parameter estimates		
Variable entered	Source	df	MS	F	R^2	Variable entered	Regression coefficient	T
Step 1 C in senesced leaves	Regression	1	0.24	71.4**	0.64	Constant	1.2	2.3**
	Residual	40	3.4×10^{3}			C in senesced leaves	-1.9×10^{-3}	−8.5**
	Total	41						
Step 2 N in senesced leaves	Regression	2	0.13	46.6**	0.71	Constant	1.1	12.3**
	Residual	39	2.8×10^{-3}			C in senesced leaves	-1.9×10^{-3}	−9.0**
	Total	41				N in senesced leaves	5.9×10^{-3}	2.9**
Step 3 Total phenolics in senesced leaves	Regression	3	39.7×10^{-3}	43.8**	0.78	Constant	1.0	10.7**
	Residual	38	2.2×10^{-3}			C in senesced leaves	-1.7×10^{-3}	−8.7**
	Total	41				N in senesced leaves	1.9×10^{-2}	4.5**
						Total phenolics in senesced leaves	-2.2×10^{-3}	−3.46**

Table 7. Simple linear regressions between decomposition rate constants (k, day^{-1}) of senesced leaves (independent variable) and (a) Soil-N concentration (g kg^{-1}), (b) Soil organic-C concentration (g kg^{-1}), (c) Soil net-N mineralisation rate (day^{-1}), and (d) Soil microbial-N flush (mg kg^{-1}), (i) ANOVA of regression and (ii) fitted parameter values. $^{**}p \leq 0.01$, $^{*}p \leq 0.05$.

(i) Analysis of variance						(ii) Parameter estimates		
Independent variable entered	Source	df	MS	F	R^2	Independent variable entered	Regression coefficient	T
(a) Dependent variable: Soil-N concentration								
Decomposition rate constant	Regression	1	2.14	227.7**	0.98	Constant non significant		
	Residual	4	9.4×10^{-3}			Decomposition rate constant	106.2	15.1**
	Total	5						
(b) Dependent variable: Soil organic-C concentration								
Decomposition rate constant	Regression	1	246.2	305.0**	0.98	Constant non significant		
	Residual	4	0.8			Decomposition rate constant	1137.7	17.5**
	Total	5						
(c) Dependent variable: net-N mineralisation rate								
Decomposition rate constant	Regression	1	788.4	10.75*	0.73	Constant	32.6	2.9*
	Residual	4	73.4			Decomposition rate constant	6536.2	3.3**
	Total	5						
(d) Dependent variable: Microbial-N flush								
Decomposition rate constant	Regression	1	87.4	8.10*	0.67	Constant	13.2	3.1*
	Residual	4	10.8			Decomposition rate constant	2176.5	2.9*
	Total	5						

other evergreen shrub species. The low values of leaf-litter of *A. lampa* on the soil, despite of the high leaf-litter production of this species, further support the high decomposability and low permanence of senesced leaves of *A. lampa* on the soil. Differences in C concentration in senesced leaves among species of evergreen shrubs may be attributed to morphofunctional differences. In comparison with *A. lampa*, the species *L. divaricata* and *J. seriphiodes* have lower leaf turnover, lower litterfall and more marked xeromorphic traits (Carrera et al. 2000), resulting in a higher ability to colonize and persist in degraded N-poor areas of bare soil (Bisigato and Bertiller 1997). *Junellia seriphiodes* also presented higher concentration of lignin in senesced leaves, a characteristic of slow growing species dominating water-limited ecosystems (Lambers et al. 1998). As suggested by several authors (Lambers et al. 1998; Aerts and Chapin III 2000; Hobbie 2000; Tutua et al. 2002), high lignin concentration may slow down litter decomposition and N cycling thus reducing plant effects on local soils. However, this rationale was not adequate to explain the pattern observed for *L. divaricata*, which showed lignin concentrations near twice lower than *A. lampa*. The presence of high concentration of total phenolics could explain the observed low decomposition rates of *L. divaricata* despite its high N, low lignin and low C/N ratio in senesced leaves. Some studies also reported that species of *Larrea* genus concentrate high quantities of nordihydroguaiaretic acid in leaves (Ruiz Leal 1972; Dimitri 1980; Hyder et al. 2002). The presence of these compounds would not only act as a defence against herbivory or to withstand water stress but also would make senesced leaves of this species recalcitrant to biodegradation (Verástegui et al. 1996; Lambers et al. 1998; del Valle and Rosell 1999; Hättenschwiler and Vitousek 2000). In coincidence with this, *L. divaricata* was one of the species exhibiting the highest leaf-litter on soil even when having a low leaf litter production. Further, the presence of high concentration of total phenolics in leaves of *L. divaricata* could explain the lower N-resorption efficiency (Carrera et al. 2000) and the high N concentrations in senesced leaves of this species, since these compounds may enhance protein precipitation before hydrolysis reducing N resorption (Aerts and Chapin III 2000).

The low intensity of effects of perennial grasses on local soil traits may be attributed to the high retention of senesced leaves in the plant after senescence along with low N concentration in senesced leaves and high N immobilisation in decaying leaves. This latter could be associated with a high saprophytic activity which may immobilise N during the initial stages of leaf decay (Ald 2003). Higher N and C concentration in the soil beneath *P. ligularis* in comparison with the other two perennial grasses could be explained by the fact that *P. ligularis* is a more mesophytic species (high N concentration in green leaves and high leaf turnover) than the other two perennial grasses, which preferentially colonize nutrient rich-soils mostly associated with evergreen shrubs (Carrera et al. 2000; Bertiller et al. 2002).

As reported for other arid ecosystems (Garcia-Moya and McKell 1970; Cross and Schlesinger 1999; Facelli and Brock 2000), our results indicate that soil fertility and the development of ''fertility islands'' in arid ecosystems of the Patagonian Monte are strongly related to quality and quantity of local species litter. Thus, the conservation of the plant cover of species such as *A. lampa* that contribute with higher quality and quantity of litter than other dominant evergreen shrubs should be a target for the conservation of ecosystem structure and functioning. High litter quality and quantity would improve physical and chemical soil properties, and would promote biological activity and nutrient cycling (Cross and Schlesinger 1999). Furthermore, high N immobilisation in microbial biomass in the soil associated with *A. lampa* implies an important mechanism to avoid N losses by leaching or denitrification but at the same time a source of labile N (Franzluebbers et al. 2001). 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 (Mazzarino et al. 1998).

In agreement with other studies (Wedin and Pastor 1993), our results indicate that litter quality and quantity are major controls of the decomposition rates of the small active soil organic matter pool of desert ecosystems. Therefore, litter changes associated with species shifting may significantly alter soil fertility. The regulatory effect of litter quantity and quality on rates of litter decomposition may be a consequence of either limiting N for

microbial activity or microbial inability to breakdown complex carbonated structures (Heal et al. 1997; Aerts and Chapin III 2000).

We concluded that litter decomposition rates along with leaf-litter production are meaningful indicators of plant local effects on soil N dynamics in shrublands of the Patagonian Monte, and probably in other similar ecosystem of the world dominated by slow growing species that accumulate a wide variety of secondary metabolites. In these cases, other indicators such as lignin concentration and C/N or lignin/N ratios widely used to predict litter decomposition at local, regional, and global scales (Fog 1988; Kemp et al. 2003) may fail in the estimation of litter decomposition and plant local effects since secondary metabolites other than lignin and low leaf-litter production may slow down litter decomposition and delay N cycling.

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