

# Relationships among plant litter, fine roots, and soil organic C and N across an aridity gradient in northern Patagonia, Argentina<sup>1</sup>

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**Abstract:** We analyzed the relationship between organic C and N in the upper soil and the quantity (mass) and quality (N, soluble phenolic, and lignin concentrations) of plant aboveground litter and upper fine roots at contrasting microsites (plant patch and bare soil) in 15 study sites across an aridity gradient in Patagonia. At each site, we estimated the total, grass, and shrub cover and randomly selected 10 plant patches of modal size (height and crown diameter) and species composition. We extracted an upper soil core (0–10 cm depth) and collected the aboveground litter underneath each plant patch canopy and at the contiguous bare soil. We separated the fine roots (< 2 mm in diameter) from the soil and assessed the biomass and the concentrations of organic C and N in soil and the lignin, soluble phenolic, and N in shrub and grass components of aboveground litter and in fine roots. Total plant and grass cover decreased with increasing aridity. Total litter mass did not vary across the aridity gradient, but the proportion of shrub components in litter increased and litter quality decreased with increasing aridity. The mass of fine roots was positively correlated to soil organic C and N and decreased with increasing aridity. All these trends were consistent at plant patch and bare soil microsites. We conclude that the decrease in soil organic C and N across the aridity gradient was the outcome of different above- and belowground controls resulting from the replacement of grasses by shrubs. Accordingly, the main controls of soil organic C and N could be the quality of aboveground litter and the quantity of the organic matter input to soil through fine-root turnover from belowground.

**Keywords:** grasses, leaf litter, litter recalcitrance, plant patch, shrubs, woody litter.

**Résumé :** Nous avons analysé la relation entre le C organique et le N de la couche supérieure du sol et la quantité (masse) et qualité (N, composés phénoliques solubles et concentrations en lignine) de la litière végétale de surface et des racines fines de la couche supérieure du sol dans des microsites contrastés (parcelles de végétation et sol nu) dans 15 sites d'étude au sein d'un gradient d'aridité en Patagonie. Pour chaque site, nous avons évalué la couverture totale d'herbes et d'arbustes et avons sélectionné au hasard 10 parcelles de végétation de taille (hauteur et diamètre des cimes) et de composition en espèces modales. Nous avons extrait une carotte de la couche supérieure du sol (profondeur 0–10 cm) et avons récolté la litière de surface sous la canopée de chaque parcelle de végétation et dans les microsites contigus de sol nu. Nous avons séparé les racines fines (< 2 mm de diamètre) du sol et avons évalué la biomasse et les concentrations de C organique et de N dans le sol ainsi que la lignine, les composés phénoliques solubles et le N dans les composantes herbacées et arbustives de la litière de surface et dans les racines fines. La couverture végétale totale et la couverture herbacée diminuaient avec une augmentation de l'aridité. La masse totale de litière ne variait pas au sein du gradient d'aridité, mais la proportion de la composante arbustive dans la litière augmentait et la qualité de litière diminuait avec une augmentation de l'aridité. La masse de racines fines était corrélée de façon positive aux C organique et N du sol et diminuait avec une augmentation de l'aridité. Toutes ces tendances étaient cohérentes entre les microsites de parcelles de végétation et de sol nu. Nous avons conclu que la diminution de C organique et N du sol au sein du gradient d'aridité était le résultat de différents contrôles de surface et souterrains entraînant un remplacement des herbes par des arbustes. En conséquence, les contrôles principaux du C organique et de N du sol pourraient être la qualité de litière de surface et la quantité d'intrants de matière organique dans le sol par le renouvellement des racines fines sous la surface.

**Mots-clés :** arbustes, herbes, litière de feuilles, litière ligneuse, litière récalcitrante, parcelle de végétation.

**Nomenclature:** Correa, 1971–1999.

## Introduction

Precipitation and temperature are the main factors influencing the spatial pattern of vegetation and the distribution of plant life forms at regional and global scales (Walter, 1985). Many studies have described the shifting of dominant plant life forms or aboveground plant traits related

to C acquisition or nutrient conservation across climatic gradients in a wide range of ecosystems (Cornelissen *et al.*, 1999; Austin & Sala, 2002; Bertiller *et al.*, 2006; Breshears, 2006; Sieben *et al.*, 2010; among others). However, few studies have included variation in plant belowground attributes, such as fine roots, which are especially relevant in relation to C and nutrient stocks and cycling in the upper soil (Jackson, Mooney & Schulze, 1997; Whitford, 2002). The quality of tissues and the patterns of biomass and litter partition between aboveground and belowground

<sup>1</sup>Rec. 2010-02-22; acc. 2010-05-24.

Associate Editor: Benjamin F. Tracy.

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DOI 10.2980/17-3-3359

plant parts are important controls of ecosystem functioning and responses to human disturbance and climate change (Schlesinger *et al.*, 1990). Accordingly, integrative studies relating above- and belowground plant attributes to soil C and N stocks and cycling across climate gradients would be useful in understanding the role of plants in the functioning of ecosystems under natural or anthropic disturbances (Breshears, 2006).

In semiarid and arid ecosystems, vegetation structure is represented by a two-phase mosaic formed by patches with high plant cover alternating with areas of scattered vegetation or bare soil (Tongway & Ludwig, 2005). Plant patches induce the formation of “fertility islands”, which concentrate soil resources such as N and organic C under plant canopies, while relatively infertile soils occur in the inter-canopy spaces (Burke *et al.*, 1999; Tongway & Ludwig, 2005; Bertiller *et al.*, 2009). In these ecosystems, increasing aridity leads to the replacement of grasses by shrubs and a decrease in plant cover and productivity (Reynolds *et al.*, 1997). This replacement of plant life forms is generally associated with changes in the dominant morphological and physiological traits of aboveground and belowground plant structures, influencing the quantity and quality of plant litterfall (Sala *et al.*, 1989; Bertiller, Beeskow & Coronato, 1991; Aerts & Chapin, 2000; Campanella & Bertiller, 2008; Carrera *et al.*, 2009). Grasses produce tissues of short lifespan, with low protection against abiotic factors and herbivores (Aerts & Chapin, 2000; Carrera *et al.*, 2005; Campanella & Bertiller, 2008). In contrast, shrubs have a great diversity of structural and chemical adaptations to cope with water shortage, herbivores, pathogens, and radiation effects (Bertiller, Beeskow & Coronato, 1991; Aerts & Chapin, 2000; Lambers, Chapin & Pons, 2000; Campanella & Bertiller, 2008; 2009; Carrera *et al.*, 2009), including species with the potential to fix N<sub>2</sub> (Rhoades *et al.*, 2008). Moreover, grasses and shrubs may make different contributions to upper soil root biomass, with grasses having a shallower root distribution than shrubs (Jackson *et al.*, 2000).

