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Cecilia Larreguy · Analía L. Carrera
Mónica B. Bertiller

Production and turnover rates of shallow fine roots in rangelands of the Patagonian Monte, Argentina

Abstract Selective sheep grazing in arid rangelands induces a decrease in total cover and grass cover and an increase in the dominance of shrubs. Both life forms differ in aboveground and belowground traits. We hypothesized that grazing disturbance leads to the replacement of grass by shrub fine roots in the upper soil, and this is reflected in changes in the seasonal dynamics of shallow fine roots at the community level. In two sites representative of non-grazed and grazed vegetation states in the Patagonian Monte, we assessed the canopy structure, and the fine root biomass, N concentration, production, and turnover during two consecutive years. The non-grazed site exhibited higher total, grass, and shrub cover than the grazed site. The grazed site had larger or equal fine root biomass than the non-grazed site except for late spring of the second year. This could be associated with the ability of shrubs to develop dimorphic-root systems occupying the soil freed by grasses at the grazed site, and with the larger contribution of grass than shrub fine roots in relation to an extraordinary precipitation event at the non-grazed site. This was consistent with the N concentration in fine roots. Fine root production was positively correlated to temperature at the grazed site and with precipitation at the non-grazed site. Fine root turnover did not differ between sites. Our results indicate that grazing leads to a shifting in the seasonality and main climatic controls of fine root production, while fine root turnover is mostly affected by changes in soil water conditions.

C. Larreguy (✉) · A. L. Carrera · M. B. Bertiller
Centro Nacional Patagónico-CENPAT (CONICET),
Boulevard Brown 2915, U9120ACV Puerto Madryn,
Chubut, Argentina
E-mail: larreguy@cenpat.edu.ar
Tel.: +54-2965-451024
Fax: +54-2965-451543

C. Larreguy · A. L. Carrera · M. B. Bertiller
Universidad Nacional de la Patagonia San Juan Bosco,
Boulevard Brown 3700, U9120ACV Puerto Madryn,
Chubut, Argentina

Introduction

Fine root production and turnover are key processes in relation to carbon and nutrient cycling in terrestrial ecosystems (Rao et al. 2001; Son and Hwang 2003). Fine-root production often exceeds shoot production (Dornbush et al. 2002), and therefore fine root decay may represent one of the major inputs of organic matter and nutrients to soil (Fernandez and Caldwell 1975; Jackson et al. 1997; Gill et al. 1999, Gill and Jackson 2000; Gordon and Robert 2000; Whitford 2002). Despite this, studies on fine root dynamics are scarce in terrestrial ecosystems (Gill and Jackson 2000; Nadelhoffer 2000; Zhao et al. 2009), and only a few addressed simultaneously the rates of production and turnover of shallow fine roots in arid ecosystems, particularly of the southern hemisphere.

In semiarid and arid ecosystems, biological activity is controlled by scarce, erratic, and discontinuous water inputs (Noy Meir 1973; BassiriRad et al. 1999). Vegetation has a patchy structure dominated by shrubs and perennial grasses alternating with areas of bare soil (Bertiller and Bisigato 1998; Aguiar and Sala 1999; Tongway and Ludwig 2005). Shrubs and perennial grasses differ in above- and belowground morphological traits related to resource acquisition and conservation and display phenological asynchronism (Sala et al. 1989; Bertiller et al. 1991; Whitford 2002). Shrubs produce long-lived tissues with large amounts of secondary compounds, such as lignin or soluble phenolics, protecting them against desiccation, herbivores, pathogens, etc. (Aerts and Chapin 2000). Species of this life form may have dimorphic or deep root systems and develop vegetative and reproductive growth independently from water inputs during spring-summer. In contrast, perennial grasses produce tissues of short lifespan, with low protection against abiotic factors and herbivores

