Plant Soil (2008) 311:39–50
DOI 10.1007/s11104-008-9655-8

REGULAR ARTICLE

Leaf litterfall, fine-root production, and decomposition in shrublands with different canopy structure induced by grazing in the Patagonian Monte, Argentina

A. L. Carrera · M. B. Bertiller · C. Larreguy

Received: 22 November 2007 / Accepted: 14 May 2008 / Published online: 3 July 2008

Abstract Selective sheep grazing in the Patagonian Monte induces the reduction of total and perennial grass cover, species replacement within life forms, and the increase in dominance of long-lived evergreen woody plants with slow growth rates and high concentration of secondary compounds in leaves. We hypothesized that these changes in the canopy structure induced by sheep grazing will affect the mass, chemistry and decomposability of leaf litter and fine roots. We selected two sites in the Patagonian Monte, representative of ungrazed and grazed vegetation states. At each site, we assessed canopy structure (total cover and absolute and relative grass and shrub cover), monthly leaf litterfall, and fine-root biomass and production in the upper soil (15 cm). We also estimated the rates of mass, C, soluble phenolics, lignin and N decay in litterbags containing both leaf litter and fine roots of each site under field conditions during two consecutive years. The ungrazed site exhibited higher total plant cover, absolute and relative grass- and shrub-cover than the grazed one. Leaf litterfall was lower at the grazed site than at the ungrazed site. Fine-root production did not vary between sites. Leaf litter and fine root tissues had higher concentration of secondary compounds at the grazed than at the ungrazed site. However, fine roots showed lower mass and C decay than leaf litter, attributable to the predominant secondary compound (lignin and soluble phenolics, respectively). Leaf litter decomposed slower but released more N during decay at the ungrazed than at the grazed site, probably due to its low concentration of secondary compounds. We concluded that changes in canopy structure induced by grazing disturbance such as those explored in our study could reduce leaf litterfall mass and increase the concentration of secondary compounds of both leaf litter and fine roots leading to slow N release to soil during decay.

Keywords Fine root chemistry · Grass cover · Lignin · Litter chemistry · N · Shrub cover

Introduction

The production and decomposition of plant litter are key processes in carbon and nutrient cycling in most terrestrial ecosystems (Lambers et al. 1998). The main

Responsible Editor: Alfonso Escudero.

A. L. Carrera · M. B. Bertiller
Centro Nacional Patagónico (CONICET),
Boulevard Brown 2825, 9120 Puerto Madryn,
Chubut, Argentina

A. L. Carrera · M. B. Bertiller · C. Larreguy
Universidad Nacional de la Patagonia San Juan Bosco,
Boulevard Brown 3700, 9120, Puerto Madryn,
Chubut, Argentina

A. L. Carrera (✉)
CENPAT,
Boulevard Brown 2825, 9120 Puerto Madryn,
Chubut, Argentina
e-mail: unanalia@cenpat.edu.ar

controls of nutrient release from litter to soil are climate, soil organisms, and litter chemistry (Aerts and Chapin 2000). Climate affects decomposition through its effects on litter production, litter quality, and microbial activity. In most arid and semiarid environments, precipitation is the main climatic factor controlling these processes (Noy Meir 1973). Under similar climatic conditions, microbial activity, decomposition processes and nutrient release can be predicted from plant litter traits reflecting entire plant or organ physiological and biochemical adaptations to the environment (Lambers et al. 1998; Xu and Hirata 2005).

In arid and semiarid ecosystems, vegetation is dominated by shrubs and perennial grasses (Whitford 2002), but grazing disturbance may induce species replacement and the increase in cover of woody plants (Reynolds et al. 1997; Bertiller and Bisigato 1998). Shrubs usually produce thick green leaves with low N concentration and large amount of secondary compounds, such as lignin, tannins, or soluble phenolics, protecting leaves against desiccation, herbivores, pathogens, and radiation effects (Aerts and Chapin 2000; Carrera et al. 2005). In contrast, perennial grasses produce leaves of short lifespan, with low protection against abiotic factors and herbivores (Aerts and Chapin 2000; Carrera et al. 2000, 2005; Campanella and Bertiller 2008). Accordingly, plant changes induced by grazing could not only affect the quantity and chemistry (concentration of secondary compounds, N, etc.) of leaf litter but also fine root traits and subsequent decomposition rates and nutrient and C cycling (Fisher et al. 2006). Studies on the effects of structural and functional traits of fine roots of both plant life forms on ecosystem processes are scarce in arid and semiarid ecosystems despite evidence of large C and nutrient inputs to the soil from decaying fine-roots (Fernandez and Caldwell 1975; Jackson et al. 1997; Whitford 2002) and larger amount of secondary compounds in fine roots of shrubs relative to those of grasses (Mun and Whitford 1998; Rodríguez et al. 2007a).

In the Patagonian Monte, vegetation is dominated by shrubs and perennial grasses arranged in a patchy structure (Bertiller and Bisigato 1998). Sheep grazing was introduced at the beginning of the twentieth century and it is an important driver of ecosystem composition and spatial structure in this region (Bertiller et al. 2002; Ares et al. 2003). Selective sheep grazing induces the reduction of total and perennial grass cover, species replacement within life forms, and the increase in dominance of long-lived evergreen woody plants with slow growth rates and high concentration of secondary compounds in leaves and roots (Bisigato and Bertiller 1997; Bertiller and Bisigato 1998; Carrera et al. 2005; Rodriguez et al. 2007a; Campanella and Bertiller 2008). Accordingly, these changes could have important effects on annual leaf litterfall, fine-root production, and litter chemistry, and consequently on decomposition and nutrient cycling. However, few studies have assessed simultaneously both leaf litterfall and upper-soil fine-root production and their effects on decomposition processes in arid and semiarid ecosystems, particularly, of the southern hemisphere (Moretto et al. 2001). We assessed the effects of changes in canopy structure (total plant cover, absolute and relative grass- and shrub-cover, and species cover) induced by grazing on leaf litterfall, upper-soil fine root production, and their decomposition rates in two sites (ungrazed vs grazed site) representative of the Patagonian Monte, Argentina. We hypothesized that changes in canopy structure induced by sheep grazing (reduction of total and perennial grass cover, species replacement within life forms, and an increase in dominance of long-lived evergreen woody plants with slow growth rates and high concentration of secondary compounds in leaves) will affect the mass, chemistry and decomposability of leaf litter and fine roots. We predicted: (1) lower leaf litterfall and upper fine root production (0–15 cm depth) due to the lower total plant cover at the grazed than at the ungrazed site; (2) increased concentrations of N, soluble phenolics, and lignin in leaf litter and fine roots due to higher shrub relative to grass contribution at the grazed than at the ungrazed site, and (3) lower mass loss and N release to soil during leaf litter and fine-root decay due to increased soluble phenolics and lignin concentrations in these tissues at the grazed than at the ungrazed site.

