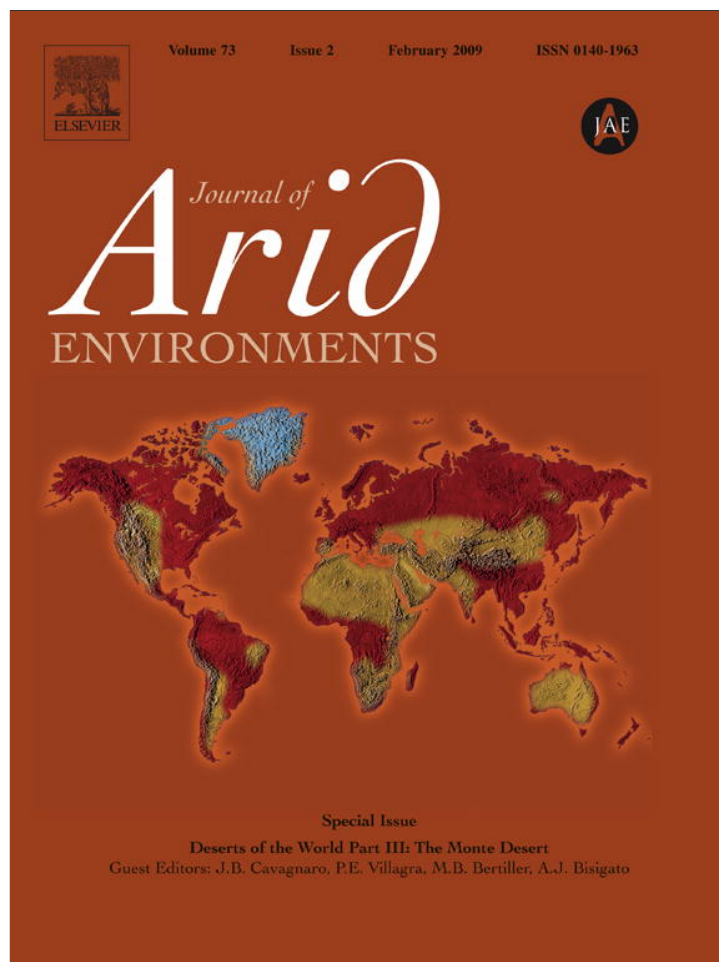


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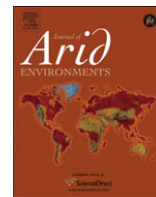
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Plant impacts on nitrogen and carbon cycling in the Monte Phytogeographical Province, Argentina

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ABSTRACT

In arid and semiarid ecosystems, primary productivity and nutrient cycling are directly related to the amount and seasonal distribution of precipitation. However, depending on morphological, phenological, physiological, and biochemical traits, plants may influence the quality and quantity of organic matter inputs to the soil and thus the biomass and activity of the soil biota responsible for carbon and nitrogen dynamics. In this paper, we review the available knowledge on plant functional traits and their impacts on ecosystem processes such as N and C cycling throughout the Monte Phytogeographical Province. We address the mechanisms of N conservation, the quantity and quality of leaf litterfall and root traits of the dominant plant life forms and their effects on decomposition processes, soil organic matter accretion, and soil-N immobilization and mineralization. We conclude that plant functional traits affect ecosystem processes in the Monte Phytogeographical Province since the chemistry of senesced leaves and root biomass exerts an important control on organic matter decomposition and N availability in soil.

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1. Introduction

Nitrogen is one of the most limiting nutrients for plant growth and exerts a strong control on plant community dynamics (Charley and Cowling, 1968). Soil-N availability depends on organic matter mineralization processes which are controlled by climate, the quantity and quality of organic debris (mostly plant litter) and microbial activity. In arid and semiarid ecosystems, the rates of these processes are primarily controlled by scarce, erratic, and discontinuous precipitation inputs (Noy Meir, 1973; Mazzarino et al., 1998a,b). Plant traits such as growth habit, phenological pattern, production of secondary compounds (lignin and other polyphenolics), nutrient resorption, and tissue lifespan are strongly associated with the quality and quantity of plant litter (Aerts and Chapin, 2000). Plant litter with high C/N or secondary compounds/N ratios generally induces low rates of organic matter decomposition, microbial activity, and soil-N mineralization (Adams and

Attiwill, 1986). Under short-N supply, many plant species enhance the production and accumulation of phenolics in tissues resulting in decelerated rates of litter decomposition and further reduction of soil-N availability (Wardle, 2002). Since secondary metabolites protect plants from herbivores, pathogens, UV-B radiation and water stress (Whitford, 2002), plants with long-lived leaves tend to invest much more C in secondary compounds than do short-lived ones. Selective grazing usually results in plant cover reduction, species substitution within the same plant life form, and plant life form replacement, especially perennial grasses by evergreen shrubs in most arid-semiarid ecosystems (Schlesinger et al., 1996; Bertiller and Bisigato, 1998). These plant life forms may strongly differ in the quantity and quality of litterfall affecting organic matter decomposition and N mineralization rates, soil fertility, and C and N cycling (Aerts and Chapin, 2000; Carrera et al., 2000, 2003, 2005; Campanella and Bertiller, 2008).

The Monte Phytogeographical Province extends from 24° 35' to 44° 20' S and from 62° 54' to 69° 05' W. In the southern Monte (Fig. 1), the mean annual temperature ranges from 12 to 14 °C and erratic precipitation events reach 200–300 mm yr⁻¹ with a trend to be concentrated in autumn and winter (Coronato and Bertiller, 1997). In the central and northern Monte (Fig. 1) mean annual

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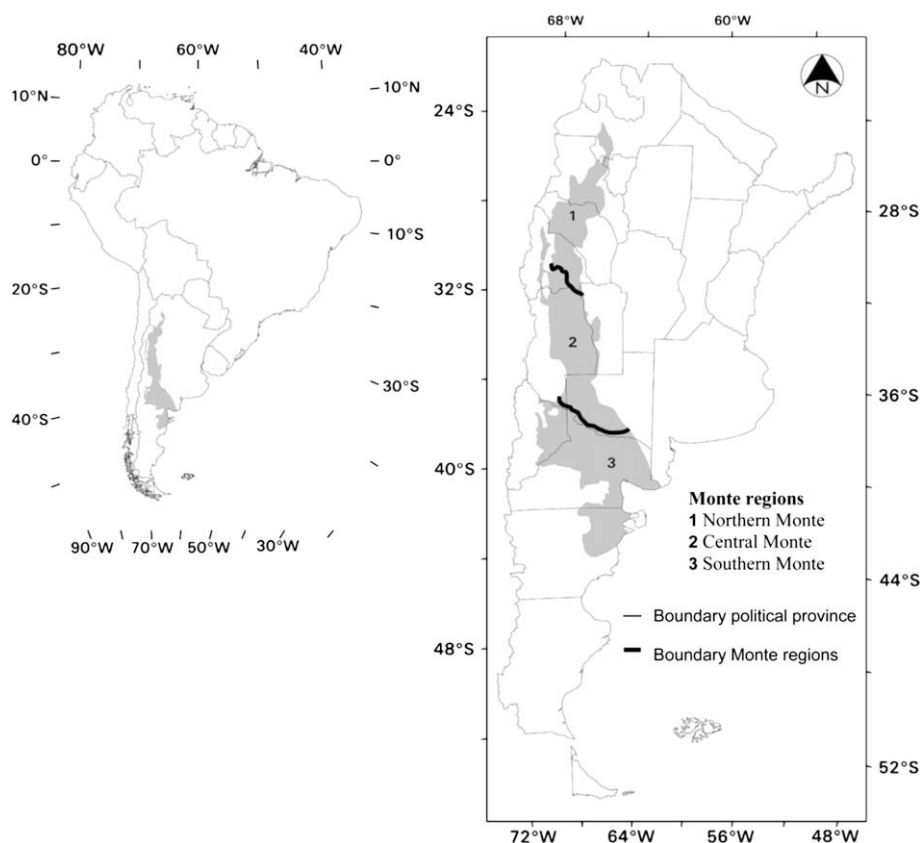


