Nutrient cycling in Patagonian ecosystems

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Abstract. *The knowledge on nutrient cycling in Patagonian ecosystems of Argentina is scarce. However, studies not directly focused on nutrient cycling provide relevant information about the mechanisms of nutrient conservation in the climatically different ecosystems of the region. Here, we identified indicators of litter decomposition and soil N mineralization rates of some representative species of the dominant plant functional groups along the wide precipitation gradient of Patagonia. Senescent leaves and litter of forest trees have higher C concentration and C/N ratio and lower N concentration than steppe shrubs. Within the tree life form, evergreen species have higher C/N ratio than deciduous species. Differences in N concentration between green and senescent leaves suggest a higher N use efficiency in forest trees than in steppe shrubs. Within the steppe, grasses have higher nutrient use efficiency than shrubs due to their higher C and much lower N, P and K content in senescent leaves and litter. Thus, we hypothesize the occurrence of (i) a gradient from nutrient-conserving ecosystems in wetter sites (Andean-Patagonian forest) to relatively nutrient-rich (low nutrient use efficient) ecosystems in drier sites (Patagonian steppe), and (ii) differences in nutrient conservation mechanisms among different functional groups: in the Andean-Patagonian forests N conservation and N use efficiency is greater in evergreens than in deciduous woody species and in conifers than in broad-leaf species, whereas in the Patagonian steppe, grasses have higher nutrient resorption than shrubs. Likely as a consequence of these differences in litter quality, potential N mineralization is greater in deciduous than in evergreen Patagonian forests. Within the steppe, N inineralization seems to depend on grass and shrub cover, which in turn is regulated by disturbance, largely grazing. Since nutrient conservation in vegetation, specially N, is associated to the rates of litter decomposition and soil N mineralization, the confirmation of these patterns would allow to predict ecosystem resilience and resistance to nutrient losses, and contribute to understand and predict the response of the different Patagonian species or functional groups to interannual climatic variability and natural or anthropogenic disturbances. There is a special need for further research on P cycling, nutrient allocation in vegetation, and field measurements of litter decomposition and N mineralization.*

Introduction

Patagonia is characterized by a distinctive longitudinal gradient of precipitation and soil types and a gradual latitudinal gradient of temperature. Precipitation decreases from the western mountains towards the east and temperature decreases from north to south (Prohaska 1976, Barros and Rivero 1982). These geographic gradients impose different structural patterns of soils and vegetation as well as different patterns of ecosystem functioning (soil water dynamics, nutrient cycling, net primary production, etc.) (Cabrera 1976, Soriano et al. 1983, Ares et al. 1990). Thus, forests dominate the more humid, western Patagonian Region, predominantly on Andisols, i.e., volcanic soils (1000-3000 mm rainfall), while a steady transition from grasslands to scattered grass and shrub steppes extends towards the east on Aridisols (from 500 to 100 mm rainfall). In the transitional zone between both regions (500-1000 mm), vegetation consists of shrub-grasses with scattered patches of *Austrocedrus chilensis* on xeric Mollisols or Alfisols. In Tierra del Fuego, soils under forests are

predominantly acid with spodic characteristics, being classified as non-allophanic Andisols, Spodosols or desaturated Inceptisols (Ferrer 1981, Lanciotti et al. 1993).

According to Schlesinger (1991), net primary production strongly depends on internal nutrient cycling (i.e., resorption and litter turnover) achieved by long-term accumulation of elements received from the atmosphere and the lithosphere. At a regional scale, annual precipitation and actual evapotranspiration are the most important factors controlling leaf litter turnover, and consequently nutrient cycling, across a wide range of ecosystems (Dyer et al. 1990). With increasing precipitation and plant cover, the increase in leaching outweighs the effect of increased weathering, resulting in decreasing concentrations of rock-derived nutrients (Austin and Vitousek 1998). Thus, a distinctive pattern of factors controlling nutrient cycling may be identified along the strong west-east gradient of precipitation, soils types, and plant cover in Patagonia. Since the knowledge of nutrient cycling in Patagonian ecosystems of Argentina is scarce and disperse, the main objectives of this paper are to compile the available information, identify some general features of nutrient cycling in this region, and outline the major trends for future research.

Nitrogen cycling

N conservation mechanisms
N cycling has received more attention in ecosystem research than any other nutrient because (i) N availability limits growth in most temperate forests and, it can have important ecological implications due to nitrate leaching, even when it is not limiting (available N > plant N uptake) (Binkley 1986); (ii) it is considered the most limiting nutrient for plant growth in arid and semiarid ecosystems (Skujins 1981).

Litter with high concentrations of plant nutrients decomposes more rapidly, and net mineralization is likely to begin earlier (Schlesinger 1991). Therefore, the mechanisms of N conservation in vegetation affect both litter decomposition and soil N availability. Greater conservation of N is associated with (i) high N resorption during senescence, (ii) high C/N ratios, lignin concentration, and lignin/N ratios in litter, (iii) low N concentrations in green leaves, and (iv) low soil N mineralization (Vitousek et al. 1982, Gower and Son 1992, Binkley 1994, Martin and Aber 1997). Although nutrient resorption is one of the most important plant strategies to conserve nutrients (Schlesinger 1991, Killingbeck 1996), there is much controversy on the apparently higher resorption of (i) plants growing in infertile vs. fertile soils, (ii) evergreens vs. deciduous woody perennials, and (iii) desert shrubs vs. non-desert woody perennials (Chapin 1980, Vitousek et al. 1982, Adams and Attiwill 1986, Vitousek and Sanford 1986, Killingbeck 1993, Aerts 1996, Killingbeck and Whitford 1996).