Materials and methods

Study area

We selected a study area located in the southern portion of the Monte Phytogeographic Province, Argentina (Patagonian Monte), 40 km west of Puerto

Madryn (42°39′S, 65°23′W, 115 m a.s.l). The mean annual temperature is 13.7°C and the mean annual precipitation is 235.9 mm (22-year average, CENPAT 2006). Soils are a complex of Typic Petrocalcids–Typic Haplocalcids (Del Valle 1998; Soil Survey Staff 1998). Vegetation corresponds to the shrubland of *Larrea divaricata* Cav. and *Stipa* spp. (Cabrera 1976; Soriano 1950) with low canopy cover (< 60% of the soil), and a random patchy structure (Bisigato and Bertiller 1997; Mazzarino et al. 1998). We selected two contiguous sites of about 2 ha each representative of conserved (ungrazed site) and disturbed (grazed site) vegetation states in ecosystems grazed by sheep of the Patagonian Monte (Bisigato and Bertiller 1997; Bertiller et al. 2002). The ungrazed site has been protected from large domestic herbivores since 1993 while the grazed site has been submitted to sheep grazing since the beginning of the last century with a stocking rate of ca. 0.14 sheep ha^{-1}. During the study period, annual precipitation was 162.7 mm and 192.5 mm for the periods July–June 2004-2005 and 2005-2006, respectively (CENPAT 2006).

Canopy structure and soil moisture at the study sites

Total and species cover was assessed at six randomly located 25-m linear transects at each site by the line intercept method (Mueller-Dombois and Ellenberg 1974) in autumn 2006. We further calculated the absolute and relative shrub and grass cover. We assessed monthly gravimetric soil moisture by extracting 20 soil cores (5.5 cm diameter and 15 cm depth) from random locations per site during the period June 2004–August 2006.

Annual leaf litterfall and fine-root production

We assessed monthly leaf litterfall at 10 randomly located litter traps (0.50×0.25 ×0.10 m) at each site during the period July 2004–June 2006. The collected leaf litterfall was cleaned of attached soil particles with a brush and separated into the two dominant plant life forms (grasses and shrubs), then dried at 60°C for 48 h and weighed. We collected 20 soil cores (5.5 cm diameter and 15 cm depth) from random locations within each site at monthly intervals during the period June 2004–June 2006. Fine roots (< 2 mm diameter) were separated from the soil cores, briefly washed in tap water to remove adhered soil particles, dried at 60°C for 48 h and weighed. We estimated the annual mass of leaf litterfall as the sum of the litterfall mass collected monthly during the two 12-month periods: July 2004–June 2005 (year 1) and July 2005–June 2006 (year 2). We estimated annual fine-root production as the sum of the significant ($P \leq 0.05$) positive increments of fine-root biomass between consecutive sampling months during each year (Defossé and Bertiller 1991; Lauenroth 2000). The sequential soil core method may lead to some underestimation in fine-root production (Makkonen and Helmisaari 1999), but it is one of the most widely used because it estimates directly fine-root biomass (Lauenroth 2000). Furthermore, because this method is so widely used, it allows comparisons between root studies across the world (Lauenroth 2000; Hertel and Leuschner 2002; Son and Hwang 2003).

Litterbag decomposition experiment and chemistry of leaf litter and fine roots

We collected leaf litter accumulated on the soil at 120 randomly selected plots (0.50×0.25 m) from an area of about 10,000 m^2 at each site during the period March–June 2004. The leaf litter collected was cleaned of attached soil particles with a brush, pooled into one sample per site, homogenized by mixing, and dried at 60°C for 48 h. After litter removal, we extracted the upper soil (15 cm depth) of each plot at each site. Fine roots (< 2 mm diameter) were separated from the soil of each plot, briefly washed in tap water to remove adhered soil particles, dried at 60°C during 48 h, pooled into one sample per site and homogenized by mixing. These fine-root samples included a mixture of both live and senesced fine-roots, due to the extreme difficulty of recognizing and separating live and dead fine roots (Ostertag and Hobbie 1999; Robinson et al. 1999; Moretto et al. 2001). The inclusion of a mixture of live and senesced roots in the litterbags of our experiment could lead to some overestimation in decomposition rates of fine roots. However, decomposition rates of mixed roots could resemble those of senesced roots due to the high turnover of fine roots and the negligible N retranslocation during fine-root senescence (Ostertag and Hobbie 1999; Gill and Jackson 2000; Moretto et al. 2001; Silver and Miya 2001).

For this experiment, we selected closed litterbags (0.3 mm mesh, 5 cm diameter) allowing for mostly microbial decay. We constructed 168 litterbags per site containing 1 g of leaf litter each obtained from the pooled and homogenized leaf-litter mass collected at the respective site. Another 168 litterbags per site were filled with 1 g of fine roots each obtained from the pooled and homogenized fine roots collected at the respective site. We randomly selected 72 bare soil and 96 canopy soil microsites at each site in the field. In August 2004, we placed one litterbag containing leaf litter and other with fine roots at each microsite. Litterbags containing leaf litter were located on the soil surface after the removal of the litter deposited on the soil, and litterbags containing fine roots were buried at 5 cm depth. We randomly collected one set of seven litterbags (three bare soil and four canopy soil microsites) per biomass type (leaf litter or fine roots) and site at monthly intervals during the period September 2004–August 2006. After collection, litterbags were cleaned of attached soil particles with a brush and the leaf litter and the fine roots from each litterbag were oven-dried at 60°C to constant weight and weighed to determine the remaining mass. One litterbag of each biomass type per microsite and date was ashed at 550°C to correct the mass remaining at each litterbag for residual attached soil particles. We expressed the mass changes per litterbag on an ash-free dry mass basis.