Several studies have addressed the effects of aridity on changes in aboveground vegetation traits or in soil resources, but few have included analysis of simultaneous changes in quantity and quality of above- and belowground attributes. Fine roots (< 2 mm diameter) may supply large quantities of C and nutrients to the soil. However, they could also contain large amounts of secondary compounds exerting an important control on nutrient and C release and cycling in soil (Cornelissen *et al.*, 1999; Hibbard *et al.*, 2001; Whitford, 2002; Carrera *et al.*, 2005; Rodríguez, Bertiller & Sain, 2007; Carrera, Bertiller & Larreguy, 2008). We addressed the relationship between soil organic C and N and the quantity (mass) and quality (N, soluble phenolic, and lignin concentrations) of plant aboveground litter (total, leaf, and woody mass) and upper fine roots (< 2 mm diameter) at contrasting microsites (plant patch and bare soil) at different sites with patchy plant structure across an aridity gradient in Patagonia. We hypothesized that decreasing soil C and N in the upper soil (0–10 cm depth) of both plant patches and bare soil with increasing aridity is related to increasing recalcitrance in aboveground litter and decreasing mass allocation to fine roots in the upper soil due to gradual replacement of grasses by shrubs.

## Methods

### ARIDITY GRADIENT AND STUDY SITES

In Patagonia, precipitation decreases from the west towards the east, while temperature increases from west to east and from south to north, creating a southwestern–northeastern aridity gradient (Bertiller *et al.*, 2005). We selected 15 study sites across an aridity gradient in Chubut Province, Patagonia (Argentina), which encompasses the Patagonian and Monte Phytogeographic Provinces. Across this gradient, mean annual precipitation varied from 125 mm to 500 mm, and the aridity index calculated as the annual potential evapotranspiration/annual precipitation ratio (Bertiller *et al.*, 2005) ranged from 1.07 to 7.31 (Table I; Figure 1). Dominant vegetation shifts from grass steppes dominated by *Festuca pallelescens* with sparse shrubs

TABLE I. Location, phytogeographical province, mean annual temperature, mean annual precipitation, and aridity index (AI) of the study sites.

Study site locations		Phytogeographical province	Mean annual temperature (°C)	Mean annual precipitation (mm)	AI*
Latitude (s)	Longitude (w)				
44° 58' 47.0"	71° 17' 00.0"	Patagonian	7.68	500.0	1.07
44° 58' 46.4"	71° 16' 59.1"	Patagonian	7.68	500.0	1.07
45° 36' 15.3"	71° 26' 11.3"	Patagonian	7.54	385.0	1.36
42° 23' 31.0"	68° 56' 41.9"	Patagonian	7.95	150.0	3.68
45° 41' 11.6"	67° 53' 26.6"	Patagonian	8.58	150.0	3.97
45° 35' 19.5"	70° 20' 14.8"	Patagonian	9.29	150.0	4.30
42° 23' 31.0"	67° 56' 42.0"	Patagonian	9.73	150.0	4.50
43° 13' 01.6"	65° 01' 29.1"	Monte	13.30	183.3	5.04
45° 27' 23.6"	69° 49' 16.5"	Patagonian	9.42	125.0	5.23
43° 51' 30.2"	68° 13' 29.4"	Patagonian	11.29	131.3	5.97
42° 33' 33.5"	66° 33' 50.4"	Monte	12.76	137.5	6.44
43° 44' 40.4"	66° 20' 21.9"	Monte	12.38	130.0	6.61
43° 40' 49.6"	66° 48' 04.6"	Monte	12.39	128.6	6.69
43° 04' 33.7"	67° 12' 49.7"	Monte	12.24	125.0	6.80
42° 45' 42.5"	66° 01' 02.5"	Monte	13.16	125.0	7.31

\*AI: aridity index = PET / P, where PET was estimated as in Le Houérou (1990):  $PET = 69.4 T$ , where T is the mean annual temperature calculated using 1991–2000 data from the CRU TS 2.1 data set (Mitchell & Jones, 2005) for each site and P is the mean annual precipitation (series 1931–1960) of each site obtained from Barros and Rivero (1982).