Differences in nutrient conservation between fertile and infertile sites are probaly not due to direct response of plants, but rather to the tendency of species with higher inherent capability for reducing nutrient losses to dominate nutrient-poor sites (Chapin 1980, Schlesinger 1991). According to some authors, this capability, commonly attributed to evergreenness in forest ecosystems, is not necessarily coupled with higher resorption, but with a longer leaf life-span and lower nutrient requirements (Enright and Ogden 1995, Aerts 1996). This results not only in higher adaptation to nutrient-poor soils, but also in lower nutrient losses by leaching. Thus, evergreen trees commonly represent the dominant species on less fertile soils of natural forests and cycle less N in litterfall than deciduous species (Gosz 1981, Nadelhoffer et al. 1985, Aerts 1996). In desert ecosystems, the general assumption of a co-occurrence of low soil N and high foliage N content or high N resorption in shrubs has been recently demonstrated to be inexact (Killingbeck 1993, Killingbeck and Whitford 1996). These authors have shown that N concentration in green leaves, and probably leaf litter, of desert shrubs are not substantially different from N concentrations in woody perennials growing in other ecosystems. The capacity of shrub species growing in N poor soils to contain foliar N concentrations similar to species of more N rich-ecosystems is attributed to the high spatial and temporal heterogeneity common to deserts (Killingbeck and Whitford 1996),

where organic matter and N are typically concentrated in "islands of fertility"; the loss of these islands would result in a more homogeneous distribution of N, and consequently in widespread N deficiency.

The inverse of nutrient concentration in annual litter or senescent leaves is an indicator of "nutrient use efficiency" and, consequently, of nutrient limitation: dry matter per nutrient unit. Higher dry matter per nutrient unit indicates higher nutrient use efficiency or higher nutrient limitation (Vitousek 1982, Aerts 1990). On the other hand, Killingbeck (1996) has recently proposed the direct use of the nutrient concentration in senescent leaves as an indicator of the "nutrient resorption proficiency" of vegetation. This author analyzed data of senescent leaf N concentration of 89 deciduous and evergreen woody perennials in order to (i) determine the minimal level below which further reductions are unlikely or biochemically impossible ("ultimate potential resorption"), and (ii) establish benchmark levels that define complete and incomplete resorption. He concluded that for both growth forms, 0.3 % N in senescent leaves represents the ultimate potential resorption, while values below 0.7% indicate highly proficient plants.

For Patagonian forests, complete data on nutrient concentration in annual litter or senescent leaves are scarce, but data on N are available and may be used to infer some general trends. Dry

Table 1. Nutrient use efficiency as the inverse of nutrient litter/senescent leaf concentration in Patagonian forests (g dry matter/g nutrient). Comparison with average values of the northern hemisphere (USA and Europe) and tropical forests.

	N	P	K	Ca
Evergreen- and deciduous shrubs and trees of the northern hemisphere[1]	137-98	2017-1260	-	-
Poor fertile soil- and montane tropical forests[2]	150-110	3950-2850	359-397	120-209
Eucalyptus calophylla, E. marginata, Agathis australis (Australia)[3]	> 300	-	-	-
Nothofagus pumilio (Tierra del Fuego)[4]	125 (133)[5]	667	267	69
Nothofagus pumilio (ChallHuaco)[6]	137	-	-	-
Nothofagus antarctica (Tierra del Fuego)[5]	90-100	-	-	-
Nothofagus dombeyi (Bariloche)[6]	200	-	-	-
Austrocedrus chilensis (Esquel-Bariloche)[7]	200	-	-	-
Discaria trinervis (Bariloche)[8]	53	-	-	-

1. Aerts (1996); 2 Vitousek and Sanford (1986); 3 Enright and Ogden (1995); 4 Calculated from fine litter (Richter and Frangi, 1992); 5 Senescent leaves (Schlichter, unpubl.); 6 Gobbi (unpubl.); 7 Buamscha et al. (1998); 8 Chaia (1997).

Table 2. C (%), N (%), lignin (%), C/N and lignin/N in senescent leaves of some tree species of Patagonian forests and potential N mineralization of soil sampled beneath trees and incubated during 16 weeks under controlled conditions of soil moisture and temperature. Values in parentheses in the last column indicate the proportion (%) of NO_3-N at the end of the incubation period.

	C	N	Lignin	C/N	Lignin/N	pot. Nmin (mg/kg)
Austrocedrus chilensis						
Dense forest (Esquel)[1]	54.0	0.48	29.5	113	62	60 (93)
Mixed forest (V. Mascardi)[1]	51.8	0.54	24.0	96	44	45 (90)
Nothofagus dombeyi (Bariloche)[2]	48.4	0.49	18.3	99	37	200 (89)
Nothofagus antarctica						
Dense forest (T.del Fuego)[3]	48.0	0.99	21.1	49	21	300 (13)
Silvopastoral (T.del Fuego)[3]	47.1	1.14	26.6	41	23	230 (50)
Nothofagus pumilio						
(ChallHuaco)[4]	47.0	0.73	13.3	64	18	300 (94)
(T. del Fuego)[3]	47.4	0.75	24.9	63	33	-

1 Buamscha et al. (1998); 2 Gobbi (unpubl.); 3 Schlichter (unpubl.); 4 Alauzis (unpubl.).

matter per unit N in annual litter or senescent leaves (N use efficiency) of the two deciduous, Patagonian species, *Nothofagus antarctica* and *N. pumilio* (90-137 g/g) are within the range for North American and European temperate forests, and nutrient-poor tropical forests (Table 1). However, data on other nutrients are much lower for Patagonian *N. pumilio* forests in Tierra del Fuego than in the other ecosystems. This suggests that N is the only limiting nutrient in these forests. N use efficiency is low (53 g/g) only in the case of *Discaria trinervis,* a deciduous actinorhizal shrub which fixes atmospheric N. Enright and Ogden (1995) have suggested that southern hemisphere conifers and some eucalyptus species are much more N use-efficient than those of the northern hemisphere, with values above 300 g dry matter/g N in senescent leaves. In our case, values for evergreen broad-leaf and conifer species (*N. dombeyi, Austrocedrus chilensis)* are about 200 g/g. N concentration in senescent leaves suggest that evergreen conifers and broad-leaf species of the Patagonian forests are highly N proficient, *sensu* Killingbeck (1996), (< 0.7% N), while broad-leaf deciduous species are less proficient (> 0.7% N), (Table 2).