We assessed the chemical composition of the pooled and homogenized samples of leaf litter and fine roots in three sub-samples of each site before the litterbag decomposition experiment and in three litterbags per site after 6, 12, 18 and 24 months of in situ decomposition. We measured the concentrations of C by dry digestion at 550°C (Schlesinger and Hasey 1981), soluble phenolics by the Folin-Ciocalteu method with tannic acid as standard (Waterman and Mole 1994), cellulose and lignin by the acid-detergent digestion technique (Van Soest 1963), and total N by semi-micro Kjeldahl (Coombs et al. 1985). All chemical traits were expressed per unit free-ash mass.

Statistical analyses

We used ANOVA to test for significant differences in: (1) total, shrub, and grass cover between sites; (2) annual leaf litter and fine root production between sites and years; and (3) chemical composition of leaf litter and fine roots between sites. In (2) we included site as fixed factor and year as random factor. In those cases in which assumptions of ANOVA were not met, variables were logarithmic transformed (Sokal and Rohlf 1981). We used a simple negative exponential model to assess decay rate (k) of dry mass, C-, soluble phenolics-, lignin-, and N-mass during the 24-month incubation period (Swift et al. 1979) as follows:

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

where y is the dry mass of leaf litter or fine roots remaining in litterbags at time t (month), a is the initial mass, and k is the decay rate. The significance of the differences in mean decay rate (k) of leaf litter and fine roots between sites and microsites was evaluated by Student *t*-test (Zar 1986). Unless otherwise noted, the level of significance throughout this study was $P \leq 0.05$. All statistical analyses were performed with SPSS 7.0 (Norusis 1997).

Results

Canopy structure and soil moisture at the study sites

Total, shrub, and grass covers were higher at the ungrazed than at the grazed site (Fig. 1a). Shrub cover was higher than grass cover ($F_{1,\ 24}=28.08$, $P<0.001$) at both study sites but the relative cover of shrubs was higher at the grazed than at the ungrazed site ($F_{1,\ 12}=28.43$, $P<0.001$). The values of canopy cover of all grass species and 12 shrub species were lower at the grazed than at the ungrazed site (Fig. 1b). Seven shrub species increased their cover at the grazed relative to the ungrazed site, but this increase did not compensate the decrease in cover of the other shrub species. Species composition was similar between both sites. Only *Prosopidastrum globosum* and *Hoffmanseggia trifoliata* were exclusively found at the ungrazed site. Soil moisture did not vary between sites ($F_{1,\ 960}=1.40$, $P=0.25$) and showed the largest values in autumn-winter (Fig. 2).

Annual leaf litterfall and fine root production

Annual leaf litterfall was higher at the ungrazed than at the grazed site (49.8 vs 30.6 g m^{-2} $year^{-1}$, respectively; $F_{1,\ 480}=189.18$, $P=0.046$), and did not differ between years ($F_{1,\ 480}=0.04$, $P=0.88$). The

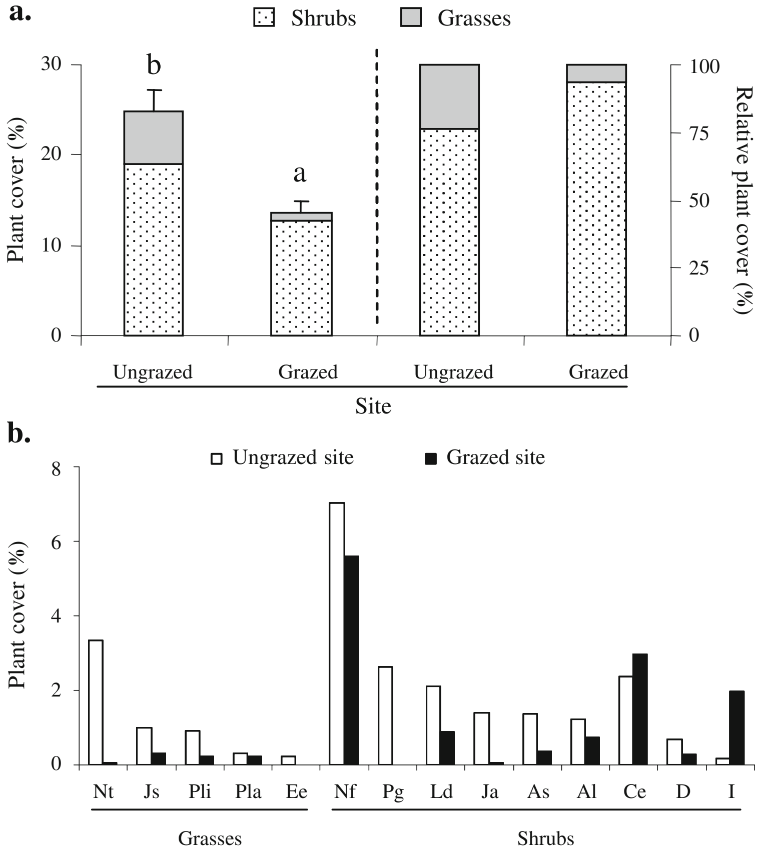


Fig. 1 **a** Mean shrub and grass cover (%) and their relative contribution to the total aboveground plant-cover at each sampling site. *Vertical lines* indicate one standard error of the total plant cover at each site. Different *lowercase letters* indicate significant differences in total plant cover between the ungrazed and the grazed site. **b** Cover of shrub and grass species at ungrazed and grazed sites. *Ns Nassauvia fuegiana* (Speg.) Cabrera, *Pg Prosopidastrum globosum* (Gill. ex Hook. & Arn.) Burkart, *Ld Larrea divaricata*, *Ja Junellia alatocarpa* (Tronc.) Moldenke, *As Acantholippia seriphioides* (A. Gray) Mold., *Al Atriplex lampa* Gill. Ex Moq., *Ce Chuquiraga erinacea* (Don) Ezcurra, *Nt Nassella tenuis* (Phil.) Barkworth, *Js Jarava speciosa* (Trin. and Rupr.) Peñailillo, *Pli Poa ligularis* Nees ex Steud, *Pla Poa lanuginosa* Poiret ap. Lamarck, *Ee Elymus erianthus* Phil.). *D* and *I* represent the total cover of other plant species with less than 1% of individual cover which decrease (*Lycium chilense* Miers ex Bert., *Boungainvillea spinosa* (Cav.) Heimerl, *Tetraglochin caespitosum* Phil., *Baccharis megapotamica* Speg., *Hoffmanseggia erecta* Philipp., *Hoffmanseggia trifoliata* Cav.) and increase their cover (*Junellia seriphioides* (Gillies and Hook) Mold., *Schinus johnstonii* Barkley, *Larrea nitida* Cav., *Aster haplopappus* (Remy) Kuntze, *Chuquiraga avellanedae* Lorentz, *Prosopis alpataco* Phil.) in the grazed relative to the ungrazed site, respectively

contribution of the different life forms to total leaf litter production differed between sites. Grasses and shrubs contributed with similar mass to annual leaf litterfall at the ungrazed site (26.1 and 23.7 g m^{-2} year^{-1}, respectively) but shrubs contributed with higher mass than grasses to annual leaf litterfall at the grazed site (26.3 and 4.3 g m^{-2} year^{-1}, respectively). Annual fine root production did not differ between the ungrazed and the grazed site (189.8 and 253.4 g m^{-2} year^{-1}, respectively; $F_{1,\ 480}$=2.78, P=0.34), or years ($F_{1,\ 480}$=1.71, P=0.42).