Fig. 1. Monte Phytogeographical Province of Argentina (gray area) indicating the northern, central, and southern regions.

temperature ranges from 15 to 19 °C, and precipitation is concentrated in the summer varying from 80 to 330 mm yr⁻¹ (Mares et al., 1985; Villagra et al., 2004). Plant cover is low (<60% of the soil) and displays a patchy structure dominated by woody plants (Bisigato and Bertiller, 1997; Villagra et al., 2004). As in other arid and semiarid ecosystems (e.g. Charley and West, 1977; Schlesinger et al., 1990), plant patches induce the creation of soil “fertility islands” due to the concentration of organic matter, microbial activity, and nutrients (Rostagno and del Valle, 1988; Rostagno et al., 1991). Vegetation is mainly represented by a shrubland of *Larrea divaricata* Cav. and C₃ perennial grasses of the genus *Stipa* in the southern Monte (Soriano, 1950; Cabrera, 1976), and by open woodlands of the tree *Prosopis flexuosa* DC. and the shrub *L. divaricata* with an herbaceous layer dominated by C₄ grasses in the central and northern Monte (Cavagnaro, 1988).

In this paper, we review the available knowledge on plant functional traits and their impacts on ecosystem processes such as N and C cycling throughout the Monte Phytogeographical Province. We address the mechanisms of N conservation, the quantity and quality of leaf litterfall and root traits of the dominant plant life forms and their effects on decomposition processes, soil organic matter accretion, and soil-N immobilization and mineralization.

2. Green leaf traits and mechanisms of N conservation in plants

Plants display different traits and mechanisms linked to N conservation. In general, plants with low growth rates and low nutrient requirements exhibit high concentration of chemical defences along with low nutrient resorption before tissues senescence. In contrast, plants with high growth rates show high

nutrient concentration in green tissues and high nutrient resorption from senescing leaves (Aerts and Chapin, 2000). These functional plant traits could in turn affect ecosystem processes since the chemistry of senesced leaves may exert an important control on organic matter decomposition and N availability in soil (Scott and Binkley, 1997; Cornelissen et al., 1999; Satti et al., 2003; Carrera et al., 2005).

2.1. Green leaf traits

In the southern Monte, leguminous deciduous shrubs have the highest and evergreen shrubs the lowest N concentration in green leaves (Fig. 2a). Perennial grasses have similar values of this trait than leguminous deciduous shrubs. Evergreen shrubs produce dense leaves with low N concentration (Fig. 2a), high leaf mass per area (LMA, Fig. 2b) and high concentration of secondary compounds (lignin and soluble phenolics, Fig. 2c and d, respectively). Deciduous shrubs (leguminous and non-leguminous) have the lowest LMA values but exhibit variable lignin concentration and low soluble phenolics concentration in green leaves. Perennial grasses show low concentrations of both lignin and soluble phenolics (Fig. 2c and d; Appendix I; Carrera et al., 2000, 2003; Bertiller et al., 2005, 2006; Moreno, 2005; Campanella and Bertiller, 2008). As in plants from other ecosystems (Aerts and Chapin, 2000), LMA is negatively related to N concentration and positively related to lignin concentration in green leaves of plant species in the southern Monte ($r = -0.62$, $p < 0.05$, $n = 12$; and $r = 0.83$, $p < 0.01$, $n = 10$, respectively).

In contrast, in the central Monte, the lowest N concentration in green leaves is shown by perennial grasses while the highest value of this leaf trait is exhibited by woody deciduous species including the N₂-fixing leguminous tree *P. flexuosa* (Fig. 2a;

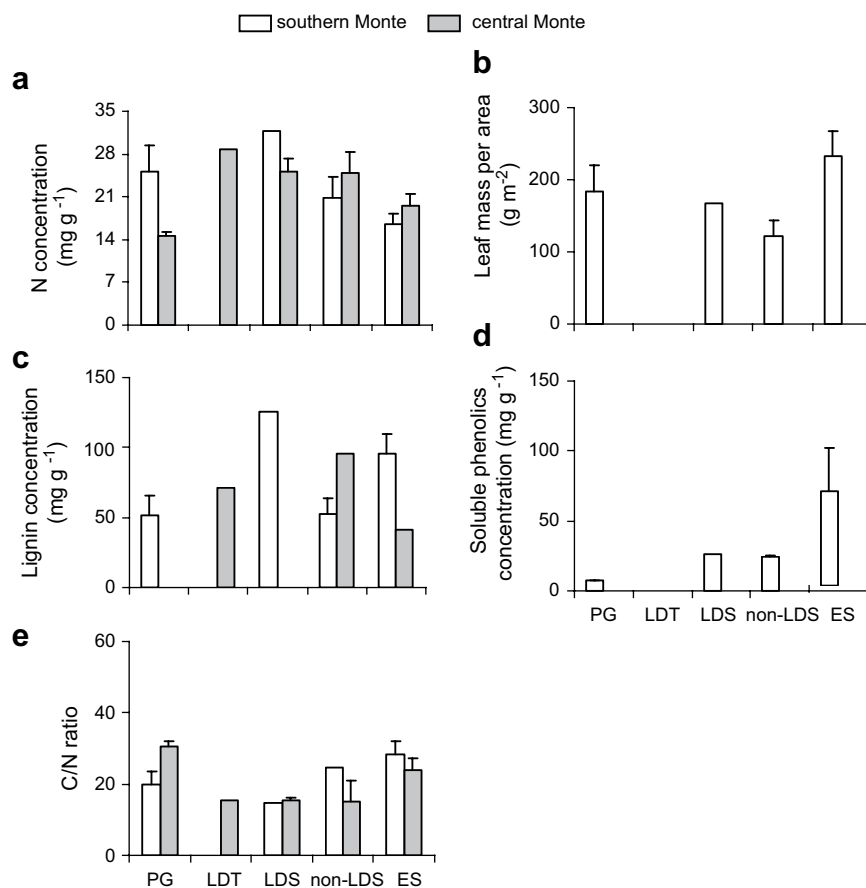


Fig. 2. Green leaf traits of life forms of the southern and central Monte: a. N concentration, b. leaf mass per area (LMA), c. lignin concentration, d. soluble phenolics concentration, e. and C/N ratio. Values of life forms were calculated from mean species value in Appendix I. PG: perennial grasses; LDT: leguminous deciduous trees, LDS: leguminous deciduous shrubs, non-LDS: non-leguminous deciduous shrubs; ES: woody evergreen (all evergreen shrubs are non-leguminous species). Vertical lines indicate 1 standard error.