Gutiérrez et al. (1991) working in *Nothofagus* forests of Tierra del Fuego, have suggested that *N. betuloides* (evergreen broad-leaf) is more adapted than *N. pumilio* to waterlogged stand conditions and subsequent reduction in N availability. They suggest that the longer leaf life span, accumulation of fine roots in the upper part of the organic H horizon (oxidant conditions), and low N requirements of *N. betuloides* are adaptations to these limiting soil characteristics. Particularly, higher C/N ratios of young and mature leaves of *N. betuloides* with respect to *N. pumilio,* 30-40 vs. 20 (Table 3) are good indicators of low N requirements. No data are available on N concentration in senescent leaves, but it might be expected that differences in C/N ratio between both species would be maintained or even widened. Armesto et al. (1992) have also suggested that the higher colonizing ability of *N. betuloides* respect to *N. pumilio* in skeletal glacial soils of Chile is related with a higher tolerance to low soil N availability. Thus, these results indicate that N conservation, i.e. higher resorption proficiency and N use efficiency, is higher in evergreen (*A. chilensis, N. dombeyi,* and probably *N. betuloides)* than in deciduous species (*N. antarctica, N. pumilio, D. trinervis).*

In the Patagonian arid and semiarid steppe, data on N content in litter of shrubs is only available for *Atriplex lampa* (evergreen) and *Prosopis alpataco* (deciduous) (Table 4). Values are higher than those of tree species of the Patagonian forest (0.8-2.4 % vs. 0.5-1.1 %). *P. alpataco,* a Mimosaceae that fixes atmospheric N, has the highest values. N content in green leaves of a large number of shrub species ranges from 0.9 to 2.9%. The minimum values are higher than those of steppe grasses and trees/shrubs of the Patagonian forests: 0.4-2.5% and 0.6-3.2%, respectively (Tables 4 and 5). Similar mean values are reported by Killingbeck and Whitford (1996) for 78

Table 3. C (%), N (%), lignin (%), C/N and lignin/N in young (1 year) and mature (> 1 year) leaves of some tree species of Patagonian forests.

SPECIES	young leaves			mature leaves			young or mature leaves	
	C	N	C/N	C	N	C/N	lignin	lignin/N
Austrocedrus chilensis								
Dense (Esquel)[1]	55	0.9	70	55.0	0.6	100	-	-
Mixed (V.Mascardi)[1]	54.5	1.2	50	52.5	0.8	70	-	-
Nothofagus betuloides								
(T.del Fuego)[2]	49.4	1.5	33	49.7	1.25	40	-	-
Nothofagus dombeyi								
(Bariloche)[3]	-	-	-	48.1	1.61	30	15.7	9.8
Nothofagus pumilio								
(T.del Fuego)[2]	45.1	2.3	20	-	-	-	-	-
(ChallHuaco)[4]	47.6	1.9	25	-	-	-	6.3	3.3
Nothofagus antarctica								
(ChallHuaco)[3]	48.1	1.9	25	-	-	-	10.2	5.4
Discaria trinervis								
(Bariloche)[5]	-	3.2	-	-	-	-	-	-

1 Buamscha et al. (1998); 2 Gutiérrez et al. (1991); 3 Gobbi (unpubl.); 4 Alauzis (unpubl.); 5 Chaia (1997).

Table 4. P (%), K (%), Ca (%), C (%), N (%), lignin (%), C/N and lignin/N in green, senescent leaves and litter of perennial grasses and shrubs of the Patagonian steppe.

Species	P	K	Ca	C	N	Lignin	C/N	Lignin/N
SHRUBS								
Atriplex lampa								
Green leaves								
Spring	0.09	0.20	2.19	-	1.5	-	-	-
Summer[1]	0.08	0.39	1.38	-	1.2	-	-	-
Litter								
Spring	0.07	0.22	2.40	33.8	1.0	-	33.8	-
Summer[1]	0.06	0.52	2.09	37.3	0.8	-	46.6	-
Prosopis alpataco								
Green leaves								
Spring	0.15	0.39	1.06	-	2.1	-	-	-
Summer[1]	0.14	0.78	1.70	-	2.9	-	-	-
Litter								
Spring	0.10	0.43	2.99	33.3	1.5	-	25.5	-
Summer[1]	0.14	0.35	2.34	42.7	2.4	-	17.8	-
Chuquiraga avellanedae								
Spring, green[2]	0.19	1.40	0.96	48.8	0.9	13.5	54.2	15.0
Mulinum spinosum								
Spring, green[2]	0.48	2.90	1.32	46.6	2.2	7.1	21.2	3.2
Nassauvia glomerulosa								
Spring, green[2]	0.30	2.22	0.55	48.0	1.4	13.0	34.3	9.3
GRASSES								
Bromus setifolius								
Green leaves (Spring)[2]	0.33	2.35	0.82	44.3	2.0	3.4	22.2	1.7
Senescent leaves[2]	0.09	0.63	0.44	42.7	0.5	7.0	85.4	14.0
Festuca pallescens								
Green leaves (Spring)	0.19	1.80	0.29	46.6	1.0	3.9	46.6	3.9
Senescent leaves[2]	0.09	0.34	0.24	47.7	0.3	8.0	159.0	26.7
Hordeum comosum								
Green leaves (Spring)[2]	0.25	2.57	0.54	43.9	2.5	3.6	17.6	1.5
Senescent leaves[2]	0.09	0.47	0.26	43.1	0.4	8.4	107.8	21.0
Poa ligularis								
Green leaves (Spring)	0.23	1.60	0.25	47.0	1.1	3.5	42.7	3.2
Senescent leaves[2]	0.05	-	0.23	45.4	0.2	6.5	227.0	32.5
Stipa speciosa var. major								
Green leaves (Spring)[3]	-	-	-	47.9	1.7	4.6	28.2	2.7
Stipa speciosa var. speciosa								
Green leaves (Spring)[3]	-	-	-	48.9	1.0	3.7	48.9	3.7