Chemistry of leaf-litter and fine-root biomass

Leaf litter had lower concentrations of soluble phenolics, lignin and nitrogen and higher cellulose concentration and cellulose/N ratio at the ungrazed than at the grazed site, while C concentration as well as C/N, soluble phenolics/N, and lignin/N ratios did not vary between sites (Table 1). Fine roots had lower C, soluble phenolics, and lignin concentrations as well as lower soluble phenolics/N and lignin/N ratios at the ungrazed than at the grazed site. Cellulose and

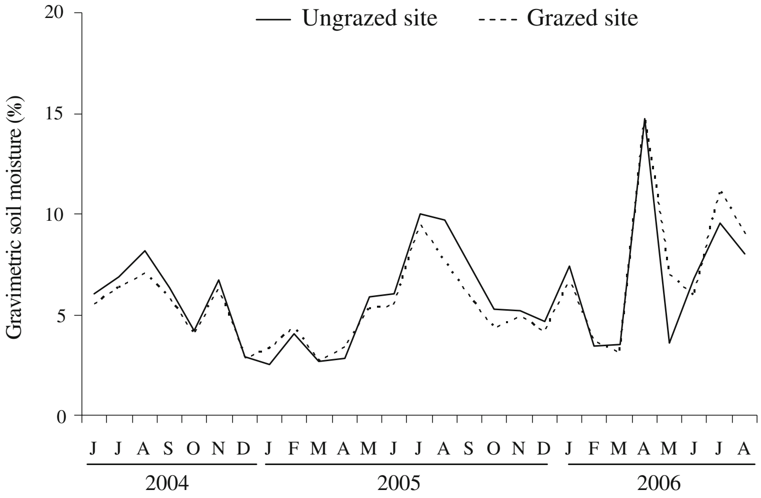


Fig. 2 Monthly gravimetric soil moisture (0–15 cm depth) at the ungrazed and the grazed site during the period June 2004–August 2006

N concentrations and C/N and cellulose/N ratios in fine roots did not vary between sites (Table 1).

Leaf-litter and fine-root decomposition in litterbags

Biomass and C-mass decay rate (*k*) of leaf litter were higher at the grazed than at the ungrazed site. Soluble phenolics- and lignin-mass decay rates of leaf litter did not differ between sites (Fig. 3a). However, N-mass decay of leaf litter was higher at the ungrazed than at the grazed site (Fig. 3a). Fine-root biomass and N-mass decay were higher at the ungrazed than at the grazed site (Fig. 3b). Carbon-, soluble phenolics- and lignin-mass decay of fine roots did not differ between sites (Fig. 3b). We did not find significant differences in leaf litter and fine root mass decay between canopy and bare soil microsites.

Relationship among mass (k_{mass}) and N (k_{N}) decay and initial chemistry traits of leaf litter and fine roots

The principal component analysis (PCA) showed a negative relationship between lignin or lignin/N ratio and decay rates on PCA axis 1 (56.5% of the total variance; Fig. 4). Accordingly, fine roots with high lignin concentration exhibited lower mass and N decay than leaf litter with low lignin concentration and lignin/N ratio in both the grazed and ungrazed site (see also Fig. 3 and Table 1). Additionally, PCA axis 2 (34.6% of the total variance) clustered high

Table 1 Mean values ± 1SE of initial concentrations of C (mg g^{-1}), soluble phenolics (mg g^{-1}), lignin (mg g^{-1}), cellulose (mg g^{-1}), N (mg g^{-1}), and C/N, soluble phenolics/ N, lignin/ N and cellulose/ N ratios in leaf litter and fine roots from each study site

	C	Soluble phenolics	Lignin	Cellulose	N	C/N	Soluble phenolics/N	Lignin/N	Cellulose/N
Leaf litter									
Ungrazed site	428.2±6.2 a	14.9±0.6 a	58.1±2.5 a	274.4±3.3 b	7.8±0.1 a	54.9±0.8 a	1.9±0.1 a	7.46±0.41 a	35.2±0.5 b
Grazed site	436.9±8.6 a	20.1±0.2 b	74.1±1.8 b	185.1±2.0 a	10.0±0.4 b	44.3±4.1 a	2.0±0.2 a	7.50±0.58 a	18.7±1.5 a
Fine roots									
Ungrazed site	417.0±4.5 a	1.0±0.1 a	115.1±3.3 a	184.1±10.2 a	8.4±0.1 a	49.7±1.2 a	0.12±0.01a	13.73±0.69 a	22.0±1.7 a
Grazed site	447.5±0.5 b	2.1±0.1 b	144.8±2.7 b	196.4±5.8 a	8.7±0.2 a	51.3±1.5 a	0.24±0.02 b	16.60±0.56 b	20.3±1.2 a

Different lowercase letters indicate significant differences between sites

Fig. 3 Mean values ± 1SE of remaining: biomass, C-, soluble phenolics-, lignin-, and N-mass (*black circles*) of **a** leaf litter and **b** fine roots as a function of time and fitted simple negative exponential curve (*solid line*) for each study site. Different *lowercase letters* indicate significant differences in dry mass decay (k) between sites