Wainstein and González, 1971; Wainstein et al., 1979; Braun Wilke, 1982; Guevara et al., 1992; Chambouleyron and Braun, 1994; Candia and Dalmaso, 1995; van den Bosch et al., 1997; Asner et al., 2003). Comparing both regions, perennial grasses display higher N concentration in green leaves in the southern than in the central Monte (Fig. 2a). This difference could be associated with the prevalence of C₄ species with low N requirements and high N-use efficiency in the central Monte. Accordingly, the C/N ratio in green leaves of perennial grasses of the central Monte is higher than that of the southern Monte (Fig. 2e). Evergreen shrubs invest more C in structural compounds (lignin) in green leaves in the southern than in the central Monte (Fig. 2c). However, these differences should be taken with caution since only few data of lignin concentration in green leaves are available for evergreen species of the central Monte (Appendix I). Patterns of green leaf traits of life forms in the Monte Phyto-geographical Province are consistent with those reported for a variety of habitats indicating that long-lived species have dense green leaves with high concentration of structural and defensive compounds (Westoby et al., 2002).

Life forms display differential seasonal patterns of N concentration in green leaves in the southern and central Monte. In the southern Monte, perennial grasses display larger seasonal variations in N concentration in green leaves (from 27.5 mg g⁻¹ in the vegetative growth period in autumn to 7.4 mg g⁻¹ in the reproductive period in late spring-early summer) than evergreen shrubs (from 18.5 mg g⁻¹ in autumn to 14.8 mg g⁻¹ in late spring-early summer; Carrera et al., 2000; Carrera, 2003). These seasonal patterns are probably associated with differences in the phenology

and in the ability to explore deep soil layers among life forms. Plant activity of perennial grasses is synchronic with precipitation and high soil moisture in the upper soil (0–0.2 m depth, Bertiller et al., 1991). Shrubs maintain phenological activity during the whole year or in the dry warm season due to their deep roots (more than 3 m depth) and to the production of long-lived well-defended leaves (Bertiller et al., 1991, 2005, 2006; Carrera, 2003; Campanella and Bertiller, 2008).

Perennial grasses of the central Monte exhibit lower seasonal variation in N concentration in green leaves (12.3 mg g⁻¹ in summer and 9.3 mg g⁻¹ in winter; Guevara et al., 1992) than woody life forms (Braun Wilke, 1982; van den Bosch et al., 1997). Green leaves of evergreen shrubs show the lowest N concentration in winter (13.1 mg g⁻¹) and the highest one in spring (21.8 mg g⁻¹). The N₂-fixing leguminous deciduous tree *P. flexuosa* (Morales, 1992), exhibits higher N concentration in green leaves in spring (32.2 mg g⁻¹) than in summer (25.2 mg g⁻¹), while the non-leguminous deciduous shrub *Lycium chilense* Mier ex Bertero shows similar values at both seasons (21.5 and 20.6 mg g⁻¹ in spring and summer, respectively). The contrasting seasonal patterns of N concentration in green leaves between both regions could be related to the fact that in the central Monte precipitation events are coupled with the highest temperatures (summer) while in the southern Monte they occur mainly during the cold seasons (autumn and winter). The simultaneous occurrence of soil humidity and high temperature could enhance organic matter decomposition and N mineralization increasing N availability in soil and luxury nutrient uptake by plants in the central Monte as it was reported for other arid ecosystems (Crawley, 1998).

2.2. N-resorption proficiency and efficiency

Nutrient resorption before leaf senescence and low N requirements associated with long-lived leaves are considered important plant strategies to conserve nutrients in nutrient-poor ecosystems (Killingbeck, 1996; Aerts and Chapin, 2000). Data related to mechanisms of N conservation are mostly available for the southern Monte (Mazzarino et al., 1998b; del Valle and Rosell, 2000; Carrera et al., 2000, 2003, 2005; Bertiller et al., 2005, 2006). Nitrogen resorption can be quantified by N-resorption proficiency (level to which plants reduce N in senesced leaves, *sensu* Killingbeck, 1996), or by N-resorption efficiency (percentage of N reabsorbed from senescing leaves with respect to green leaves). Accordingly to Killingbeck (1996) and Aerts and Chapin (2000), woody species with high N concentrations in senesced leaves ($>7.0 \text{ mg g}^{-1}$) are not N-proficient while perennial grasses with values $<7.0 \text{ mg g}^{-1}$ are high N-proficient (Fig. 3a, Appendix I). Nitrogen concentration in senesced leaves of perennial grasses (4.6 and 4.0 mg g^{-1} in autumn and late spring-early summer, respectively), and evergreen shrubs (11.7 and 9.3 mg g^{-1} in autumn and late spring-early summer, respectively) does not show seasonal fluctuations and does not vary among years with different annual precipitation in the southern Monte (Carrera et al., 2000, 2003). Temporal data on N concentration in senesced leaves are not available for species of the central Monte.

Woody species of the southern and central Monte also display lower N-resorption efficiency than perennial grasses of the southern Monte (Fig. 3b, Appendix I). Perennial grasses with short leaf lifespan reallocate a high proportion of N from senesced leaves to new growth, seeds, or other organs and produce leaf litter with high C/N ratio (Fig. 3c, Appendix I). In contrast, evergreen shrubs mostly retain their leaves for more than one growing season (Carrera et al., 2000, 2005; Campanella and Bertiller, 2008), allowing the increase of the canopy photosynthetic capacity across an extended activity period with a more prolonged use of N (Aerts and Chapin, 2000). The high concentration of secondary compounds in green leaves of evergreen shrubs may enhance protein

precipitation before hydrolysis reducing N-resorption during the leaf senescence (Aerts and Chapin, 2000). Consequently, N concentration in senesced leaves is positively related to soluble phenolics concentration in plant species of the southern Monte (Appendix I) ($r = 0.58, p < 0.05, n = 12$). As in other ecosystems, low N-resorption in shrubs of the Monte Phytogeographical Province is associated with N-rich litter (Fig. 3d). Thus, non-reabsorbed N may circulate in the ecosystem through litterfall and subsequent decomposition process (Aerts and Chapin, 2000).

3. Litter production

Plant litter production is the main input of C to soil and decomposition of plant debris affects the balance between the C returned to the atmosphere and the C sequestered in plants and soils. Plant litterfall is also the main pathway of nutrient return to soil (Whitford, 2002). Despite of this, our understanding of the rates and controls of litter production and decomposition is scarce mainly in non-forest ecosystems of the south hemisphere including the Argentinean Monte.

3.1. Annual leaf-litter production of plant life forms

The mass of annual leaf litterfall varies among dominant life forms and sites within the Monte Phytogeographical Province. Leaf litter production is higher at the central (northern Mendoza) than at the southern (north-eastern Chubut) Monte (Fig. 4a). This could be associated with the distribution of annual precipitation at both sites (predominant autumn-winter precipitations in the southern Monte and summer precipitations in the central Monte) and is consistent with general models relating actual evapotranspiration and litter production (Meentemeyer et al., 1982).