1 del Valle (1996), del Valle and Rosell (1999); 2 Somlo et al. (1985); 3 Somlo and Cohen (1995)

shrubs growing in 11 desert on five continents (2.2%). Senescent leaves of two steppe grasses (*Festuca pallescens* and *Poa ligularis* show extremely low N contents (0.2-0.3%), probably as a result of a strong mechanism of N conservation. N use efficiency of these Patagonian grasses is much higher than the mean value given by Aerts (1996) for 22 graminoids of the Northern Hemisphere (330-500 vs. 150 g/g).

Soil N mineralization
Soil N mineralization (N_{min}) is directly related to the total content of organic N in the soil, but it is also closely linked to the availability of C (Schlesinger 1991). Vegetation with a high C/N ratio in litterfall generally shows low rates of N_{min}, nitrification is minimal or proceeds after a lag, and ammonification is the prevailing process (Vitousek et al. 1982, Adams and Attiwill 1986). This has

Table 5. C (%), N (%), lignin (%), C/N and lignin/N in green and senescent leaves of perennial grasses and shrubs of the Patagonian steppe and trees of the Patagonian forest. Values in parentheses indicate number of species.

	Forest trees	Steppe grasses	Steppe shrubs
Green leaves			
C (%)	45-55 (5)[1]	44-49 (6)[4]	47-49 (5)[5]
N (%)	0.6-1.9 (5)[1]//3.2 (1)*	1.0-2.5 (6)[4]	0.9-2.9 (5)[5]
C/N	20-100 (5)[1]	18-49 (6)[4]	21-54 (5)[5]
Lignin/N	3-10 (3)[2]	2-4 (6)[4]	7-27 (5)[5]
Senescent leaves or litter			
C (%)	47-54 (4)[3]	43-48 (4)[6]	33-43 (2)[7]
N (%)	0.5-1.1 (4)[3]//1.9 (1)*	0.2-0.5 (4)[6]	0.8-2.4 (2)[7]
C/N	40-100 (4)[3]	86-227 (4)[6]	18-47 (2)[7]
Lignin/N	18-62 (4)[3]	14-27 (4)[6]	-

* *Discaria trinervis* (deciduous shrub) (Chaia, 1997). 1 Buamscha et al. (1998), Gutiérrez et al. (1991), Alauzis, (unpubl.), Gobbi (unpubl.). 2 Gobbi (unpubl.), Alauzis (unpubl.). 3 Buamscha et al. (1998), Gobbi (unpubl.), Schlichter (unpubl.), Alauzis (unpubl.). 4 Somlo et al. (1985), Somlo and Cohen (1995). 5 del Valle (1996), del Valle and Rosell (1999), Somlo et al. (1985). 6 Somlo et al. (1985). 7 del Valle (1996), del Valle and Rosell 1999)

important implications on the analysis of disturbance effects. Thus, ecosystems with a dominance of high C/N in litterfall would show high resistance to N losses after disturbance (< nitrates < leaching < denitrification), but also low N availability for plant regrowth (low resilience). Since the quality of the C sources is more important than total C, the ratio lignin/N has been proposed as a more adequate index than C/N to predict the rates of litter decomposition and N_{min} (Melillo et al. 1982, Parton et al. 1988, Gower and Son 1992, Binkley 1994).

Field measurements of litter decomposition by the "litter bag" technique, and N_{min} by the "buried bag" or "PVC tube" method are laborious and time consuming, but currently constitute the most frequently useded approaches to examine both processes. A more simple method is to estimate the potential N_{min} (pN_{min}) in laboratory incubations under controlled (optimum) soil moisture and temperature conditions. This type of assays allows to estimate both N mineralization potential and nitrate production (nitrifier activity) under comparable conditions (Vitousek et al. 1982).

An indicator of substrate quality is given by the amount of microbial-N, considered as a regulator of N dynamics in arid and mesic environments (e.g. Robertson et al. 1988, García and Rice 1994). Microbial biomass acts as a sink and source of nutrients and represents the chief component of the active soil organic matter pool (McGill et al. 1986). As a sink, microbial biomass constitutes a mechanism for conserving N, thus reducing losses by leaching or denitrification (Vitousek and Matson 1985, García and Rice 1994), but it is retained in labile, easily mineralizable N forms. Thus, in arid-semiarid environments, microbial mortality during dry periods may account for 40% or more of the gross N_{min} produced during subsequent wet periods (Bernhard-Reversat 1982, Mazzarino et al. 1991). Microbial biomass-N levels mainly depend on C sources, which are usually limiting in arid-semiarid ecosystems (West and Skujins 1978, Mazzarino et al. 1991, Gallardo and Schlesinger 1992), and are obviously higher under vegetated patches.