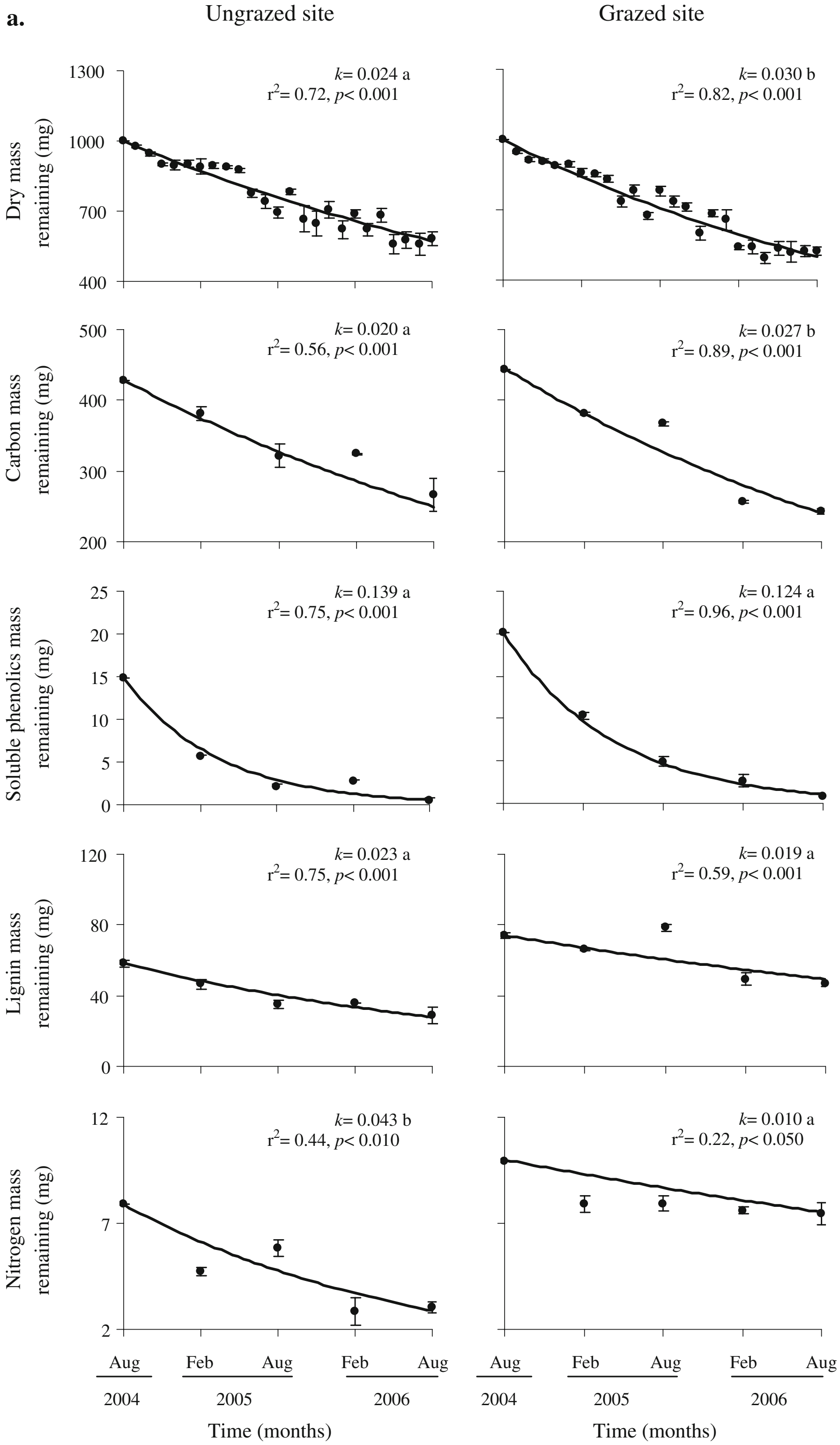


Fig. 3 (continued)

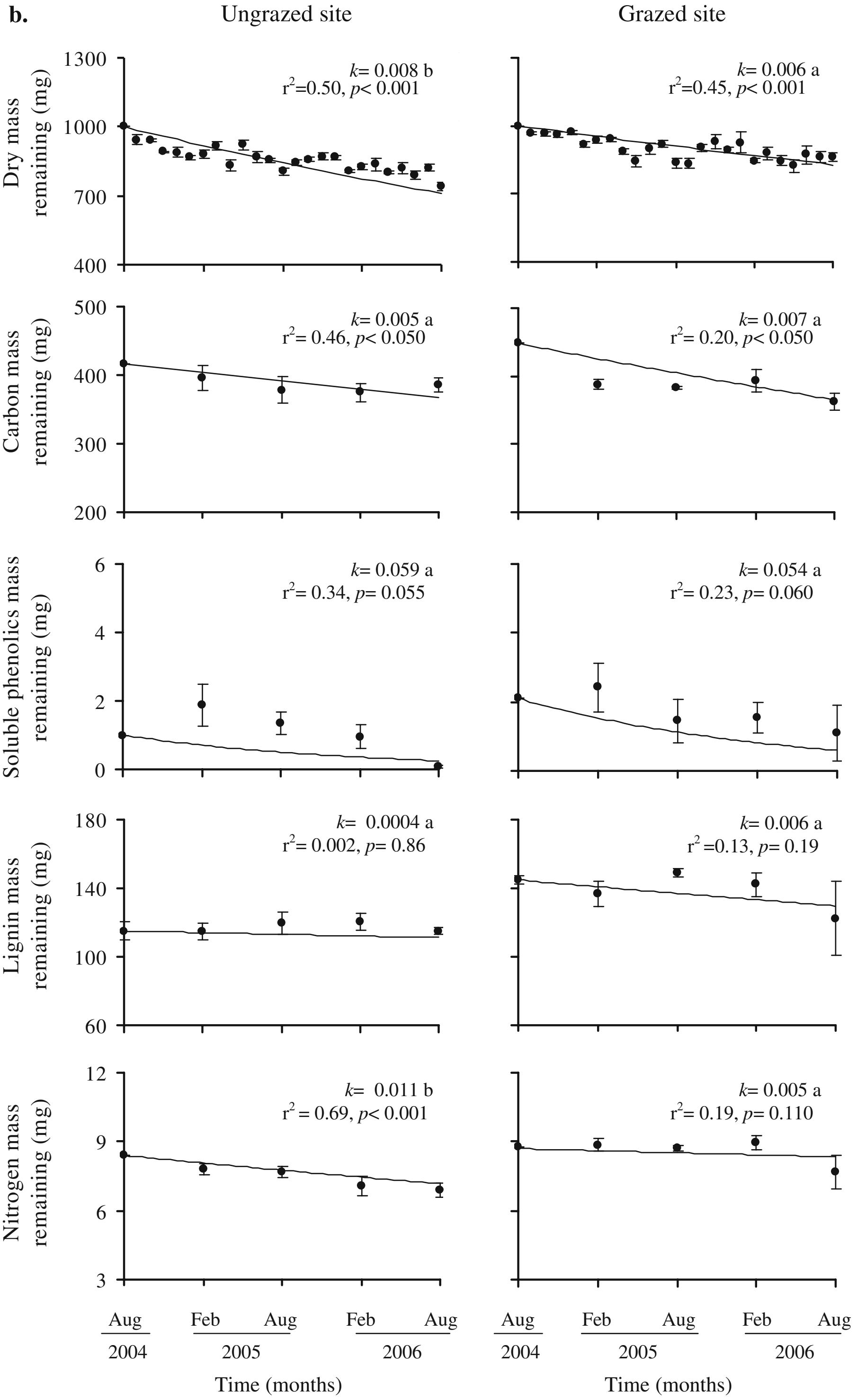
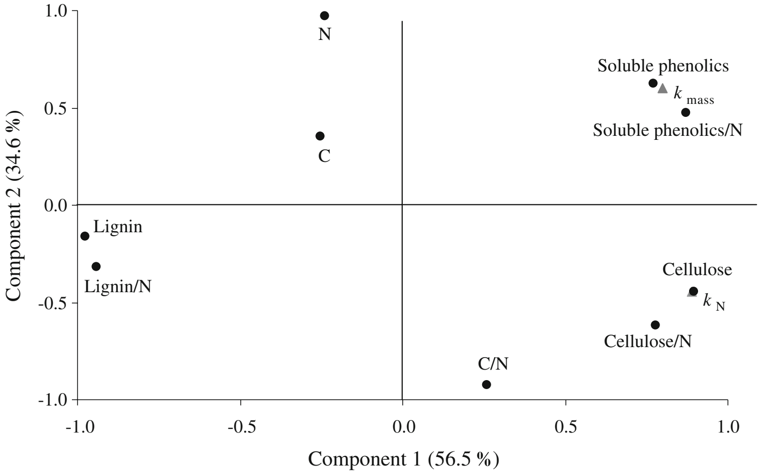