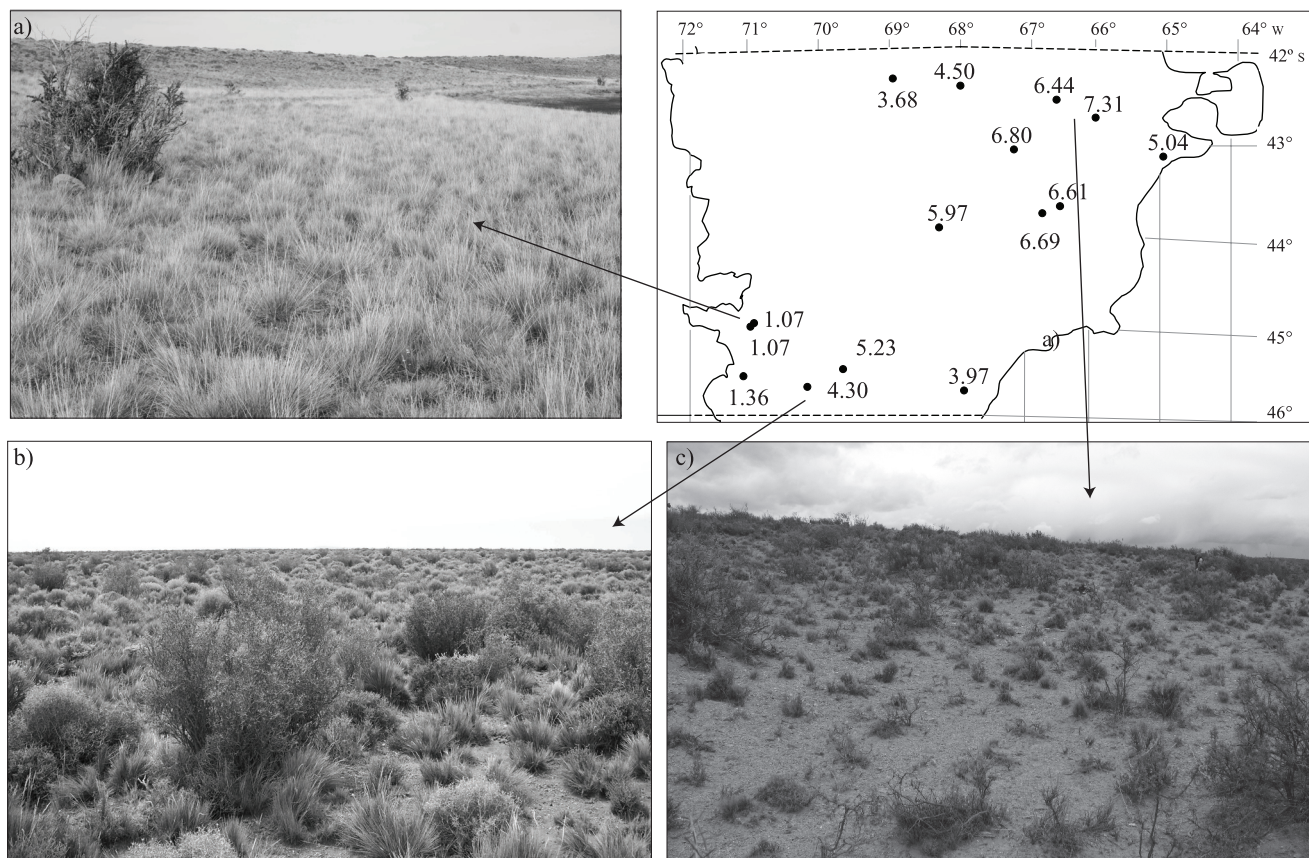


FIGURE 1. Geographical location and aridity index of the 15 study sites in Chubut Province, Patagonia (Argentina), with 3 selected photographs of the study sites showing the shift from grass steppes to arid shrublands with increasing aridity index. a) aridity index = 1.07, b) aridity index = 4.30 and c) aridity index = 7.31.

of *Mulinum spinosum* to arid shrublands dominated by *Larrea divaricata* and *Stipa* spp. (Bertiller *et al.*, 1995; Correa, 1971–1999; León *et al.*, 1998) with increasing aridity. This shift in dominant plant life forms is frequently associated with increasing vegetation patchiness (Burke *et al.*, 1999; Pazos, Bisigato & Bertiller, 2007; Figure 1). Across the aridity gradient, soils vary from Mollisols and Entisols at the most humid sites to Aridisols at the driest ones (Soil Survey Staff, 1999; Godagnone *et al.*, 2008).

#### SAMPLING

At each study site, we visually estimated total plant, grass, and shrub canopy covers using cover categories with increments of 1% (Bertiller & Ares, 2008) in November 2007 (vegetative/early reproductive growth period of shrubs and grasses). We also registered the total cover of leguminous plant species with the potential to fix  $N_2$  at each site. We randomly selected 10 plant patches of modal size (height and diameter) and species composition on a representative minimal area (*sensu* Mueller-Dombois & Ellenberg, 1974) of about 10 000  $m^2$  per site. We collected the litter accumulated on the soil within 1 rectangular plot of 0.30 × 0.15 m located beneath the canopy of each plant patch (plant patch microsite) and on the contiguous bare soil (bare soil microsite). We further extracted 1 soil core (10 cm diameter and 10 cm depth) at 5 randomly selected microsites of each type per site.

The collected litter was carefully cleaned to remove soil particles and separated into woody tissues and leaves of shrubs and grasses. The litter components were then dried at 60 °C for 48 h and weighed. Fine roots (< 2 mm diameter) were separated from the soil of each core, briefly washed in tap water to remove adhered soil particles, dried at 60 °C for 48 h, and weighed. Coarse roots (> 2 mm diameter) were not included in this study since they are associated with low turnover rates (Gill & Jackson, 2000). The high turnover rates of fine roots may represent a major contribution of nutrient and carbon inputs to the soil (Jackson, Mooney & Schulze, 1997). As other authors have reported, it was extremely difficult to recognize and separate the fine roots of each life form and distinguish between live and dead fine roots in the samples (Ostertag & Hobbie, 1999; Robinson *et al.*, 1999; Rodríguez, Bertiller & Sain, 2007; Carrera, Bertiller & Larreguy, 2008). Accordingly, our data include a mixture of shrub and grass live and senesced fine roots. After the separation of fine roots, all soil samples were air-dried and sieved to 2 mm.

In 3 randomly selected replicates per microsite and site of aboveground litter components (woody litter, shrub leaf litter, and grass leaf litter) and fine roots, we assessed N concentration by the semi-micro Kjeldahl method (Coombs *et al.*, 1985), total soluble phenolics by the Folin–Ciocalteu method, using 50% methanol as extract solution and tannic acid as standard (Waterman & Mole, 1994), and

lignin by the van Soest (1963) procedure. All soil samples were analyzed for soil organic C concentration by wet combustion (Nelson & Sommers, 1982) and for soil N concentration by semi-micro Kjeldahl method (Bremner & Mulvaney, 1982). This study was conducted for only 1 y, but we did not expect significant variation in soil attributes and litter quality over the short term since previous studies in arid ecosystems of the Patagonian Monte indicated that N and organic C concentration in the soil and leaf litter of perennial grasses and evergreen shrubs did not significantly vary among 3 consecutive years (Carrera *et al.*, 2003; 2005).

STATISTICAL ANALYSES

We evaluated the relationships between the aridity index and plant cover, total and per component aboveground litter, upper fine roots, and soil traits at plant patch and bare soil microsites by regression analysis using means per site as replicates (Sokal & Rohlf, 1981). The significance of differences in total and per component aboveground litter, upper fine roots, and soil traits between microsites was evaluated by ANOVA. In cases where the assumptions of ANOVA were not met, variables were transformed logarithmically (Sokal & Rohlf, 1981). We also evaluated the relationships among all plant and soil variables and the aridity index by principal component analysis. Unless otherwise noted, the level of significance throughout this study was  $P < 0.05$ . All statistical analyses were performed with SPSS 7.0 (Norusis, 1997).

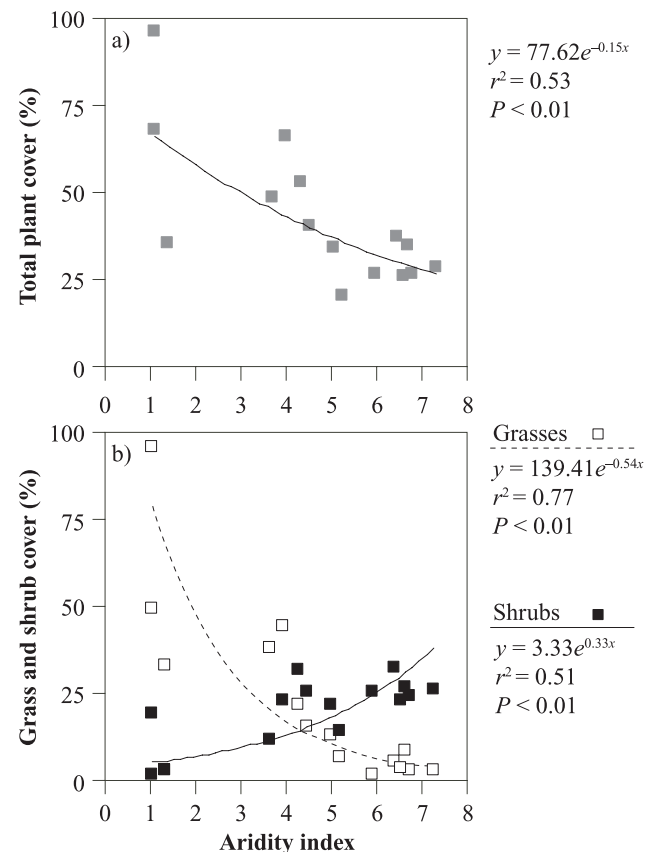


FIGURE 2. a) Total plant and b) grass and shrub cover across the aridity gradient.