(Asner and Beatty 1996; Aerts and Chapin 2000; Roumet et al. 2006) and are shallow-rooted species displaying vegetative and reproductive growth in autumn-late spring, coupled with precipitation inputs (Bertiller et al. 1991; Peláez et al. 1994; Gebauer et al. 2002; Snyder and Tartowski 2006; Rodríguez et al. 2007b; Campanella and Bertiller 2008). Moreover, these life forms may differ in the chemical composition of their fine roots, with shrubs showing higher N concentration in fine roots than perennial grasses (Kemp et al. 2003; Moretto and Distel 2003; Rodríguez et al. 2007a). These differences in N concentration in fine roots have been used in other studies to evaluate the contribution of different species and life forms to the total fine root biomass (Corre-Hellou and Crozat 2005; Rodríguez et al. 2007a).

In arid environments, belowground biomass could be four times higher than aboveground biomass (Jackson et al. 1997; Peek et al. 2004), and a high proportion of fine roots are located in the upper soil (Gill et al. 1999; Silva and Rego 2003). In general, plants tend to maximize resource acquisition balancing above- and belowground growth rates, nitrogen concentration, and longevity (Bloom et al. 1985). In this sense, fast-growing structures such as fine roots tend to have relatively high nitrogen concentrations and high turnover rates, whereas slow-growing structures have relatively low nitrogen concentrations and long life spans (Valverde-Barrantes et al. 2007). Accordingly, carbon and nutrient mass returned to soil through fine roots could be higher than the decomposition of aboveground litter since fine root growth and turnover are usually faster than those of other plant parts (Gill and Jackson 2000; Nadelhoffer 2000; Zhao et al. 2009).

Disturbance such as grazing usually alters the relative aboveground abundance and spatial distribution of grass and shrub species, and these changes might influence belowground biomass and C allocation patterns as well as C and nutrient cycles (Ludwig and Tongway 1995; Gill and Jackson 2000; Snyman 2009; Zhao et al. 2009). Our understanding of the effects of grazing on belowground components and processes and their eventual consequences on C and nutrient cycling in arid ecosystems is still scarce. Previous studies in the Patagonian Monte of Argentina reported that total and perennial grass aboveground cover decreased, but fine root biomass did not change across grazing gradients (Rodríguez et al. 2007a). This was associated with the ability of shrubs to allocate fine roots in the upper soil compensating the eventual reduction of perennial grass fine roots induced by grazing (Rodríguez et al. 2007b). Also changes in fine root chemistry, such as increased concentration of N, lignin, and soluble phenolics, were associated with grazing (Rodríguez et al. 2007a; Carrera et al. 2008). Based on this preliminary evidence, our objective was to evaluate the production and turnover rates of shallow fine roots in rangelands of the Patagonian Monte, Argentina. We hypothesized that grazing disturbance leads to the replacement of perennial grass fine roots by shrub fine roots (< 2 mm diameter) in the

upper soil, and this is reflected in changes in the seasonal dynamics of shallow fine roots (0–15 cm soil depth) at the community level. We predicted that (1) grazing would lead to the concentration of fine root production in summer while fine root production would be concentrated in autumn-late spring in non-grazed vegetation states and (2) fine root turnover would be higher in non-grazed than grazed vegetation states.

Materials and methods

Study area

The study area is located in the northeastern region of the Chubut Province (Argentina), 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, http://www.cenpat.edu.ar). Precipitation is slightly concentrated in autumn–winter or evenly distributed during the year (Coronato and Bertiller 1997). Vegetation is representative of the shrubland of *Larrea divaricata* Cav. and *Stipa* spp., characteristic of the southern portion of the Monte Phytogeographic Province, Argentina (Soriano 1950; Cabrera 1976). Both Typic Petrocalcids and Typic Haplocalcids soils are present in the area (del Valle 1998; Soil Survey Staff 1998). Sheep have been grazed in the area since the beginning of the last century (Ares et al. 1990). The study was conducted within a typical paddock of about 2,500 ha with a single watering point in a corner, subjected to continuous grazing all year round with a historical stocking rate of ca. 0.14 sheep ha^{-1} (Bertiller et al. 2002). Within this paddock, we selected a floristically homogeneous vegetation stand 600 m from the watering point. At this stand, we installed a 2 ha enclosure (excluding domestic herbivores) and selected an adjacent grazed site of about 2 ha in 1993 (Mazzarino et al. 1998; Bertiller et al. 2002). Based on sheep fecal counts (Bisigato and Bertiller 1997), the cover of perennial grasses (Rodríguez et al. 2007a), and remote sensing analyses (Ares et al. 2003), the grazed site is characterized by high grazing intensity (Bertiller et al. 2002). Our study was carried out in the enclosure and in the grazed site. Both areas are representative of conserved (non-grazed) and disturbed (grazed site) vegetation states of the Patagonian Monte (Bisigato and Bertiller 1997; Bertiller et al. 2002).