Fig. 4 Principal component analysis of the correlation matrix of fine roots and leaf litter mass (k_{mass}) and N (k_N) decay rates and initial fine root and leaf litter chemical traits (C, soluble phenolics, lignin, cellulose and N concentrations, and C/N, soluble–phenolics/N, lignin/N, and cellulose/N ratios)



mass decay with high concentration of soluble phenolics and soluble phenolics/N ratio (positive values) while high N decay was associated with high cellulose concentration, and high ratios of cellulose/N and C/N in decaying tissues (negative values; Fig. 4).

Discussion

Our findings partially supported the hypothesis of the study since differences in canopy structure induced by grazing were reflected in the mass, chemistry and decomposability of leaf litter, but did not account for differences in some of those attributes in fine roots. In agreement with our first prediction, annual leaf litterfall was lower at the grazed than at the ungrazed site. This is likely a consequence of the reduction in the aerial plant cover caused by grazing as reported in other studies (e.g., Schlesinger et al. 1990; Bisigato and Bertiller 1997; Bertiller and Bisigato 1998; Whitford 2002) but also may be the result of larger shrub than grass contribution to the canopy cover. Shrubs usually have longer leaf lifespan, lower leaf turnover, and lower leaf shedding than grasses (Whitford 2002; Carrera et al. 2000, 2003; Bertiller et al. 2006; Campanella and Bertiller 2008). In contrast to our first prediction, fine root production did not vary between sites. This finding is consistent with results of other study in the Patagonian Monte (Rodríguez et al. 2007a) indicating that the reduction of total and grass cover induced by grazing was not necessary associated with the reduction of fine root biomass in the upper soil layers during the wet season (autumn). This fact was related to the ability of shrub fine-roots to occupy the upper soil freed by fine roots of grasses in these ecosystems (Rodríguez et al. 2007b). Our findings further supported this evidence since the concentration of secondary compounds (lignin and soluble phenolics) in fine roots was higher at the grazed than at the ungrazed site and this could be attributable to larger proportion of shrub fine-roots (Rodríguez et al. 2007a).

Accordingly to our second prediction, the relative increase of shrubs in canopy cover at the grazed site was associated with increased concentration of N and secondary compounds in leaf litter and increased concentration of secondary compounds in fine roots. Changes in chemical traits of leaf litter and fine roots related to grazing disturbance could be associated with changes in plant community structure due to extinction or replacement of species with different physiological and biochemical adaptations to the environment (Wardle et al. 2002). But, also, changes in chemical traits in plant tissues could result from physiological changes at the individual plant level (Findlay et al. 1996) in response to herbivory or other environmental stresses (Holland and Detling 1990; Bryant and Reichart 1992; Wardle et al. 2002). Differences in tissue chemistry found in our study could not be attributed to species replacement since both the grazed and the ungrazed site showed nearly the same floristic list. We also discarded eventual changes in chemical traits of plant tissues at the individual level since studies in the area showed little variation within species in the chemistry of green and senesced leaves and litter among sites with different aridity or disturbance regimes at local or regional scales (Carrera el al. 2005; Moreno 2005; Campanella and Bertiller 2008). Thus, the most probable cause of chemistry variation in leaf litter and fine roots in our study is the variation in the relative contribution of grass and shrub species to the above-and below-ground biomass.

According to our third prediction, the increasing proportion of shrubs relative to grasses was related to reduced rate of N release from leaf litter and both mass and N decay from fine roots at the grazed site. This could be directly attributable to differences in tissue chemistry. Structural C pools such as lignin, cellulose and other cell wall components are resistant to enzymatic attack and microbial degradation (Melillo et al. 1982; Hoorens et al. 2003). Soluble phenolics could retain N in litter through the formation of phenol-protein complexes and/or inactivation of microbial enzymes (Aerts and Chapin 2000). Thus, both structural C and soluble phenolic compounds may interfere in decomposer metabolism, decelerating litter decay by microorganisms (Palm and Sanchez 1991; Lambers et al. 1998; Aerts and Chapin 2000). Leaf litter and fine roots had more compounds recalcitrant to degradation at the grazed than at the ungrazed site. However, in contrast to the third prediction, the increase in the proportion of shrubs relative to grasses in leaf litter did not reduce its mass decay at the grazed site. Leaf litter mass and C decay were higher at the grazed than at the ungrazed site despite higher concentrations of lignin and soluble phenolics. Probably, the high N concentration in leaf litter at the grazed site could enhance microbial activity and mass decay, but, at the same time, the breakdown of leaf litter with high concentration of phenolics could release precursors that immobilize N, reducing N release (Mun and Whitford 1998; Mutabaruka et al. 2007). Furthermore, other studies have reported that a substantial fraction of the carbon fixed in the aboveground plant biomass as lignin, cellulose and soluble phenolics could be lost through photodegradation by UV radiation (Schade et al. 1999; Austin and Vivanco 2006; Brandt et al. 2007; Parton et al. 2007). Photodegradation could account for high mass loss of leaf litter with high concentration of phenolics at the grazed area with low plant cover.