Results

PLANT COVER

Total plant (Figure 2a) and grass cover decreased with increasing aridity, while the reverse occurred with shrub cover (Figure 2b). The mean value of leguminous plant cover across the aridity gradient was 3.5% and did not significantly vary across the gradient (data not shown).

SOIL ORGANIC C AND TOTAL N

Soil organic C and total N decreased with increasing aridity at both the plant patch and the bare soil microsites (Figures 3a and 3b, respectively). Soil organic C and total N were higher underneath plant patches than in bare soil microsites across the whole aridity gradient ( $F_{1, 150} = 11.50, P < 0.01; F_{1, 150} = 9.09, P < 0.01$ , respectively).

ABOVEGROUND LITTER

Total aboveground litter mass did not vary across the aridity gradient at either type of microsite, but it was

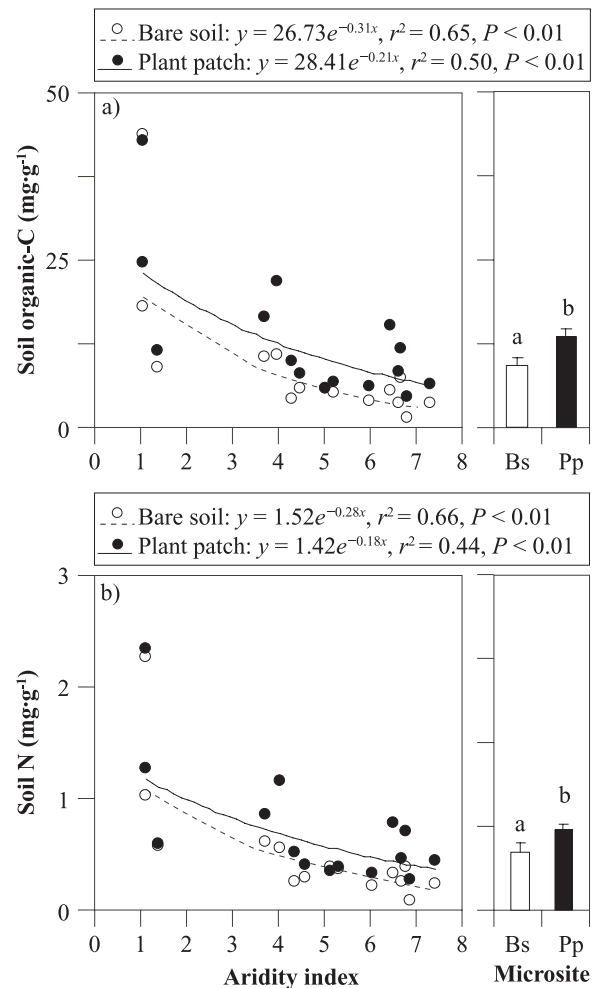


FIGURE 3. Mean values of a) organic C concentration and b) total N concentration in soil underneath plant patches (black circles) and in bare soil (white circles) at each site across the aridity gradient and mean value + SE (bars) of each attribute at each microsite (bare soil: Bs; plant patch: Pp). Different lowercase letters indicate significant ( $P \leq 0.05$ ) differences among mean values of each attribute between microsites.

higher underneath plant patch than in bare soil microsites ( $F_{1,300} = 11.83, P < 0.01$ ; Figure 4a). The shrub woody and leaf components in aboveground litter increased with increasing aridity only under patch canopies (Figures 4b and c, respectively). In contrast, the mass of the leaf litter of grasses decreased with increasing aridity at both types of microsite (Figure 4d). The mass of woody litter and the leaf litter of shrubs and grasses were higher underneath plant patch than in bare soil microsites across the whole aridity gradient ( $F_{1,300} = 61.36, P < 0.01$ ;  $F_{1,300} = 112.81, P < 0.01, F_{1,300} = 51.13, P < 0.01$ , respectively).

The nitrogen concentration in the aboveground plant litter components beneath plant patches increased with aridity (Figures 5a-d), whereas at bare soil microsites N concentration increased with increasing aridity only in total aboveground plant litter and in grass leaf litter (Figures 5a and d, respectively). Soluble-phenolic concentration in total aboveground plant litter and in shrub-leaf litter increased with increasing aridity beneath plant patches (Figures 6a and c, respectively), but this chemical attribute was not significantly correlated to the aridity index at bare soil microsites (Figures 6a to d). Lignin concentration in total aboveground plant litter and in woody litter increased

with increasing aridity beneath plant patches (Figures 6e and 6f, respectively). Lignin concentration increased with increasing aridity only in total aboveground litter at bare soil microsites (Figure 6e). The different litter components (woody, shrub-leaf and grass-leaf) were not correlated to aridity at bare soil microsites (Figures 6e to h). No differences in chemical traits of aboveground litter were found between microsites (Figures 5 and 6).

FINE ROOTS

Fine root mass decreased with increasing aridity and did not vary between plant patch and bare soil microsites ( $F_{1,150} = 0.06, P = 0.80$ ; Figure 7a). Nitrogen and lignin concentrations in fine roots did not vary across the aridity gradient at any microsite (Figures 7b and 7d, respectively), while soluble phenolic concentration in fine roots decreased with increasing aridity only at plant patch microsites (Figure 7c). No differences in chemical traits of upper fine roots were found between microsites (Figures 7b to d).