Characterization of study sites: climatic conditions, soil moisture, and canopy structure

Monthly air temperature and monthly precipitation from July 2004 to June 2006 were obtained from a weather station located 40 km from the study area (http://www.cenpat.edu.ar). We assessed the gravimetric soil moisture at monthly intervals in 20 soil cores (5.5 cm diameter and 15 cm depth) randomly extracted

at each site during the study period (July 2004–June 2006). We recorded the total plant cover and the absolute and relative shrub and perennial grass cover along six randomly located 25-m linear transects by the line intercept method (Mueller-Dombois and Ellenberg 1974) at each sampling site.

Root biomass and annual and seasonal fine root production and turnover rate

During the period July 2004–June 2006, we randomly collected 20 soil cores (5.5 cm diameter and 15 cm depth) per site at monthly intervals. Fine (< 2 mm diameter) and coarse (> 2 mm diameter) roots 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 accumulated fine root production as the sum of the significant ($p < 0.05$) positive increments of fine root biomass between consecutive sampling months (Defossé and Bertiller 1991; Lauenroth 2000) during both years: July 2004–June 2005 (year 1) and July 2005–June 2006 (year 2). Similarly, we calculated the accumulated fine root decay as the sum of the significant ($p < 0.05$) decrements of fine root biomass between consecutive sampling months minus the sum of the significant increases in coarse root biomass during both years (Defossé and Bertiller 1991; Lauenroth 2000). Then, we calculated the production of fine roots by season at each site and year. Annual fine root turnover rate (year^{-1}) was calculated according to Gill and Jackson (2000) as follows:

$$\text{Annual fine root turnover rate} = \frac{\text{annual fine root production}}{\text{maximum fine root standing biomass}}$$

Nitrogen concentration in fine roots

We assessed the N concentration of fine roots by semi-micro Kjeldahl (Coombs et al. 1985) in five randomly selected subsamples at each site and season in both sampling years.

Statistical analyses

We used ANOVA to test for significant differences in (1) total and absolute and relative shrub and perennial grass cover between sites; (2) fine and coarse root biomass between sites, months, and years, (3) soil gravimetric moisture, fine root production, and N concentration in fine roots between sites, seasons, and years, (4) annual fine root turnover rate and accumulated fine root production and decay between sites. Variables were logarithmically transformed in those cases in which assumptions of ANOVA were not met (Sokal and Rohlf

1981). These statistical analyses were performed with the statistical package SPSS 7.5 for Windows (Norusis 1997). We also evaluated the relationship among climatic factors (precipitation, temperature, and gravimetric soil moisture) and seasonal fine root production by detrended component analysis using PAST package (Hammer et al. 2001) and by correlation analysis. Unless otherwise noted, the level of significance throughout this study was $p \leq 0.05$.

Results

Characterization of study sites: climatic conditions, soil moisture, and canopy structure

Precipitation was 162.5 and 192.5 mm for year 1 (July 2004–June 2005), and year 2 (July 2005–June 2006), respectively. Precipitation events occurred throughout the year. The highest precipitation event occurred at the end of spring of the second year associated with high temperatures (Fig. 1a). Soil moisture did not differ between sites ($F_{1,960} = 1.40$, $p = 0.25$) but differed between years, being higher in year 2 than in year 1 ($F_{1,48} = 7.94$, $p < 0.01$). The largest values of soil moisture occurred in autumn and winter (Fig. 1b).