Finally, results on mass decay of leaf litter obtained in the ungrazed and the grazed site (0.024 and 0.030 month^{-1}, respectively) of the Patagonian Monte were within the range of variation reported for several plant species from other semiarid and arid ecosystems (0.015–0.600 month $^{-1}$; Koukoura et al. 2003; Arriaga and Maya 2007; Brandt et al. 2007). In contrast, values of mass decay of fine roots in the grazed and the ungrazed site (0.006 and 0.008 month^{-1}) were mostly lower than those reported for other ecosystems (0.008–0.0575 month^{-1}; Scheffer and Aerts 2000; Silver and Miya 2001).

We concluded that changes in canopy structure induced by grazing disturbance such as those explored in our study were related to reduced mass of leaf litterfall and increased concentration of secondary compounds of both leaf litterfall and fine roots. This in turn affected mass decay and N release to soil from decomposing tissues probably through the effect of tissue chemistry on microbial activity. Accordingly, we could conclude that changes in the relative contribution of life form or species to the total plant cover could have a significant impact on ecosystem processes in these environments.

Acknowledgements This research was funded by PICTs 08–11131, 08–6027, 08–20454 and 02192 BID 1201–1728/OC-AR of the National Agency for Scientific and Technological Promotion. Recognition is also given to Mr Fermín Sarasa who allowed access to the study area in Estancia “San Luis”. Claudia Sain helped with field work.

References

Aerts R, Chapin FS (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv Ecol Res 30:1–67

Ares JO, Bertiller MB, Bisigato A (2003) Modeling and measurement of structural changes at a landscape scale in dryland areas. Environ Model Assess 8:1–13

Arriaga L, Maya Y (2007) Spatial variability in decomposition rates in a desert scrub of Northwestern Mexico. Plant Ecol 189:213–225

Austin AT, Vivanco L (2006) Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. Nature 442:555–558

Bertiller MB, Bisigato AJ (1998) Vegetation dynamics under grazing disturbance. The state-and-transition model for the Patagonian steppes. Ecol Aust 8:191–199

Bertiller MB, Ares JO, Bisigato AJ (2002) Multi-scale indicators of land degradation in the Patagonian Monte, Argentina. Environ Manage 30:704–715

Bertiller MB, Mazzarino MJ, Carrera AL, Diehl P, Satti P, Gobbi M et al (2006) Leaf strategies and soil N across a regional humidity gradient in Patagonia. Oecologia 148:612–624

Bisigato AJ, Bertiller MB (1997) Grazing effects on patchy dryland vegetation in northern Patagonia. J Arid Environ 36:639–653

Brandt LA, King JY, Milchunas DG (2007) Effects of ultraviolet radiation on litter decomposition depend on precipitation and litter chemistry in a shortgrass steppe ecosystem. Glob Change Biol 13:2193–2205

Bryant JP, Reichart PB (1992) Controls over secondary metabolite production in arctic woody plants. In: Chapin FS, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J (eds) Arctic ecosystems in a changing climate: an ecophysiological perspective. Academic Press, New York, pp 377–390

Cabrera AL (1976) Las Regiones Fitogeográficas Argentinas. Enciclopedia Argentina de Agricultura, Jardinería y Horticultura. ACME, Buenos Aires

Campanella MV, Bertiller MB (2008) Plant phenology, leaf traits, and leaf litterfall of contrasting life forms in the arid Patagonian Monte, Argentina. J Veg Sci 19:75–85

Carrera AL, Sain CL, Bertiller MB (2000) Patterns of nitrogen conservation in shrubs and grasses in the Patagonian Monte, Argentina. Plant Soil 224:185–193

Carrera AL, Bertiller MB, Sain CL, Mazzarino MJ (2003) Relationship between plant nitrogen conservation strategies and the dynamics of soil nitrogen in the arid Patagonian Monte, Argentina. Plant Soil 255:595–604

Carrera AL, Vargas DN, Campanella MV, Bertiller MB, Sain CL, Mazzarino MJ (2005) Soil nitrogen in relation to quality and decomposability of plant litter in the Patagonian Monte, Argentina. Plant Ecol 181:139–151

CENPAT (2006) Estación meteorológica. Unidad de Investigación de Oceanografía y Meteorología-CENPAT-CONICET. http://www.centropatagonico.com

Coombs J, Hind G, Leegood RC, Tienszen LL, Vonshsk A (1985) Analytical techniques. In: Coombs J, Hall DO, Long SP, Scurlock JMO (eds) Techniques in bioproductivity and photosyntesis. Pergamon Press, Oxford, pp 219–228

Defossé GE, Bertiller MB (1991) Comparison of four methods of grassland productivity assessment based on *Festuca pallescens* phytomass data. J Environ Manage 44:199–203

Del Valle HF (1998) Patagonian soils: a regional synthesis. Ecol Aust 8:103–123

Fernandez OA, Caldwell MM (1975) Phenology and dynamics of root growth of three cool semi-desert shrubs under field conditions. J Ecol 63:703–714

Findlay S, Carreiro M, Krischik V, Jones C (1996) Effects of damage to living plants on leaf litter quality. Ecol Appl 6:269–275

Fisher DG, Hart SC, Rehill BJ, Lindroth RL, Keim P, Whitham TG (2006) Do high-tannin leaves require more roots? Oecologia 149:668–675

Gill RA, Jackson RB (2000) Global patterns of root turnover for terrestrial ecosystems. New Phytol 147:13–31

Hertel D, Leuschner C (2002) A comparison of four different fine root production estimates with ecosystem carbon balance data in a *Fagus–Quercus* mixed forest. Plant Soil 239:237–251