At both sites, woody deciduous have larger leaf litter production than grasses and evergreen species, but differences are more marked at the central Monte than at the southern Monte. This could be associated with a large contribution of deciduous tree species

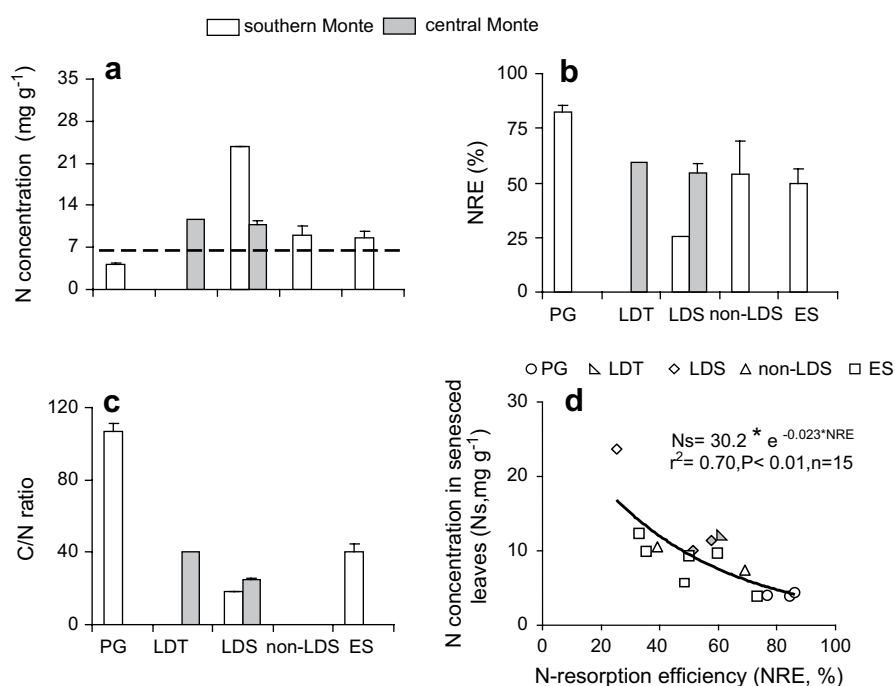


Fig. 3. Mean values of a. N concentration in senesced leaves (the horizontal line indicates the benchmark level of resorption proficiency, Killingbeck, 1996), b. N-resorption efficiency, and c. C/N ratio in senesced leaves of dominant life forms in the southern and central Monte, d. relationship between N-resorption efficiency and N concentration in senesced leaves. Values of life forms were calculated from mean species value in Appendix I. Vertical lines indicate 1 standard error. Acronyms of plant life forms as in Fig. 1.

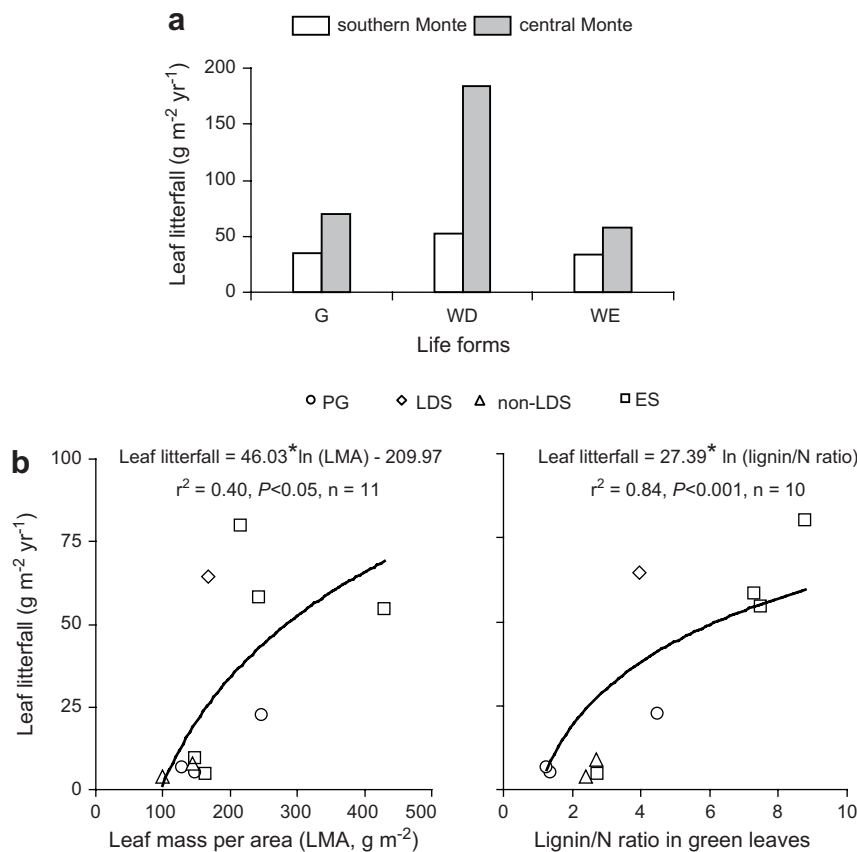


Fig. 4. a. Annual leaf litterfall of dominant life forms (G: grasses, WD: woody deciduous, WE: woody evergreens) at the southern and central Monte. Data of central Monte were recalculated from Martínez Carretero and Dalmasso (1992): shrublands dominated by *Larrea cuneifolia* (1130 m.a.s.l.), and *Larrea divaricata* (1500 m.a.s.l.) and Villagra (2000): shrublands of *Prosopis flexuosa*. Data of southern Monte correspond to the shrubland of *L. divaricata* and *Stipa* spp. and were recalculated from del Valle et al. (1999), Carrera et al. (2005), and Campanella and Bertiller (2008); b. Relationship between annual leaf litterfall and leaf mass per area and lignin/N ratio in green leaves of dominant life forms at the southern Monte. Data were taken from Bertiller et al. (2005, 2006), Carrera et al. (2005) and Campanella and Bertiller (2008).

(*P. flexuosa*) to the total cover in the former. Grasses and woody evergreens yield similar amounts of leaf litterfall at both sites, indicating that the annual production of leaf litter does not depend on life form. In the southern Monte, species producing dense green leaves (high LMA) with high lignin/N ratio contribute with the largest mass of leaf litterfall (Fig. 4b).