The non-grazed site exhibited higher total, shrub, and perennial grass covers than the grazed site (Fig. 2). At both sites shrub cover was higher than perennial grass cover ($F_{1,24} = 28.08$, $p < 0.001$), and the relative cover of shrubs was higher at the grazed than at the non-grazed site ($F_{1,12} = 28.43$, $p < 0.001$).
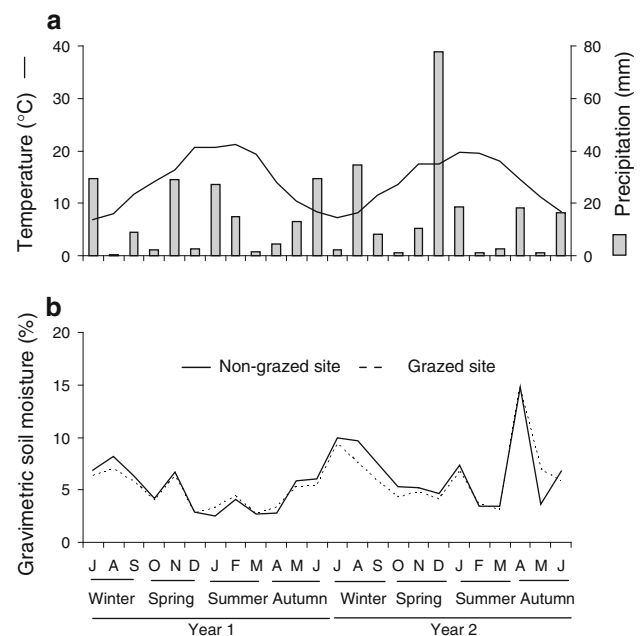

Fig. 1 a Mean monthly temperature and monthly precipitation in the study area, and b monthly gravimetric soil moisture (0–15 cm soil depth) at the non-grazed and grazed site during the period July 2004–June 2006
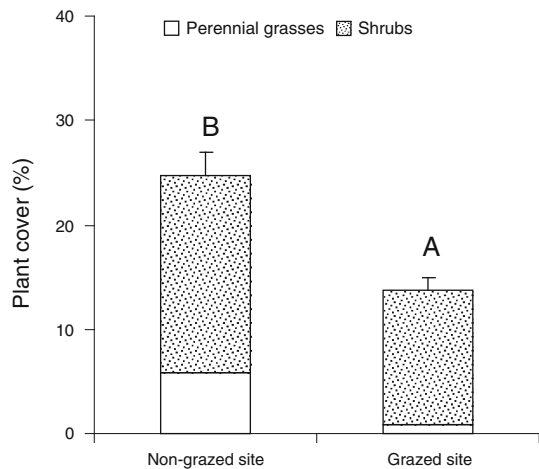
Fig. 2 Total, shrub, and perennial grass covers (%) at the non-grazed and grazed site. *Vertical lines* indicate one standard error of the total plant cover at each site. *Different capital letters* indicate significant differences in total plant cover between sites
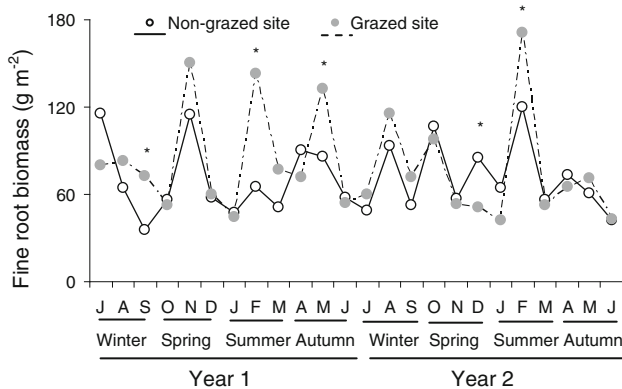