Forest soils. For the forests of the Andean-Patagonian region, no data on N mineralization-immobilization under field conditions are currently available. Assays on potential N mineralization under controlled laboratory conditions during 16 week incubation periods (Table 2), produced the following results:
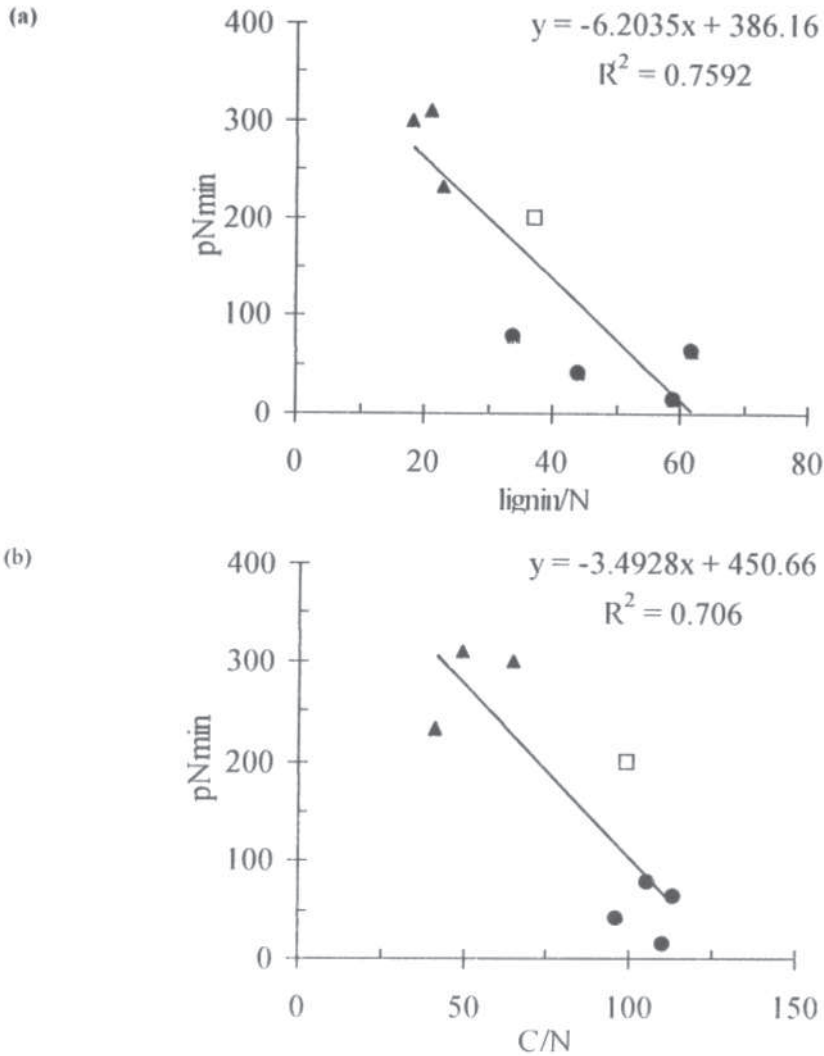
(a)

$$y = -6.2035x + 386.16$$
$$R^2 = 0.7592$$

(b)

$$y = -3.4928x + 450.66$$
$$R^2 = 0.706$$

Figure 1. Relation of potential N mineralization (pNmin) to lignin/N ratio (a), and to C/N ratio (b) for Patagonian forest species. Symbols: ▲ : deciduous broadleaf species (*N. antarctica, N. pumilio*); ●: evergreen conifer (*A. chilensis* along a moisture-soil fertility gradient); □ : broadleaf evergreen (N. *dombeyi).*

(i) pN_{min} is very high in forests of *N. antarctica* (broad-leaf deciduous tree) in Tierra del Fuego: up to 300 mg N/kg soil in closed forests, decreasing to 230 mg N/kg under trees in savanna-type silvopastoral systems, and to 100 mg N/kg in the interspaces between trees and in pure grasslands from deforested sites. Coupled to the decrease of pN_{min} from closed forests to pure grasslands, a marked increase of the NO_3-N fraction occurs. NH_4-N represents 87% of total mineralized N in the closed forest, 50% in the grassland, and 35% in the silvopastoral system. This suggests that silvopastoral and grassland systems have a higher risk of N losses (NO_3-N) through leaching and denitrification than closed forests. The predominant ammonification in the closed forest probably stems from limiting conditions for nitrifiers. The shift to NO_3-N in the savanna-type system implies a change to more suitable conditions for nitrifiers and higher substrate quality, since grass composition under trees also changes (Schlichter, unpubl.). (ii) Near Bariloche, pN_{min} values reach 300 mg N/kg soil in *N. pumilio* forests (broad-leaf deciduous) and 200 mg N/kg for *N. dombeyi* (broad-leaf evergreen), while values are quite low, 20-80 mg N/kg, in A. *chilensis* forests (evergreen conifer) along a soil moisture-fertility gradient (Esquel-Bariloche). In all cases, NO_3-N represents the main form of mineralized N (Buamscha et al. 1998, Alauzis, unpubl., Gobbi,

unpubl.). (iii). In general, higher pN_{min} is associated with lower C/N and lignin/N ratios in senescent leaves (Figure 1, Table 2), as suggested by other authors previously mentioned. Apparently, the lignin/N ratio in green leaves (young and mature), although lower than in senescent leaves, can also be used as indicator of N_{min} since differences among species are maintained (Table 3).

All these data indicate that systems dominated by evergreens have a lower capacity to mineralize N than systems dominated by deciduous species, due to a higher N conservation mechanism (higher C/N and lignin/N ratios, lower N concentration in young, mature, and senescent leaves, and long life-span). Data on fine litter decomposition agree with this preliminary conclusion, since evergreens have substantially lower fine litter decomposition than deciduous species (see below). After disturbance, it might be then expected higher losses of N under deciduous thand under evergreen species. These pN_{min} patterns must be translated to field conditions with caution: N_{min} will be affected by the mediterranean-type climate of the region, with inadequate conditions for microbial activity (rainfall concentrated during winter), and the predominant soil types, very well-drained, but with a high capacity to retain water at depth, might enhance nitrate movement during wet periods and leave them available for deep-rooted vegetation.