RELATIONSHIP AMONG PLANT LITTER, FINE ROOTS, SOIL TRAITS, AND THE ARIDITY GRADIENT

The principal component analysis (PCA) showed a negative relationship between aridity and soil traits (organic

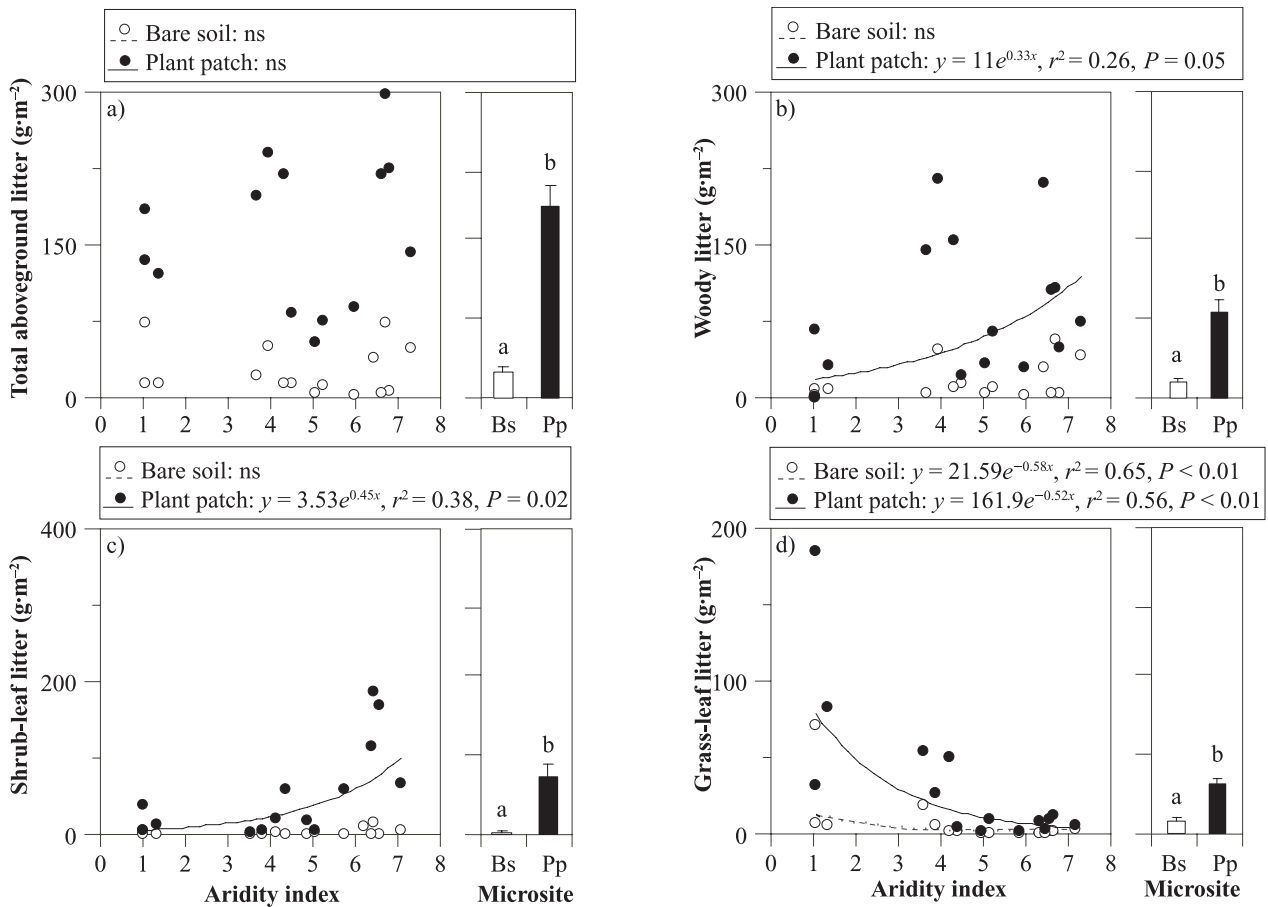


FIGURE 4. Mean values of a) total aboveground litter, b) woody litter, c) shrub-leaf litter, and d) grass-leaf litter mass underneath plant patches (black circles) and in bare soil (white circles) microsites at each site across the aridity gradient and mean value + SE (bars) of each attribute at each microsite (bare soil: Bs; plant patch: Pp). Different lowercase letters indicate significant ( $P \leq 0.05$ ) differences among mean values of each attribute between microsites. ns: not significant.