3.2. Spatial pattern of leaf litter

The spatial pattern of plant litter is quite heterogeneous in relation to patchy structure of arid plant communities (Bisigato and Bertiller, 1997; Villagra et al., 2004). del Valle et al. (1999) reported that the accumulation of litter within the patches of *Prosopis alpataco* Philippi and *Atriplex lampa* Gill. ex Moq. is 6–8 fold higher than in the bare soil surrounding their canopies (263.2 g m⁻², 182.0 g m⁻², 28.2 g m⁻², respectively) in the southern Monte. Likewise, in the community of *Larrea cuneifolia* Cav. and *L. divaricata* at the central Monte, litter production is higher under shrub canopies (409.0 g m⁻² yr⁻¹ and 231.4 g m⁻² yr⁻¹, respectively) than under the herbaceous layer (191.4 g m⁻² yr⁻¹ and 144.3 g m⁻² yr⁻¹, respectively) or on the bare soil (175.6 g m⁻² yr⁻¹ and 122.4 g m⁻² yr⁻¹, respectively; Martínez Carretero and Dalmasso, 1992). Additionally, microrelief, wind, water movement, and live-stock grazing may further increase the spatial heterogeneity of leaf litter after litterfall in arid ecosystems (Rostagno and del Valle, 1988). As a consequence, leaf litter tends to accumulate under shrub patches (Whitford, 2002) promoting the formation of fertility islands which are usually characterized by high nutrient

concentration and microbial activity (Rostagno et al., 1991; van den Bosch et al., 1997; Mazzarino et al., 1998a,b).

3.3. Total leaf litterfall

Total litterfall in plant communities of the Monte Phytogeographical Province varies between 134.9 g m⁻² and 471.0 g m⁻² in the shrublands dominated by *Larrea* spp. (Martínez Carretero and Dalmasso, 1992; Carrera et al., 2005). These values are similar to those reported for other desert ecosystems of the world (Table 1).

4. Litter decomposition

The decomposition of plant litter is a key process in C and nutrient cycling and thereby is critical to maintain plant productivity in most terrestrial ecosystems (Wardle, 2002). Main controls of nutrient release from litter to soil are climate, soil organisms and litter chemistry (Aerts and Chapin, 2000). These controls operate at different spatial scales. At a regional scale, climate affects decomposition through its effect on litter production, litter quality, and the activity of soil microorganisms. In most arid and semiarid ecosystems, precipitation is the main climatic factor controlling microbial decomposition (Noy Meir, 1973), but also solar radiation could also induce mechanical fragmentation of litter (Austin and Vivanco, 2006; Gallo et al., 2006). At a local scale, microbial activity, decomposition processes, and nutrient release in the Monte Phytogeographical Province can be predicted from plant/litter traits reflecting morpho-physiological and biochemical adaptations to

Table 1
Total aboveground litterfall ($\text{g m}^{-2} \text{yr}^{-1}$) in arid and semiarid ecosystems.

Plant community and location	Total litterfall
Monte desert	
Northern Mendoza, Argentina (central Monte)	
Piedmont shrubland of <i>Larrea cuneifolia</i> Cav.	471.0 ^b
Piedmont shrubland of <i>Larrea divaricata</i> Cav.	202.0 ^b
Woodlands of <i>Prosopis flexuosa</i> DC.	410.6 ^c
North-eastern Chubut, Argentina (southern Monte)	
Shrubland of <i>L. divaricata</i> and <i>Stipa</i> spp. (Five dominant species)	134.9 ^{a,d}
Sonora desert	
Baja California Sur, Mexico	
Shrubland of <i>Jatropha cinerea</i> (Ortega) Muell. Arg., <i>Jatropha cuneata</i>	120.0 ^e
Wiggins-Rollins, <i>Fouquieria diguetii</i> (Tiegh.) IM. Johnston,	
<i>Bursera microphylla</i> A. Gray, <i>Cyrtocarpa edulis</i> (Brandegee) Standl. and	
<i>Prosopis articulata</i> S. Watson.	
Plains: Isolated trees of <i>Olneya tesota</i> A. Gray and <i>Cercidium microphyllum</i>	59.5 ^f
(Torr.) Rose & Johnst. and shrubs of <i>Encelia farinosa</i> Torr. & A. Gray and	
<i>Jatropha cardiophylla</i> (Torr.) Muell. Arg.	
Hillsides: scrub of <i>Croton sonora</i> Torr., <i>Jatropha cordata</i> MüllArg. and	157.4 ^f
<i>Mimosa distachya</i> Cav.	
Arroyos: dominated by <i>O. tesota</i> , <i>Coursetia glandulosa</i> Gray, <i>Eysenhardtia</i>	357.0 ^f
<i>orthocarpa</i> (Gray) S. Wats. and <i>M. distachya</i> .	
Mojave desert	
Nevada, USA	53.0 ^g
Russian desert	
<i>Artemisia terrae-albae</i> Krasch. community	128.0 ^h

^a Data of total litterfall were computed from leaf litter data using the equation in Meentemeyer et al. (1982).

^b Martínez Carretero and Dalmasso (1992).

^c Villagra (2000).

^d Carrera et al. (2005).

^e Maya and Arriaga (1996).

^f Martínez-Yrizar et al. (1999).

^g Strojan et al. (1979).

^h Kurochkina and Borovskaya (1976) in Strojan et al. (1979).

the environment (Carrera et al., 2005; Vargas et al., 2006; Carrera et al., 2008) as in other ecosystems of the world (Aerts and Chapin, 2000).

4.1. Effect of leaf litter chemistry on decomposition rates

Perennial grasses of the southern Monte (*Poa ligularis* Nees ap. Steud., *Stipa tenuis* Phil., *Stipa speciosa* Trin. & Rupr.) produce leaf litter with low concentrations of N and secondary compounds and high C/N ratio (Appendix I) which shows the lowest decomposition rates (k) under laboratory incubation (0.0039 day^{-1} to 0.0044 day^{-1} ; Carrera et al., 2005; Vargas et al., 2006). This plant life form exhibits low variation in leaf litter decomposition rates among plant species in comparison with evergreen shrubs. The wide variation in leaf litter decay rates in evergreen shrubs may be associated with differences in the concentration and type of secondary compounds. *A. lampa* with low soluble phenolics and intermediate lignin concentrations shows the highest decomposition rate (0.0091 day^{-1}). However, decomposition rates of *L. divaricata* and *Junellia seriphioides* (Gillies & Hook.) Mold. show intermediate values (0.0047 day^{-1} and 0.0056 day^{-1} , respectively) probably related to high concentrations of soluble phenolics and lignin, respectively (Appendix I; Carrera et al., 2005; Vargas et al., 2006). Under field conditions, leaf litter of *L. divaricata* at the northern Monte (Pucheta et al., 2006), and *L. cuneifolia* at the central Monte (Lupiañez, 1999) exhibits lower decomposition rates (0.0035 day^{-1} and 0.0015 day^{-1} , respectively), than leaf litter of *L. divaricata* (southern Monte) under laboratory incubation (0.0047 day^{-1}). Other studies in semiarid and arid ecosystems of the world, also report a slight variation in litter decomposition among grass species (e.g. 0.0012 day^{-1} to 0.0018 day^{-1} ; Montaña et al., 1988; Koukoura et al., 2003), and a wide range of variation in litter

decomposition rates among woody species (e.g. 0.0027 day^{-1} to 0.0201 day^{-1} , Arriaga and Maya, 2007). This is probably associated with both the quantity and quality of C compounds in litter. The secondary compounds in litter may affect its decomposability by retaining N in litter through the formation of phenol–protein complexes of low decomposability, and/or inactivation of microbial enzymes, thus slowing down the N release to the soil and N cycling (Aerts and Chapin, 2000; Vargas et al., 2006; Carrera et al., 2008). These observations show that single chemical traits such as C/N ratio or lignin concentration commonly used to predict decomposition rates in mesic environments do not apply to deserts shrubs (Schaefer et al., 1985; Whitford, 2002). Accordingly, species replacement induced by grazing (i.e. grasses or shrubs with low concentration of secondary compounds in leaves by shrubs with high concentration of secondary compounds) could affect the nutrient and C cycling in arid and semiarid rangelands.