Apparently, there are interspecific differences in rates and patterns of pN_{min} within both life-forms (evergreen and deciduous). Within deciduous species, *N. antarctica* has higher resistance to N losses than *N. pumilio* because NH_4-N is the predominant form of mineralized N. This comparison is not completely valid since data for *N. pumilio* correspond to soils under more favorable conditions for nitrifiers (ChallHuaco, near Bariloche) than those of *N. antarctica* (Tierra del Fuego). Within evergreens, *A. chilensis* and *N. dombeyi* show similar C/N ratios and N proficiency, but pN_{min} is higher in *N. dombeyi,* possibly due to lower lignin contents.

Steppe soils. In the northeastern Patagonian steppe of *Larrea divaricata* and *Stipa* spp., as in other arid ecosystems, soil organic matter and N are concentrated beneath vegetation patches (Rostagno and del Valle 1988, Rostagno et al. 1991). Field measurements of N mineralization (N_{min}) and immobilization in microbial biomass (N-MB) under different vegetation patches during two years (Figure 2) (Mazzarino et al. 1996, 1998) indicate that:

(i) N_{min} rates are very low, with peaks of 4 mg N/kg soil during a very dry year (180 mm) and of 8 mg N/kg during a wet year (311 mm). However, differences between years are more marked in vegetated patches with mixed canopies (GSP), i.e., undisturbed patches, and incipient patches of *Larrea divaricata* (IGSP) than in grass patches (GP) and bare soil (BS). Ammonification is the predominant process of N_{min} in the field; only when soil moisture was > 10%, was nitrate a considerable proportion of total mineralized N. Conversely, under controlled laboratory conditions (20% soil moisture, 25 °C), N_{min} proceeds mainly to nitrification. These results suggest that the substrate has an inherent capability to mineralize to nitrates and that nitrifier activity depends markedly on soil moisture pulses.

(ii) N immobilized in microbial biomass is largest in vegetated patches and lowest in grass patches and bare soil. Incipient patches of *Larrea divaricata* are intermediate (Table 6). During a wet year, N_{min} increased in all patches, but N-MB increased only in the vegetated patches and decreased in all other patches. The decrease of N-MB coupled with higher N_{min} implies a net loss of labile N. This effect is less marked in the incipient patches of *Larrea divaricata* and indicates a more rapid recovery of soil fertility than under grass patches.

These data indicate that (i) under field conditions, this ecosystem shows strong mechanisms of N conservation that result in low losses by leaching and denitrification (N is considerably immobilized in microbial biomass and NH_4-N is the predominant form of mineralized N), and (ii) N-MB is strongly related to the type of vegetation cover and constitutes an important indicator of the state of the vegetation. When the cover of the complex patches is reduced by grazing disturbance, i.e., losses of grasses and tall shrubs (Bisigato et al. 1997), N-MB is reduced and consequently the source of soil N-labile forms increases.
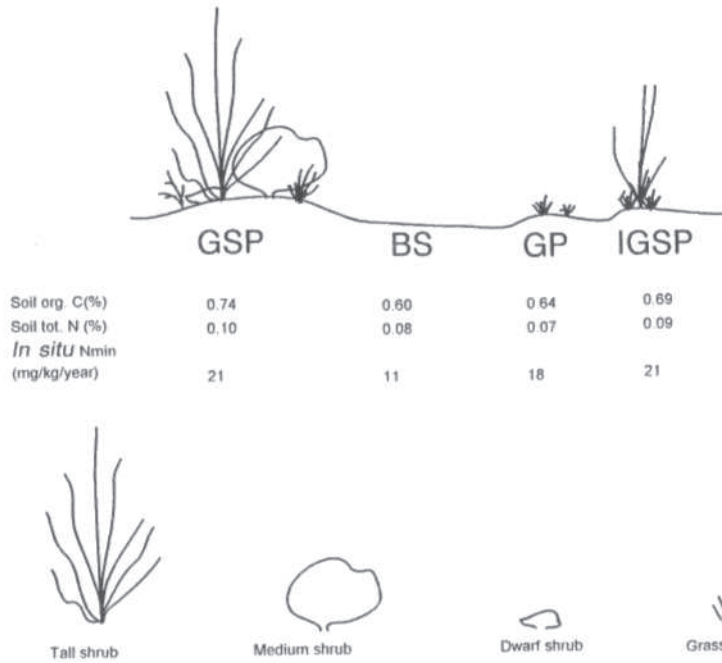
Figure 2. Diagram of the main vegetation patches and some soil characteristics of the *Larrea divaricata* and *Slipa spp.* shrub- steppe in northeastern Patagonia. GSP: Grass-shrub patches, IGSP: Incipient grass-shrub patches, GP: grass patches, and BS: Bare soil.

Forest-steppe ecotone. Austin and Vitousek (1998) suggested that "along moisture gradients a shift in the relative importance of C versus nutrient resources occurs, i.e. that moisture gradients also represent a gradient from relatively nutrient-rich, water-use efficient systems in drier sites to relatively C-rich, nutrient-use-efficient ecosystems in wetter sites". Based on the increase in plant cover and the decrease in nutrient concentration along increasing precipitation gradients, they conclude that water availability, rather than nutrient availability, is the main limiting factor for production in drier sites. When comparing some representative species of the main plant functional groups dominating the precipitation gradient of Patagonia, a similar trend for forest trees vs. steppe shrubs was observed (Table 5). C concentrations and C/N ratios are higher and N concentrations lower in senescent leaves or litter of forest trees than in steppe shrubs. Likewise, differences in N concentration between green and senescent leaves suggest a higher N use efficiency in forest trees. However, steppe grasses behave as a nutrient-use-efficient group with higher values of C and much lower values of N in senescent leaves and litter than shrubs. Shrubs and grasses, the main dominant functional groups in arid and semi-arid ecosystems of Patagonia, differ not only in their structure (life form, size, rooting depth) but also in their functioning (phenorhytmics) (Sala et al. 1989, Bertiller et al. 1991). Shallow-rooted grasses behave as opportunistic or aridopasive species (Fisher and Turner 1978, Bertiller 1984, Sala et al. 1989, Bertiller et al. 1991) because they mostly grow in the wet season (autumn to late spring) and have a rest period, with an important leaf senescence, during the driest part of the year (Soriano 1981, Soriano et al. 1983, Soriano and Sala 1983, Soriano et al. 1987, Bertiller et al. 1991). The high C/N ratio and N resorption proficiency in senescent leaves of grasses suggest strong mechanisms of N conservation in accordance with the high leaf turnover exhibited by this functional group. Consequently, a lower pool of mineralizable N might be expected under grass patches than under shrubs, as has been determined in assays of