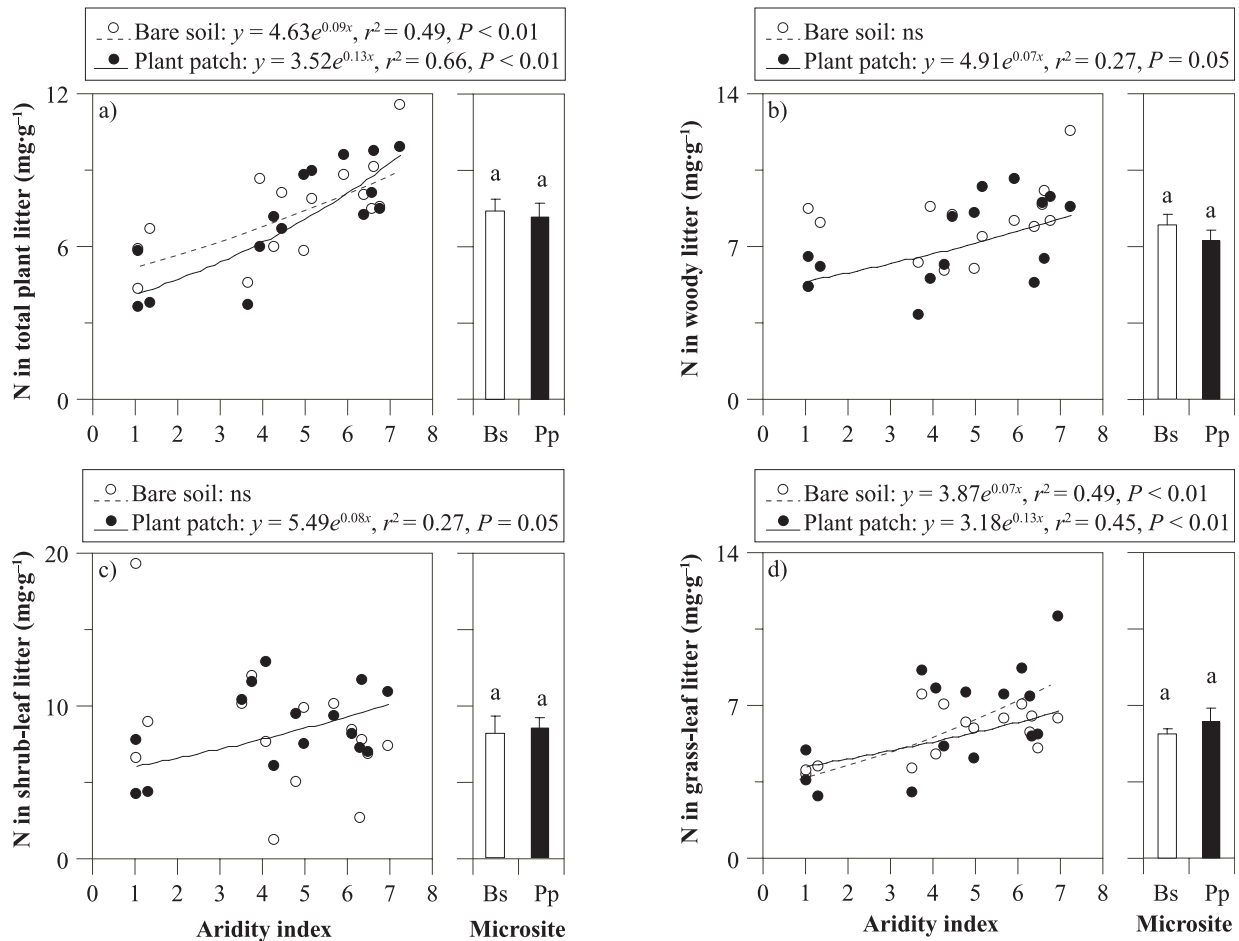


FIGURE 5. Mean values of N concentration in a) total aboveground plant litter, b) woody litter, c) shrub-leaf litter, and d) grass-leaf litter underneath plant patches (black circles) and in bare soil (white circles) at each site across the aridity gradient and mean value + SE (bars) of each attribute at each microsite (bare soil: Bs; plant patch: Pp). Different lowercase letters indicate significant ( $P \leq 0.05$ ) differences among mean values of each attribute between microsites. ns: not significant.

C and N concentrations) on PCA axis 1 (40.97% of the total variance; Figure 8). Soil traits were grouped with upper fine root mass and soluble phenolic concentration in fine roots (positive values of axis 1; Figure 8). Moreover, the aridity index was clustered with aboveground litter traits (mass, N, soluble phenolic, and lignin concentrations) and N concentration in fine roots at both microsites (negative values of axis 1 and positive values of axis 2; Figure 8). The variable that explained the largest variation in soil organic C and N was the mass of fine roots (74% and 72 % of the total variance, respectively, in both cases positively correlated). Other aboveground variables were not correlated or explained only a low percentage of variance in soil organic C and N. Lignin concentration in aboveground litter, for example, was negatively correlated to soil organic C and N, explaining only 19.4% and 18.8 % of the total variance, respectively.

## Discussion

In northern Patagonia, the decrease in organic C and N in the upper soil with increasing aridity at both plant patch and bare soil microsites was related to the reduction of total plant cover and a gradual replacement of grasses by

shrubs. These changes in aboveground plant cover were not associated with the reduction of the mass of aboveground plant litter, but they led to an increasing contribution of shrub components with a high concentration of secondary compounds in the aboveground litter underneath plant patches. In semiarid and arid ecosystems, shrubs usually display a wide range of morphophysiological and chemical traits that enable them to withstand water shortage, herbivore attack, and radiation effects (Aerts & Chapin, 2000; Austin & Sala, 2002; Bertiller *et al.*, 2006; Carrera *et al.*, 2009). Shrubs with long-lasting tissues generally have high concentrations of secondary compounds that lead to low nutrient resorption during tissue senescence (Bertiller, Beeskow & Coronato, 1991; Aerts & Chapin, 2000; Lambers, Chapin & Pons, 2000; Campanella & Bertiller, 2008) and to the production of litter that is nutrient rich but has high concentrations of secondary metabolites. This was the most probable cause of increasing N concentration in total and shrub litter with increasing aridity. We discarded the eventual contribution of leguminous plants with the potential to fix  $N_2$  since their cover did not vary across the aridity gradient. Our findings were consistent with studies reporting that the shift of plant life forms and/