4.2. Microsite effects on litter decomposition rates

Spatial variation in microclimate and physicochemical soil properties induced by plant canopies could influence decomposition, mineralization and soil organic matter accumulation in soil (Whitford, 2002). Soils from different microsites exert a strong differential effect on decomposition processes in the northern Monte (Pucheta et al., 2006). Canopy soils underneath shrubs such as *Bulnesia retama* (Gillies ex Hook & Arn.) Gris. and *L. divaricata* promote higher leaf litter decomposition rates (k) of litter of *L. divaricata* than bare soil (0.0043 day^{-1} , 0.0035 day^{-1} , and 0.0028 day^{-1} , respectively) under field conditions. The higher rate of leaf litter decomposition on the soil under *B. retama* relative to the soil beneath *L. divaricata* could be probably associated with higher microbial activity due to higher nutrient concentration and water content and lower temperature (Pucheta et al., 2006). Lupiañez (1999) also found that the litter of *L. cuneifolia* decomposes at higher rates on the canopy soil (0.0023 day^{-1}) than on the bare soil (0.0007 day^{-1}) or at positions elevated from the soil surface both under canopies (0.0008 day^{-1}) or at the bare soil (0.0012 day^{-1}). The evidence found by Lupiañez (1999) highlights the importance of microsites associated with shrub canopies for microbial activity and litter decomposition in accordance with the paradigm of “islands of fertility” in arid ecosystems. These islands of fertility might differ in the quality of the C compounds depending on the dominant shrubs of the patch. In the southern Monte, del Valle et al. (1999) identified C compounds released from decaying litter of *P. alpataco* and *A. lampa* in the soil under their respective canopies using a ¹³C Nuclear Magnetic Resonance spectroscopy. They found that litter decomposition of *P. alpataco* leads to higher concentration of aromatic compounds in soil (from 28.5% to 40.3%) than that of *A. lampa* (from 20.2% to 24.8%). This suggests that not only the total amount of soil organic C accretion, but also the quality of the C compounds released during litter decay could have important implications on the nutrient cycling under patch canopies.

5. Root traits

Although belowground processes are important in the regulation of soil organic C accretion in semiarid ecosystems (Jobbagy and Jackson, 2000), studies on fine-root biomass and activity and root production and turnover are very scarce in the Monte ecosystems.

5.1. Root biomass and activity

Rodríguez et al. (2007a) reported a total root biomass of 1043.1 g m^{-2} within the first 50 cm of soil in the southern Monte.

Most of this biomass (63%) corresponds to fine roots (≤ 1.4 mm), 18.3% to intermediate roots (between 1.4 and 4 mm in diameter) and the rest to thick roots (> 4 mm in diameter). They found also that fine-root biomass is concentrated (59.5%) in the upper soil (0–20 cm depth) as in other sclerophyllous shrub/tree communities and desert ecosystems (79 and 60% of the fine-root biomass is located in the upper 30 cm soil, respectively, Jackson et al., 1997). Simultaneously, the horizontal distribution of root biomass is heterogeneous (del Valle and Rosell, 1999). Root biomass under shrub canopies is not only higher than in bare soil (1250 vs. 200 g m^{-2}) but also differs among species or patch types. *P. alpataco* shows higher values of root biomass than *A. lampa* (733 vs. 566 g m^{-2}) under its canopy. Mixed patches of *L. divaricata* (shrub) and *S. tenuis* (grass) have higher fine-root biomass in the upper 50 cm soil (361 g m^{-2}) than those composed by only perennial grasses (270 g m^{-2}). The upper soil under shrub patches of *L. divaricata* (316 g m^{-2}) does not differ in fine-root biomass from the two former (Rodríguez et al., 2007b). Rodríguez et al. (2007b) found that soil water availability may exert an important control on fine-root biomass and activity in the southern Monte. Both the perennial grass *S. tenuis* and the evergreen shrub *L. divaricata* are able to have active fine roots in the upper soil (0–50 cm depth) when the soil is wet (soil moisture $> 8\%$). Accordingly, the large moisture fluctuations and extreme dry conditions in the upper soil may induce high fine-root turnover in these ecosystems.

Studies on root biomass are very scarce in the central Monte. *L. divaricata* shows lower root biomass in the upper soil (0–25 cm depth) than *L. cuneifolia* (0.30–1.06 kg plant^{-1} vs. 1.54–6.91 kg plant^{-1} , respectively), and both species exhibit higher root biomass in lowlands than in piedmont environments (Martínez Carretero et al., 2007).

5.2. Root chemistry

Nitrogen concentration in fine roots (< 1.4 mm in diameter) is higher in tall evergreen shrubs such as *L. divaricata* and *A. lampa* (15.2 mg g^{-1} and 14.4 mg g^{-1} , respectively) than in evergreen dwarf shrubs and perennial grasses of the southern Monte (6.9 mg g^{-1} and 6.1 mg g^{-1} , respectively; Appendix I, Rodríguez et al., 2007a). Evergreen dwarf shrubs (mainly *J. serphioides* and *Nassauvia fuegiana* (Speg.) Cabr.) show the highest concentration of soluble phenolics in fine roots (5.3 mg g^{-1}) (Appendix I). Probably, this is associated with the fact that these species persist and/or increase their covers in areas disturbed by grazing in which species with low anti-herbivore defences reduce their covers or disappear (Bertiller and Bisigato, 1998). In the central Monte, fine roots of the deciduous leguminous tree *P. flexuosa* exhibit higher concentrations of N and C (20.1 mg g^{-1} and 500.0 mg g^{-1} , respectively) than those of deciduous leguminous shrubs such as *Acacia furcatispina* Bukart (11.5 mg g^{-1} and 370.0 mg g^{-1} , respectively), and *Cercidium praecox* (Ruiz & Pav.) Harms (12.6 mg g^{-1} and 420.0 mg g^{-1} , respectively; Appendix I, Chambouleyron and Braun, 1994).

As is reported for other ecosystems (Huxman et al., 2004), water shortage and grazing disturbance could reduce the nutrient resorption and/or increase the concentration of recalcitrant C compounds in roots (e.g. suberin, tannin and lignin). This in turn could directly affect the metabolic functioning of soil microbial communities controlling the rate and extent of organic matter decomposition and consequently the C and N cycling in the Monte ecosystems.

6. Soil organic matter, N immobilization in microbial biomass, and N mineralization in soil

Studies on N cycling related processes are scarce in arid-semiarid ecosystems. In the Monte Phytogeographical Province, most of them refer to laboratory measurements under controlled

conditions or to short incubation periods in the field (Mazzarino et al., 1996). Studies on N mineralization provide information on N availability for plants, the predominant form of inorganic N, and risks of N losses by leaching, denitrification, and volatilization according to the dominant ionic form (Hart et al., 1994). Other key measurement is the amount of N retained in microbial biomass that mainly depends on C sources usually limiting in arid-semiarid ecosystems. Nitrogen retained in microbial biomass represents an important indicator of soil-N conservation and of the source of labile N after microorganism death (West and Skujins, 1978; Mazzarino et al., 1991; Gallardo and Schlesinger, 1992).