Holland EA, Detling JK (1990) Plant response to herbivory and belowground nitrogen cycling. Ecology 71:1040–1049

Hoorens B, Aerts R, Stroetenga M (2003) Does initial litter chemistry explain litter mixture effects on decomposition? Oecologia 442:578–586

Jackson RB, Mooney HA, Schulze ED (1997) A global budget for fine root biomass, surface area, and nutrient contents. Proc Natl Acad Sci USA 94:7362–7366

Koukoura Z, Mamolosb AP, Kalburtji KL (2003) Decomposition of dominant plant species litter in a semi-arid grassland. Appl Soil Ecol 23:13–23

Lambers H, Chapin FS, Pons T (1998) Plant physiological ecology. Springer, Berlin

Lauenroth WK (2000) Methods of estimating belowground net primary production. In: Sala OE, Jackson RB, Mooney HA, Howarth RW (eds) Methods in ecosystem science. Springer, Berlin, pp 58–71

Makkonen K, Helmisaari HS (1999) Assessing fine-root biomass and production in a Scots pine stand – comparison of soil core and root ingrowth core methods. Plant Soil 210:43–50

Mazzarino MJ, Bertiller MB, Sain CL, Satti P, Coronato F (1998) Soil nitrogen dynamics in northeastern Patagonia steppe under different precipitation regimes. Plant Soil 202:125–131

Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621–626

Moreno L (2005) Variación conjunta en los atributos morfológicos y funcionales de los órganos fotosintéticos de arbustos dominantes del norte de la Patagonia árida. Tesis de Licenciatura. Universidad Nacional de la Patagonia San Juan Bosco, Argentina

Moretto AS, Distel RA, Didoné NG (2001) Decomposition and nutrient dynamic of leaf litter and roots from palatable and unpalatable grasses in a semi-arid grassland. Appl Soil Ecol 18:31–37

Mueller-Dombois D, Ellenberg H (1974) Aims and methods of vegetation ecology. Wiley and Sons, New York

Mun HT, Whitford WG (1998) Changes in mass and chemistry of plant roots during long-term decomposition on a Chihuahuan Desert watershed. Biol Fertil Soils 26:16–22

Mutabaruka R, Hairiah K, Cadisch G (2007) Microbial degradation of hydrolysable and condensed tannin polyphenol–protein complexes in soils from different land-use histories. Soil Biol Biochem 39:1479–1492

Norusis MJ (1997) SPSS advanced statistics 7.5. SPSS, Chicago

Noy Meir I (1973) Desert ecosystems: Environment and producers. Annu Rev Ecol Syst 4:25–52

Ostertag R, Hobbie SE (1999) Early stages of root and leaf decomposition effects of nutrient availability. Oecologia 121:564–573

Palm CA, Sanchez PA (1991) Nitrogen release from the leaves of some tropical legumes as affected by their lignin and polyphenolic contents. Soil Biol Biochem 23:83–88

Parton W, Silver WL, Burke IC, Grassens L, Harmon ME, Currie WS et al (2007) Global-scale similarities in nitrogen release patterns during long-term decomposition. Science 315:361–364

Reynolds HL, Hungate BA, Chapin FS, D'Antonio CM (1997) Soil heterogeneity and plant competition in an annual grassland. Ecology 78:2076–2090

Robinson CH, Kirkham JB, Littlewood R (1999) Decomposition of root mixtures from high arctic plants: a microcosm study. Soil Biol Biochem 31:1101–1108

Rodríguez MV, Bertiller MB, Sain CL (2007a) Spatial patterns and chemical characteristics of root biomass in ecosystems of the Patagonian Monte disturbed by grazing. J Arid Environ 70:137–151

Rodríguez MV, Bertiller MB, Bisigato AJ (2007b) Are fine roots of both shrubs and perennial grasses able to occupy the upper soil layer? A study case in the arid Patagonian Monte of Argentina with non-seasonal precipitation. Plant Soil 300:281–288

Schade GW, Hofmann RM, Crutzen PJ (1999) CO emissions from degrading plant litter. Tellus 51:889–908

Scheffer RA, Aerts R (2000) Root decomposition and soil nutrient and carbon cycling in two temperate fen ecosystems. Oikos 91:541–549

Schlesinger WH, Hasey MM (1981) Decomposition of chaparral shrubs foliage: losses of organic and inorganic constituents from deciduous and evergreen leaves. Ecology 62:762–774

Schlesinger WH, Reynolds JF, Cunningham GL, Huenneke LF, Jarrell WM, Virginia RA et al (1990) Biological feedbacks in global desertification. Science 247:1043–1048

Silver WL, Miya RK (2001) Global patterns in root decomposition: comparisons of climate and litter quality effects. Oecologia 129:407–419

Soil Survey Staff (1998) Keys to soil taxonomy. USDA, Washington, DC, p 324

Sokal RR, Rohlf FJ (1981) Biometry. Freeman, San Francisco, C A, p 797

Son Y, Hwang JH (2003) Fine root biomass, production and turnover in a fertilized *Larix leptolepis* plantation in central Korea. Ecol Res 18:339–346

Soriano A (1950) La vegetación del Chubut. Rev Arg Agron 17:30–66

Swift MJ, Heal OW, Anderson JM (1979) Decomposition in Terrestrial Ecosystems. Blackwell, Cambridge, Mass.

Van Soest PJ (1963) Use of detergents in the analysis of fibrous feeds. II A rapid method for the determination of fibre and lignin. J Assoc Off Anal Chem 46:830–835

Wardle DA, Bonner KI, Barker GM (2002) Linkage between plant litter decomposition, litter quality, and vegetation responses to herbivores. Funct Ecol 16:585–595

Waterman PG, Mole S (1994) Extraction and chemical quantification. In: Waterman PG, Mole S (eds) Methods in ecology, analysis of phenolic plant metabolites. Blackwell, Cambridge, Mass., pp 66–103

Whitford W (2002) Decomposition and nutrient cycling. In: Whitford W (ed) Ecology of desert systems. Academic Press, San Diego, CA, pp 235–274

Xu X, Hirata E (2005) Decomposition patterns of leaf litter of seven common canopy species in a subtropical forest: N and P dynamics. Plant Soil 273:279–289

Zar JH (1986) Biostatistical analysis. Prince-Hall International, Englewood Cliffs, N.J., USA