Fig. 3 Monthly fine root biomass at the non-grazed and the grazed site during the period July 2004–June 2006. The *asterisks* indicate significant differences in fine root biomass between sites for the corresponding month

Fine and coarse root biomass

Fine root biomass did not significantly differ between years ($F_{1,960} = 0.76$, $p = 0.54$) but differed between grazed and non-grazed sites depending on the sampling month (significant interaction site × sampling month: $F_{11,960} = 2.18$, $p = 0.01$). In general, the grazed site showed larger or equal monthly values of fine root biomass than the non-grazed one during years 1 and 2 except for December year 2 when fine root biomass was larger in the non-grazed than in the grazed site (Fig. 3). Monthly values of coarse root biomass (data not shown) did not significantly differ between sites, sampling years, or months ($F_{1,960} = 0.23$, $p = 0.71$; $F_{1,960} = 16.09$, $p = 0.16$; $F_{11,960} = 0.92$, $p = 0.52$, respectively). Fine root biomass was larger than coarse root biomass at both sites (77.3 and 77.2% at the non-grazed and grazed site, respectively).
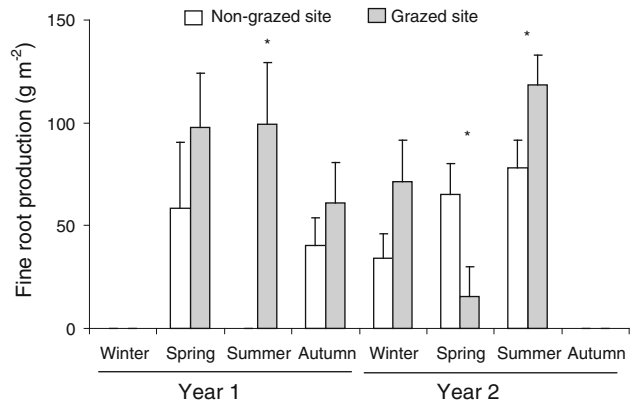

Fig. 4 Seasonal fine root production (g m^{-2}) at the non-grazed and grazed site during the period July 2004–June 2006. *Vertical lines* indicate one standard error of seasonal fine root production at each site and year. The *asterisks* indicate significant differences in fine root production between sites for the corresponding season

Seasonal fine root production

Seasonal fine root production differed between sites depending on the sampling season and year (significant effect of the interaction site × sampling season × year: $F_{1,320} = 6.64$, $p < 0.001$). In the first year, we did not observe fine root production during summer and winter at the non-grazed site and in winter at the grazed site. In the second year, fine root production was higher at the non-grazed than grazed site in spring while the reverse occurred in summer ($F_{1,40} = 5.45$, $p = 0.02$; $F_{1,40} = 4.42$, $p = 0.04$, respectively). We did not observe fine root production in autumn at any site in the second year (Fig. 4).

Accumulated fine root production and decay and annual turnover rates

Accumulated fine root production and decay did not differ between sites ($F_{1,40} = 0.05$, $p = 0.82$; $F_{1,40} = 3.12$, $p = 0.09$, respectively). Accumulated fine root production equaled fine root decay at the non-grazed and grazed site ($F_{1,40} = 1.2$, $p = 0.28$; $F_{1,40} = 0.71$, $p = 0.40$, respectively). In general, fine root decay lagged about 1–2 months behind fine root production (Fig. 5). Annual fine root turnover rate did not differ between sites ($F_{1,4} = 2.40$, $p = 0.26$, Fig. 5).