Despite the differences in climate and vegetation among regions within the Monte Phytogeographical Province, patches dominated by woody plants have a pronounced effect on soil properties with respect to grass patches and bare soil interspaces. The patchy structure of different plant cover determines different patterns of soil-N fertility and dynamics in the southern Monte (Rostagno et al., 1991; Mazzarino et al., 1996). When comparing plant patches and bare soil, the highest organic C and N concentrations in the upper 20 cm of soil are found in the large shrub-grass patches (7.4 vs. 6.0 mg C g^{-1} , 1.0 vs. 0.8 mg N g^{-1} , respectively, Mazzarino et al., 1996). Studies of soil-N dynamics conducted in the field during two consecutive years with contrasting precipitation also show marked differences among these microsites, and a differential effect of water availability on N mineralization (N_{min}) and N retained in microbial biomass (N_{MB} ; Mazzarino et al., 1998a). Annual accumulated mineralized N at 0–20 cm depth is almost negligible during a dry year, while during a wet year it is higher in large and incipient shrub-grass patches than in isolated grass patches and bare soil (Table 2). Monthly values of N_{min} during the dry year are less than 4 mg N kg^{-1} , and net-N immobilization occurred frequently. In contrast, during the wet year frequent pulses of 4–8 $\text{mg N kg}^{-1} \text{ month}^{-1}$ are observed, and immobilization is less frequent. Nitrification is low in the field and ammonium represents from 65 to 80% of inorganic N. However, nitrates increase at all microsites when soil moisture rises above 10%. Nitrates also prevail (80–90%) under optimum soil moisture in laboratory incubations being higher in the large shrub-grass patches than in the other patch types. Inorganic N at 20–40 cm depth is quite similar to values at the surface soil during the wet year (2.9–3.5 mg kg^{-1} vs. 2.7–3.9 mg kg^{-1}) and mainly in form of ammonium, suggesting downward movement of ammonium or N mineralization at depth possibly from root decay. This available N is coupled with higher water availability at depth than at the surface (7.5–8.8% vs. 5.7–6.3% of soil moisture), representing an advantage for deep-rooted shrubs. During both years, N_{MB} ranged from 10 to 23 mg kg^{-1} , the highest values corresponding to the large shrub-grass patches and the lowest to the isolated grass patches and the bare soil (Table 2). Except in the large shrub-grass patches, N_{MB} decreases at all microsites during the wet year while N_{min} increases, implying a net loss of labile N. In summary, results indicate that ecosystems of the southern Monte display a strong mechanism of soil-N conservation minimizing losses by leaching and denitrification. Nitrogen is fairly immobilized in microbial biomass under more vegetated patches, and ammonium is the main form of inorganic N. However, information about soil ammonia volatilization is scarce in the Monte ecosystems. This process could represent a potential risk of N losses in alkaline desert soils (Schlesinger, 1991) such as those in the southern Monte with pH values > 8.0 (del Valle and Rosell, 1999; Carrera, 2003).

Besides the primary effects of water availability and plant cover on soil-N dynamics, plant species play a major role through the quantity and quality of litter. This was demonstrated in long term studies of potential-N mineralization (pN_{min}) and N_{MB} in canopy soils from evergreen shrubs (*L. divaricata*, *A. lampa*, *J. serphioides*)

Table 2

Mean values of net-N mineralization (Nmin) and N retained in microbial biomass (N-MB) under different plant patches and bare soil during a dry and a wet year in: a. southern Monte (precipitations concentrated in autumn-winter) and b. Dry Chaco plain (precipitations concentrated in spring-summer).

	Nmin (mg kg ⁻¹ yr ⁻¹)	N-MB (mg kg ⁻¹)	Nmin (mg kg ⁻¹ yr ⁻¹)	N-MB (mg kg ⁻¹)
a. Southern Monte	Dry year (178 mm)		Wet year (311 mm)	
Large shrub-grass patches	1.7 Ba	19 Ba	21Aa	23 Aa
Incipient patches	0.1 Ba	15 Ab	21Aa	13 Bb
Isolated grasses	2.0 Ba	13 Ac	19 Aab	11 Bc
Bare soil	1.2 Ba	12 Ac	11 Ab	10 Bc
b. Dry Chaco Plain	Dry year (361 mm)		Wet year (780 mm)	
<i>Prosopis flexuosa</i>	150 Aa	44 Aa	153 Aa	38 Ba
<i>Larrea divaricata</i>	–	–	96 bc	20 b
Grass interspaces	75 Ab	26 Ab	70 Ac	17 Bb

At each site different letters indicate significant differences ($P < 0.05$): capital letters between years for the same treatment, and lowercase letters among treatments for the same year. N-MB was determined by the fumigation-incubation method and was not corrected by a recovery factor (k_N). Measurements were conducted at 0–20 cm depth in the southern Monte (Mazzarino et al., 1996) and at 0–10 cm depth in the Dry Chaco Plain (Mazzarino et al., 1991).

and perennial grasses (*S. tenuis*, *S. speciosa* and *P. ligularis*) (Carrera et al., 2003, 2005). The highest soil C and N concentrations correspond to *A. lampa* (9.8 mg C g⁻¹ and 0.9 mg N g⁻¹) and the lowest to *J. seriphioides*, *S. tenuis* and *S. speciosa* (5.3 mg C g⁻¹ and 0.5 mg N g⁻¹). Similarly, the highest values of pNmin and N-MB, measured in 16-wk incubations under optimum temperature and soil moisture, correspond to the soil beneath *A. lampa* (93.6 and 34.3 mg kg⁻¹, respectively) and the lowest to *S. tenuis* (55.3 and 19.9 mg kg⁻¹, respectively). Soils beneath other species show intermediate values of all parameters (Appendix II). Results are closely associated with litter production, which is higher in *A. lampa* than in all other species, but also with litter chemistry (Carrera et al., 2005; Campanella and Bertiller, 2008). Although shrubs have significantly higher N concentrations and lower C/N ratio in senesced leaves than perennial grasses, they also show much higher concentrations of lignin (*J. seriphioides*, *A. lampa*) and soluble phenolics (especially *L. divaricata*; Appendix I)

In the central and northern Monte, data on soil fertility and N dynamics are scarce. In the central Monte, Rossi and Villagra (2003) found a strong effect of *P. flexuosa* on soil chemical properties with significantly higher values of organic matter and N under tree canopies than in inter-canopy areas (21 and 1.5 mg g⁻¹ vs. 7 and 0.9 mg g⁻¹, respectively). They also found different life forms dominating these habitats, i.e. shrubs under canopies, and grasses and perennial forbs outside the canopies.