potential N_{min} under different vegetated patches of the NE Patagonian steppe of Larrea divaricata and Stipa spp. (Mazzarino et al. 1996, 1998). Conversely, deep-rooted shrubs develop biological activity during the dry period (aridoactive species sensu Fisher and Turner 1978) in relation to their capacity to exploit water from deeper soil layers, and to morphological adaptations to conserve water (small leaves, thick cuticle, epicuticular waxes, foliar thorns, etc.). The yearly reposition of leaves in the evergreen shrubs may vary among species, but it is quite small in relation to the green leaves that remain in the plant and maintain high N content during the whole year. Thus, in this functional group, mechanisms to conserve water and to maintain high N content in tissues prevail over mechanisms of N conservation or high N resorption proficiency. This agrees with the pattern of nutrient-rich, water-use efficient species proposed by Austin and Vitousek (1998).

These features have implications on the dynamics, conservation, and restoration of vegetation in arid and semiarid ecosystems of Patagonia in which grazing is an important disturbance agent (Soriano et al. 1983, Ares et al. 1990). As in similar areas of the world, long-term effects of grazing may be traced back to changes in the spatial and temporal patterns of vegetation and, subsequently, to physical and chemical changes in soils (León and Aguiar 1985, Soriano and Movia 1986, Schlesinger et al. 1990, Bertiller 1996, del Valle et al. 1998). Under different disturbance scenarios, both functional groups exhibit different behaviours. While grasses tend to reduce their abundance and cover in disturbed ecosystems, shrub may increase their cover, both in relative and absolute terms (Paruelo et al. 1993, Beeskow et al. 1995, Bisigato and Bertiller 1997). Reduction of plant cover by disturbances increases the loss of organic matter and mineralizable N in the upper soil by erosion. Recolonization of bare soil by shrubs may be an important, necessary step to recover soil fertility (Mazzarino et al. 1996, 1998). The importance of shrubs as triggers of the colonization and establishment of grasses has been studied in Patagonian rangelands (Soriano et al. 1994, Aguiar and Sala 1994). In these studies differences in root density, soil water potential and evaporation have been identified as the main factors involved in the facilitation processes around shrubs. The results shown here give additional information about the factors involved in facilitation processes around shrubs in the Patagonian steppe, since they are probably not only related to water conservation but also to nutrient conservation and dynamics in soil.

Considering the Patagonian forest trees, which behave as a whole as C-rich, nutrient-use-efficient species (sensu Austin and Vitousek 1998), some distinctive patterns have been observed among life forms, but also among species within each life form. Studies on N conservation mechanisms of Austrocedrus chilensis (evergreen conifer) along a moisture-soil fertility gradient indicate that this species shows a strong inherent capacity to conserve N independent of site characteristics (Buamscha et al. 1998). These authors conclude that A. chilensis shows consequently a high capacity to dominate poor sites, which explains its wide distribution in the region. However, nutrient conservation mechanisms such as N resorption may imply a higher consumption of energy and represent a disadvantage when coexisting with less nutrient-use-efficient species in fertile sites. Thus, in mixed forests with *N. dombeyi*, an evergreen with higher rates of pN_{min} and less lignin contents, long-term coexistence might be conditioned by the site soil fertility (Dezzotti 1994).

Phosphorus cycling

Killingbeck (1996) developed the concept of "phosphorus resorption proficiency" in a similar way as for N. In the case of P, he found differences between evergreen and deciduous species: average resorption proficiency for P in senescent leaves was < 0.04% and < 0.05, respectively. P resorption proficiency of *N. pumilio*, calculated from Richter and Frangi (1992), is 0.15% P in fine litter (Table 1), a very high value only comparable to some species of *Betula*, *Fraxinus*, *Larix* and *Quercus* (Killingbeck 1996) These results suggest that P does not represent a limiting factor in *N. pumilio* forests. As mentioned above, N seems to be the most limiting nutrient in these forests consistent with other temperate forests. The comparison of P use efficiency with average values of temperate evergreen- and deciduous shrubs and trees reviewed by Aerts (1996), also shows that P is

Table 6. Mean values of microbial N (N-MB, mg kg^{-1}) during a dry and a wet year under different vegetated patches in the shrub steppe of *Larrea divaricata* and *Stipa* spp. (from Mazzarino et al. 1998).