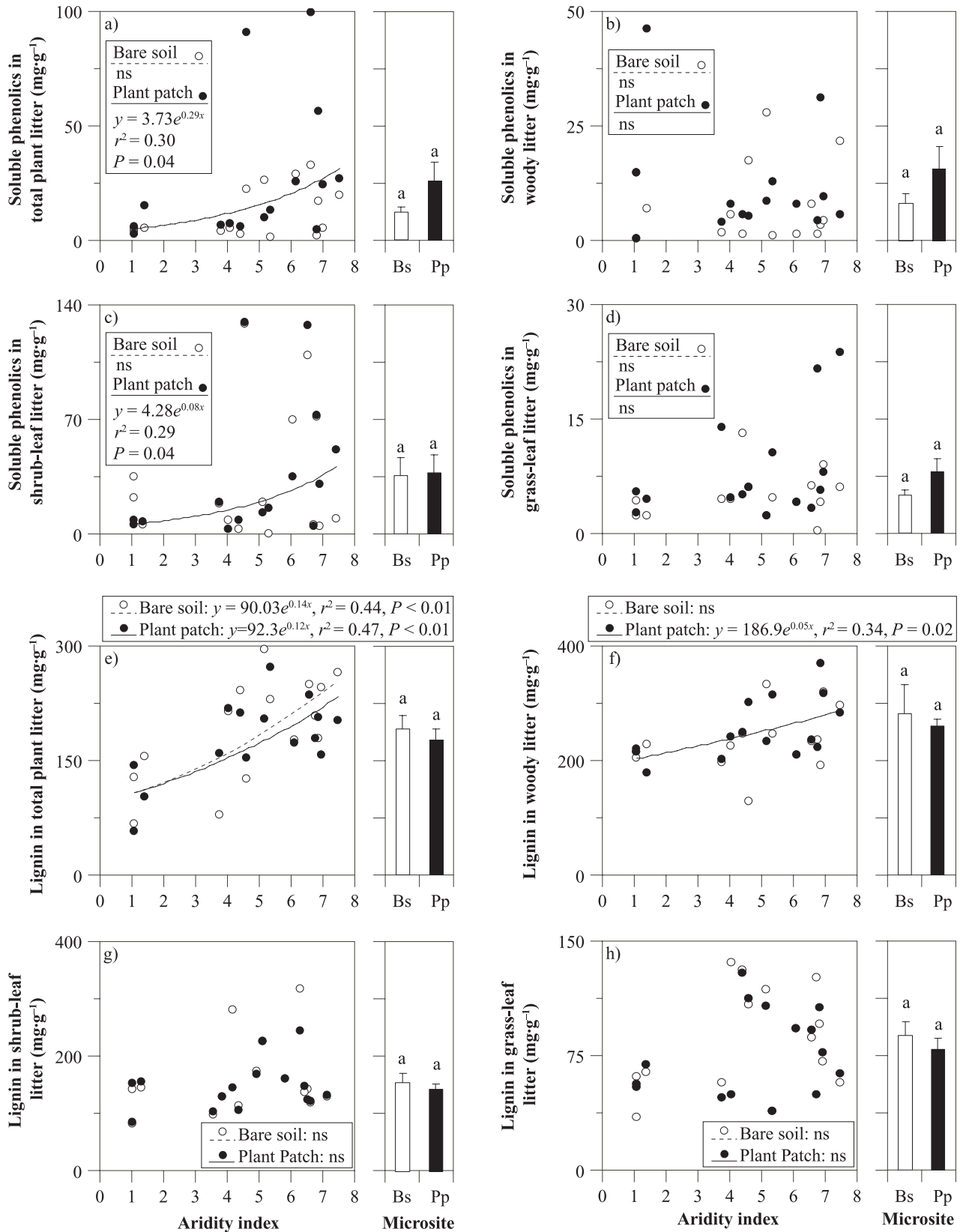


FIGURE 6. Mean values of soluble phenolic concentration in a) total aboveground plant litter, b) woody litter, c) shrub-leaf litter, and d) grass-leaf litter and lignin concentration in e) total aboveground plant litter, f) woody litter, g) shrub-leaf litter, and h) grass-leaf litter underneath plant patches (black circles) and in bare soil (white circles) at each site across the aridity gradient and mean value + SE (bars) of each attribute at each microsite (bare soil: Bs; plant patch: Pp). Different lowercase letters indicate significant ( $P \leq 0.05$ ) differences among mean values of each attribute between microsites. ns: not significant.

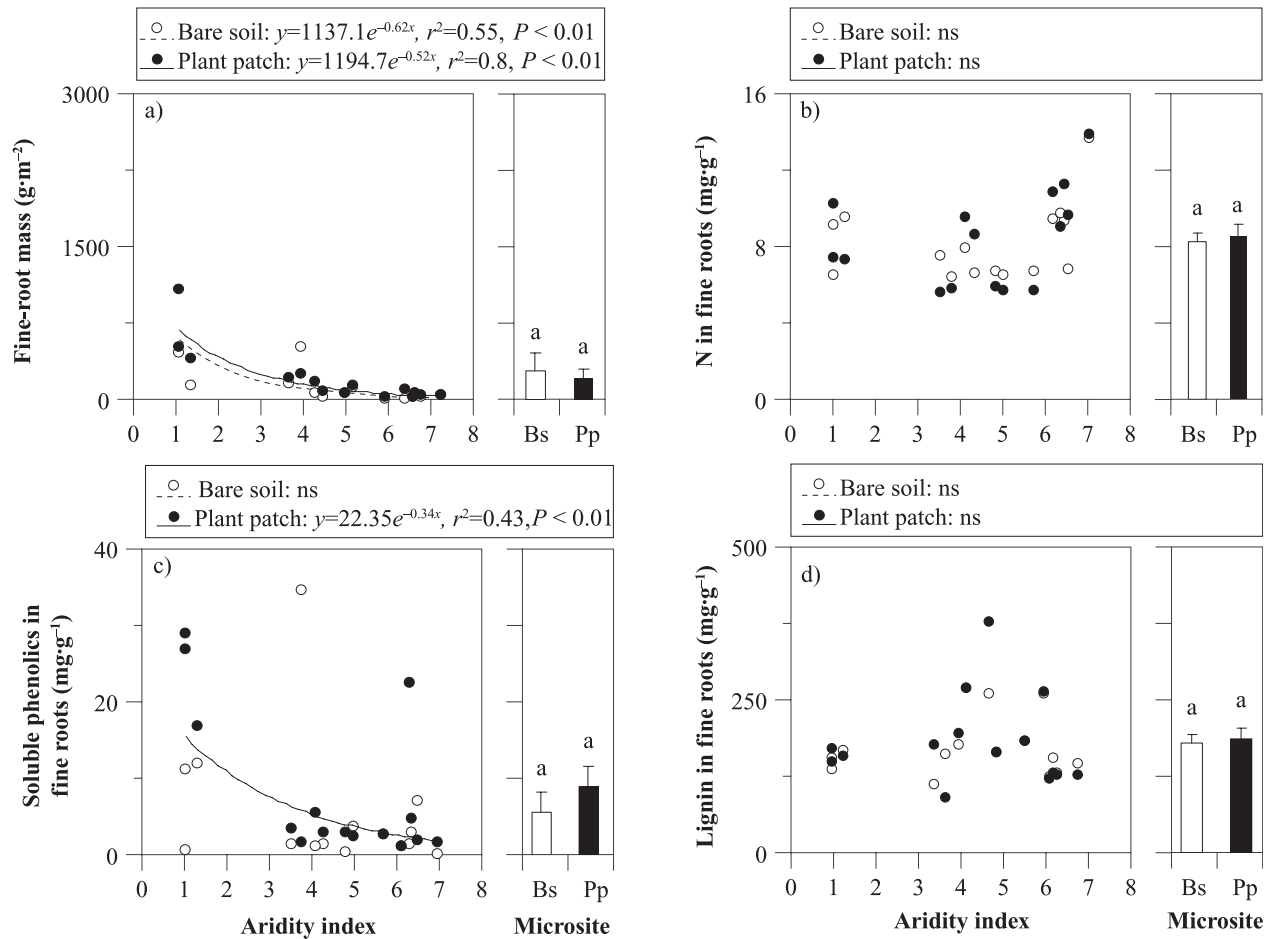


FIGURE 7. Mean values of a) upper fine root mass, b) N concentration, c) soluble phenolic concentration, and d) lignin concentration in fine roots underneath plant patches (black circles) and in bare soil (white circles) at each site across the aridity gradient and mean value + SE (bars) of each attribute at each microsite (bare soil: Bs; plant patch: Pp). Different lowercase letters indicate significant ( $P \leq 0.05$ ) differences among mean values of each attribute between microsites. ns: not significant.

or species may exert an important control on total litter quality (e.g., Aerts & Chapin, 2000; Lambers, Chapin & Pons, 2000). Water can strongly limit plant productivity and consequently litter production and litter quality in the most arid sites (Whitford, 2002). Litter decomposition can slow down at such sites, and recalcitrant litter of woody species may accumulate on the soil surface (Cromack, Todd & Monk, 1974; Boutton *et al.*, 1998). This in turn could have negative feedbacks on soil nutrient cycling and nutrient release to soil (Aerts & Chapin, 2000; Lambers, Chapin & Pons, 2000; Wardle, 2002; Carrera *et al.*, 2005; 2009), as observed in the driest portion of our study gradient. Moreover, increasing N concentration in grass leaf litter without a simultaneous increment of recalcitrant components could lead to an increase in grass leaf litter decay (Wardle, 2002; Vargas *et al.*, 2006), which would also account for the relative increase in shrub components in aboveground litter with increasing aridity. The increase of N concentration in leaf litter of grasses with increasing aridity could be explained by the fact that grasses display more mesophytic traits at arid than at humid Patagonian sites (Bertiller *et al.*, 2005). This is probably related to the fact that, at the shrubby communities, grasses preferentially