Though studies on soil-N dynamics are lacking for the central Monte, those conducted in the Dry Chaco plain provide useful values for comparison with the southern Monte, since they also refer to open woodlands of *P. flexuosa* and *L. divaricata* with precipitations distributed in spring-summer (Mazzarino et al., 1991; Hang et al., 1995). However, mean annual precipitation and plant diversity and productivity are higher in the latter than in the Monte Phytogeographical Province, and the tree stratum is co-dominated by *Aspidosperma quebracho-blanco* Schldl. (Morello et al., 1985). Main results indicate that surface soils beneath *P. flexuosa* have higher organic C and total N (19.2 and 1.8 mg g⁻¹, respectively), than beneath grasses in the interspaces (13.0 and 1.2 mg g⁻¹, respectively) and *L. divaricata* (12.8 and 0.9 mg g⁻¹, respectively). Soils beneath *P. flexuosa* also show higher Nmin and N-MB than soils underneath grasses and *L. divaricata* (Table 2). Further, the highest values of Nmin and N-MB are always in spring-summer. During a dry year, Nmin was very similar to an exceptionally wet year (Table 2), but concentrated in a marked pulse after a heavy rain event (110 mg kg⁻¹ month⁻¹) vs. several peaks of 10–40 mg kg⁻¹ month⁻¹ during the wet year. While Nmin

correlates strongly with soil moisture pulses, N-MB increases at the onset of the rainy season and then remains high and relatively constant with values ranging from 17 to 44 mg kg⁻¹. Nitrates comprise the highest proportion of mineralized N (70–85%). High Nmin and N-BM in soils beneath trees is associated with high litter production as well as high N concentration and low C/N and lignin/N ratios in litter. The patterns of organic C and several nutrients change at deep soil layers (25–75 cm), where values are significantly higher in soils under *L. divaricata* and grasses (clear of trees and shrubs for at least 15 yr) than under trees, suggesting a differential effect of life forms in the deep soil.

As compared to the southern Monte, N-BM and Nmin are higher in the Dry Chaco plain, but differences are more marked for Nmin (5–9 times higher) than for N-MB (only 1.3–1.5 higher). In the Dry Chaco, higher Nmin values and predominance of nitrates coupled with water availability during the growing season are certainly related to greater productivity but also to higher risk of N losses by leaching and denitrification (Mazzarino and Bertiller, 1999). No information is available in relation to inorganic N form preferences for plant uptake in the Monte Phytogeographical Province. Due to differences in the main available forms of soil-inorganic N (nitrate at the central Monte vs. ammonium at the southern Monte) plants could preferably take up different inorganic N forms across the Monte ecosystems. This hypothesis could be supported by evidence that nitrate may be the preferred N source of inorganic N for seedlings of *P. flexuosa* in laboratory experiments (Causin et al., 2004).

Besides the effect of plant litter, biological soil crusts in desert ecosystems can play an important role on N cycling (Schlesinger, 1991). Biological crusts are frequent in the Monte ecosystems (Tanquilevich, 1971; Scutari et al., 2002, 2004). In the southern Monte the lichen *Collema coccophorum* (Tuck.) is an important component of biological soil crusts and one of its components is a N₂-fixing cyanobacteria (Scutari et al., 2004) probably having an important impact on N dynamics in soils of the southern Monte (Scutari et al., 2004).

7. Final remarks

Studies on the topics addressed in this review are quite limiting in the Monte Phytogeographic Province. As in other water/nutrient-poor ecosystems, plant life forms differ in the leaf traits and in the mechanisms to conserve nutrients within the plant. The main mechanisms in the Monte plants are related to (i) the conservation of long-lasting dense green leaves with low concentrations of N and high concentrations of secondary compounds (mainly in evergreen shrubs) that protect them against water stress, pathogen and herbivores; (ii) leaf shedding during the periods of water shortage thus avoiding the high costs of maintaining resistant dense leaves. This mechanism is characteristic of species with high N concentration in green leaves and intermediate N-resorption efficiency and proficiency (e.g. deciduous tree *P. flexuosa* and deciduous shrubs); and (iii) high foliar N-resorption efficiency and proficiency associated with short leaf lifespan (mainly in perennial grasses).

Leaf traits are strongly related to litter production, i.e. plants with low N-resorption produce denser leaves and higher litterfall than plants with high N-resorption and low mass per area. However, leaf litter production is not completely associated with life forms indicating species-specific responses. In general, plant species with the highest leaf litterfall also produce the most recalcitrant leaf litter, excepting leguminous species. The fate of dead plant material varies as a function of its physical-chemical composition and its physical location in the environment. Litter chemistry exerts an important control on decomposition processes. In this review we identify three contrasting cases: (i) litter with low concentrations of N and secondary compounds that decomposes

slowly probably due to high values of C/N ratio (e.g. perennial grasses); (ii) litter with high concentrations of N and secondary compounds that decomposes also slowly possibly due to the negative effect of plant secondary metabolites on microbial activity (some woody species), and (iii) litter with high concentrations of N and intermediate concentrations of secondary compounds that decomposes at high rates (e.g. the shrub *A. lampa*, and probably the leguminous tree *P. flexuosa*). The micro-environmental conditions play also an important role in determining the decomposition rates of the organic matter. The attenuation of climatic conditions and the higher organic matter and nutrients concentrated under plant canopy enhance microbial activity resulting in higher decomposition rates than in the surrounded bare areas. However, not all the plant species within a life form (mainly in the case of shrubs), would have the same impact on C and N cycling.

Results further show that ecosystems of the southern Monte have strong mechanisms of soil-N conservation such as high N retention in microbial biomass and low risk of N losses by leaching and denitrification. Considering that N is a strong selective factor in plant communities of arid–semiarid ecosystems and that data on N dynamics are lacking for the central and northern Monte, information on the Dry Chaco plain has been included for comparison with the southern Monte. From this comparison, it is evident that the seasonal distribution of precipitation plays a major role on soil-N dynamics. While in the north precipitation coincides with the growing season (summer), in the southern Monte it occurs mainly in autumn–winter. Consequently, soil organic matter and N mineralization are lower in the southern Monte with predominance of ammonium in the soil solution, while nitrates are the main form of available inorganic N in the north. Inter-annual variation of precipitation also influences N mineralization, available N being higher and more evenly distributed in wet years. Nitrogen retained in microbial biomass is less dependant on precipitation and only slightly lower in the southern than in the northern Monte.

The differential effect of plant life forms and species of the Monte Province on soil organic matter accretion and N cycling suggests that changes induced by deforestation, grazing, and probably climate change could modify N availability affecting primary productivity. As a result of the present review, we can remark that further research is needed on:

- Litter production and root turnover along the whole Monte Phytogeographical Province, including decomposition of leaf litter and roots of isolated species and mixtures under field conditions.
- Soil-N dynamics in the central and northern Monte.
- N₂ fixation by free and symbiotic bacteria.
- N losses by volatilization from alkaline soils.
- Effects of life forms or species on C and nutrient distribution in deep soil layers.
- Identification of prevalent forms of N uptake (ammonium, nitrate or organic compounds) by plant species and/or life forms.
- Long term effects of life form or species shifting on soil organic matter quality. Although easily degradable or labile organic matter enhances biological activity and N availability, slow decomposable or recalcitrant organic matter is also important because it contributes to improve water and nutrient storage, soil structure, and resistance to erosion.
- Effects of global climatic change on N dynamics in vegetation and soil.

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Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jaridenv.2008.09.016.

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