Treatments	Dry year (180 mm)	Wet year (360 mm)
Border of patches with perennial grasses and shrubs (GSP)	18.6 Ba	23.1 Aa
Incipient patches of *L. divaricata* and perennial grasses (IGSP)	15.3 Ab	13.1 Bb
Patches of perennial grass *Stipa tenuis* (GP)	13.2 Ac	11.4 Bc
Bare soil (BS)	11.5 Ac	10.4 Bc

Common letters indicate no significant differences (p<0.05): capital letters between years for the same treatment, and small letters among treatments over the same year

not limiting in these ecosystems. This would mean a paradox, considering that the predominant soil types in the analyzed forest are Andisols or acid soils with spodic characteristics, i.e. soils with low contents of bioavailable P (high capacity to retain P). Gutiérrez et al. (1991) also found that under N. pumilio stands, values of water-soluble P in the organic H layer (80 mg/kg) are higher than average annual requirements of forest ecosystems in different environments, and attribute this fact to a high mycorrhizal infection. Conversely, they found lower soluble P (46 mg/kg) and mycorrhizal infection in *N. betuloides* stands, probably due to the predominant waterlogged conditions of the soils. Ectotrophic mycorrhizal associations seem a very effective mechanism of *Nothofagus* genera to cope with P-deficient soils, as it has also been reported in reviews from New Zealand, Australia, New Guinea, New Caledonia, and Argentina (see Veblen et al., eds. 1996). In *A. chilensis* forests, roots are associated with endomycorrhizae (vesicular-arbuscular or VA mycorrhzae) (Fontenla et al. 1991).

In the Patagonian steppe the concentration of P in green, senescent tissues, and litter varies among species (Table 4). In green leaves of shrubs, P content ranges from 0.08 to 0.48% and in grasses from 0.19 to 0.33%. In senescent tissues and litter, P varies between 0.06 and 0.14% in shrubs, and between 0.05 and 0.09% in grasses. These values indicate that grasses have higher P conservation or P resorption proficiency than shrubs, a pattern already observed for N. Additionally, grasses show a high resorption of potassium (from 1.4-2.9% in spring green leaves to 0.34-0.63 % in summer green- and senescent leaves) (Table 4).

Nutrient allocation and decomposition rates

Data on nutrient allocation and decomposition rates of fine and coarse debris are only available for forest trees of Tierra del Fuego (Table 7). Applying the mass-balance approach, Richter and Frangi (1992) conclude that in *Nothofagus* pumilio forests in Tierra del Fuego, root storage of nutrients represents a high proportion of the total nutrient pool (42%). Nutrient concentration was especially high in fine roots. Fine twigs and leaves, although representing only 3 % of total biomass, stored 13% of the total pool. This agrees with data on other mature forests, in which leaves account for less than 5% of total biomass, but represent 5-20% of the total nutrient pool in vegetation (Waring and Schlesinger 1985). The nutrient storage in stem and branches represents only 45% of the total nutrient pool, a value considerably lower than those reported by Vitousek et al. (1988) for various types of mature forests (70-80%).

The forest floor is mainly comprised of coarse debris (93%) with extremely low rates of decomposition (500 years for boles and 270 years for large branches). Thus, the role of fine debris with much higher rates of decomposition (k= 0.56 for leaves and 0.47 for fine twigs per year) is fundamental for the short-term supply of nutrients. Due to the magnitude of root biomass and nutrient concentration, the belowground transfer of nutrients must also be important. Assuming a mean k value of 0.5/year, the nutrient contribution of *N. pumilio* in litterfall amounts to figures strikingly similar to those reported for *N. truncata* in New Zealand (18.7-18.3 kg N, 34.9-36.5 kg

Table 7. Biomass and nutrient storage in different compartments of *N. pumilio* forests in Laguna Victoria, Tierra del Fuego (from Richter and Frangi, 1992).

Compartments	Dry matter (t/ha)	Ashes (t/ha)	N (kg/ha)	P (kg/ha)	K (kg/ha)	Ca (kg/ha)
Above-ground biomass	431.9	2.9	791	126	629	997
Below-ground biomass	66.3	2.1	218	40	176	238
Litter coarse debris	58	1.3	152	14	57	347
Litter fine debris	4	0.4	32	6	15	58

Ca, and 65.3-73 kg total nutrients per ha and year) (calculated from Richter and Frangi 1992, and Ogden et al. 1996). Decomposition rates of *N. pumilio* fine debris in Tierra del Fuego (Richter and Frangi 1992) are similar to those reported by Godeas (1988) for stands near Bariloche and San Martín de los Andes (k=0.47/year, without distinction between leaves and fine twigs). This last author determined a lower k value (0.23-0.31/year) for *N. dombeyi,* confirming again differences among evergreen and deciduous broad-leaf species in litter decomposition and, consequently, in nutrient conservation and soil mineralization rates. According to Frangi et al. (1997), fine twig decomposition rates also vary among species being higher for *N. pumilio* than for *N. antarctica* and *N. betuloides* (k=0.47, 0.23 and 0.17/year, respectively). Decomposition rates of branches ≥ 1 cm (coarse debris) are not significantly different among species, but decrease with diameter increase. They conclude that k values for large branches (8-17 cm) and boles (19-60 cm) of *N. pumilio* are similar or slightly higher than those of cold temperate conifers and lower than those of cold and warm temperate hardwoods of the northern hemisphere.

Further research

- Very few data are available on nutrient allocation in vegetation, litterfall, and decomposition rates. Only some local studies were carried out in forest stands (Tierra del Fuego).
- Data on N mineralization and N immobilized in microbial biomass under field conditions are only available for the northeastern Patagonia steppe of *Larrea divaricata* and *Stipa* spp.
- Despite the importance of Andisols as high P fixing soils, almost no data are available on P cycling in this type of soils.
- The potential use of indicators of litter decomposition and N mineralization should be validated with field measurements of both processes. From these indicators differences between evergreen and deciduous woody perennials in Patagonian forests, as well as, between shrubs and grasses of the steppe have been identified, which should be further investigated in relation to the response of these ecosystems to disturbance.
- In general, available data were collected with different objectives that in most cases were not focused on specific questions or hypothesis related to ecosystem functioning and nutrient cycling. However, the data are significant enough to provide some advise about the mechanisms of nutrient conservation in Patagonian ecosystems with different water inputs, and constitutes a base for specific studies.

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