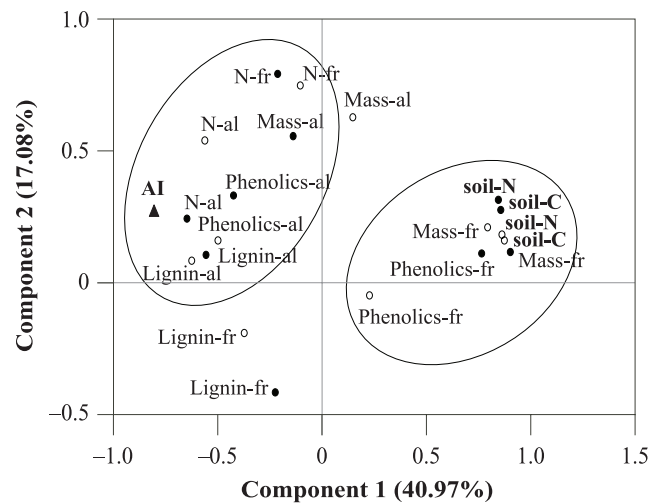


FIGURE 8. Principal component analysis of the correlation matrix of mass, N, soluble phenolics, and lignin concentrations in aboveground plant litter (al) and fine roots (fr), organic C and total N concentrations in soil (soil C and soil N, respectively), and aridity index (AI, black triangle) at plant patch (black circles) and in bare soil (white circles) microsites. Ovals indicate closest affinity among litter, upper fine roots, and soil traits and aridity index.



grow under or at the border of shrub canopies, which confer protection against biotic and abiotic adverse factors (Rebollo *et al.*, 2002; Bertiller & Ares, 2008).

In comparison with vegetation patches, bare soil microsites exhibited lower litter mass and fewer changes in litter traits across the aridity gradient. This was consistent with studies reporting stronger effects of the presence or absence of plant cover than of canopy composition on the spatial patterning of litter and soil attributes in ecosystems with patchy vegetation (Rostagno, del Valle & Videla, 1991; Zaady, Groffman & Shachak, 1996; Mazzarino *et al.*, 1998; Burke *et al.*, 1999; del Valle, Rosell & Bouza, 1999; Tongway & Ludwig, 2005; Carrera *et al.*, 2009). This could be explained by the low effect of plant canopies on neighbouring denuded areas and by the fact that bare soil was more exposed to wind and water erosion than the soil beneath plant patches (Zaady, Groffman & Shachak, 1996; Tongway & Ludwig, 2005). Accordingly, our results provide further evidence of the importance of maintaining patch canopies for ecosystem processes (Adler *et al.*, 2001).

Unlike aboveground plant litter, upper fine root mass declined but did not increase in recalcitrance with increasing aridity at both microsites. In contrast, soluble phenolics in fine roots decreased with increasing aridity at plant patch microsites, indicating that fine roots may have lower decomposability and may be better chemically defended, probably against herbivores (Stevens & Jones, 2006; Meier, Keyserling & Bowman, 2009), in humid sites than in arid sites. Reduced fine root mass with increased aridity was probably the consequence of the reduction of plant cover and the replacement of grasses by shrubs across the aridity gradient (Jackson, Mooney & Schulze, 1997; Gill & Jackson, 2000). Jackson *et al.* (2000) reported a larger contribution of grasses (75%) than shrubs (45%) to the cumulative root biomass in the top soil (30 cm depth). In general, fine roots have high annual turnover and negligible N retranslocation during senescence (Jackson, Mooney & Schulze, 1997; Gill & Jackson, 2000), thus influencing the input of C and N into soil. Moreover, shrubs may have lower annual fine root turnover and thus less effect on soil N and C pools than grasses (Wilson, 1998; Gill & Jackson, 2000). Accordingly, we found that fine root mass in the upper soil was the variable explaining the largest variance in soil organic C and N. This was consistent with many studies highlighting the importance of belowground mass as a source of soil organic C and nutrients in water-limited ecosystems (Jackson, Mooney & Schulze, 1997; Gill & Jackson, 2000; Hibbard *et al.*, 2001; Carrera *et al.*, 2007).

As reported in other studies (McNaughton, Banyikwa & McNaughton, 1998; Robinson *et al.*, 1999), upper fine root mass did not vary between microsites. However, our results did not support the idea of fine root proliferation in nutrient-rich soil microsites reported in other studies (Robinson *et al.*, 1999). Other factors, such as dryness under the plant canopy, could promote root growth in comparatively more humid bare soil microsites, explaining the lack of a patchy spatial distribution of fine roots in the upper soil (Robinson *et al.*, 1999; Bertiller *et al.*, 2002; Kröpft *et al.*, 2002; Bisigato *et al.*, 2009).

We conclude that the decrease in soil organic C and N across the aridity gradient could be the outcome of

different above- and belowground controls resulting from the replacement of grasses by shrubs. This replacement led to (1) an increase in aboveground litter recalcitrance due to an increased contribution of recalcitrant shrub litter components and a reduced contribution of low recalcitrant leaf litter of grasses, and (2) a decrease in upper fine root mass. Based on these changes, we suggest that litter quality could be the main control of soil fertility in terms of soil organic C and N from above ground, while the quantity of organic matter input to soil through fine root turnover could be the major control of soil fertility from below ground. However, belowground components could exert a relatively larger effect on soil fertility than aboveground components due to the strong relationship between upper fine root mass and soil organic C and N. These results also provide evidence of the effects that global climate change could have on plant distribution and soil resources over the long term. Predicted increases in temperatures in arid and semiarid ecosystems (Zhuguo & Congbin, 2003; Labraga & Villalba, 2009) could lead to the encroachment of woody plants (Wardle, 2002). This in turn could lead to a reduction in aboveground-litter quality and mass allocation to fine roots in the upper soil, with important consequences for C sequestration in plants and soil.

#### Acknowledgements

This research was funded by projects PICTs 08-20454 and 02-02192 BID 1728/OC-AR of the National Agency for Scientific and Technological Promotion. O. Frumento from the Oceanographic and Meteorological Research Unit of CENPAT-CONICET calculated the mean annual air temperature of each site using the CRU TS 2.1 data set.

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