Nitrogen concentration

Nitrogen concentration in fine roots differed between sites depending on the season (significant effect of the interaction site × sampling season: $F_{1,80} = 3.36$, $p = 0.024$). In spring of the second year, the N concentration in fine roots was lower at the non-grazed than grazed site ($F_{1,10} = 8.19$, $p = 0.021$), while no differences were observed between sites in the other seasons (Fig. 6).
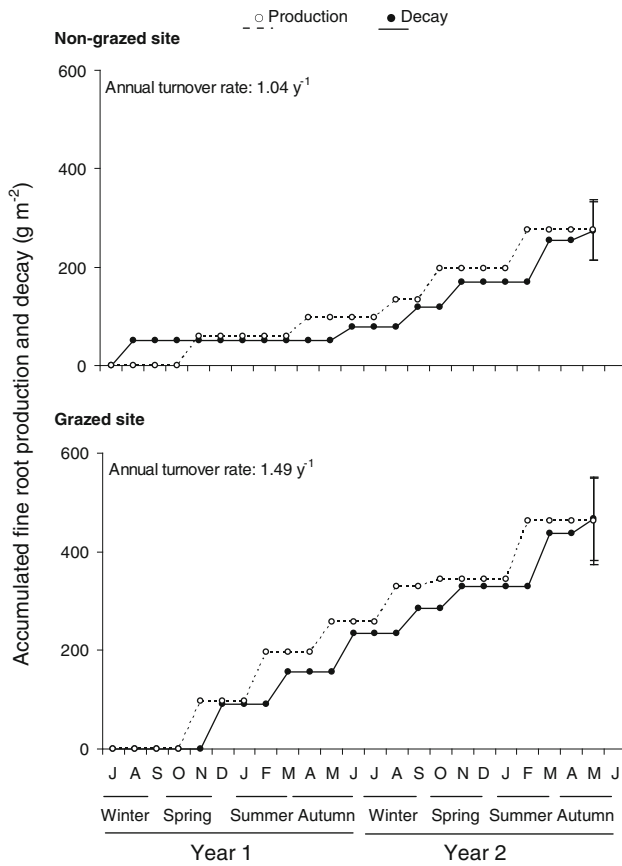
Fig. 5 Accumulated fine root production and decay (g m^{-2}) at the non-grazed and grazed site during the study period (July 2004–June 2006). *Vertical lines* indicate one standard error of annual fine root production and decay at each site. Annual turnover rates of fine roots are given in the *top left*

Relationship between climatic factors (precipitation, temperature, gravimetric soil moisture) and seasonal fine root production

The detrended correspondence analysis (DCA) and the correlation analysis showed that precipitation was the main climatic variable positively associated with production of fine roots at the non-grazed site (positive values in DCA axes 1 and 2, Fig. 7; and $r = 0.739$, $p = 0.05$, respectively). In contrast, the production of fine roots at the grazed site was associated with high temperature (negative values in DCA axis 2, Fig. 7; and $r = 0.731$, $p = 0.04$, respectively).

Discussion

Biomass and production of fine roots

Our findings supported our first prediction that changes in canopy structure (reduced total and perennial grass cover) induced by grazing disturbance are reflected in the seasonal dynamics of shallow fine roots at the community level. We found larger or equal fine root
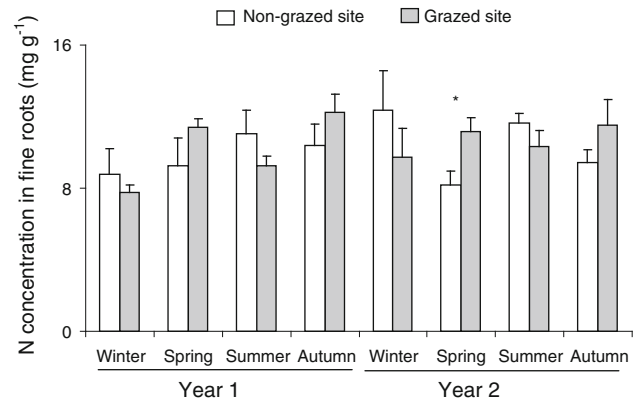

Fig. 6 Seasonal N concentration in fine roots (mg g^{-1}) at the non-grazed and grazed site during the study period (July 2004–June 2006). The *asterisk* indicates significant difference between sites in the corresponding season
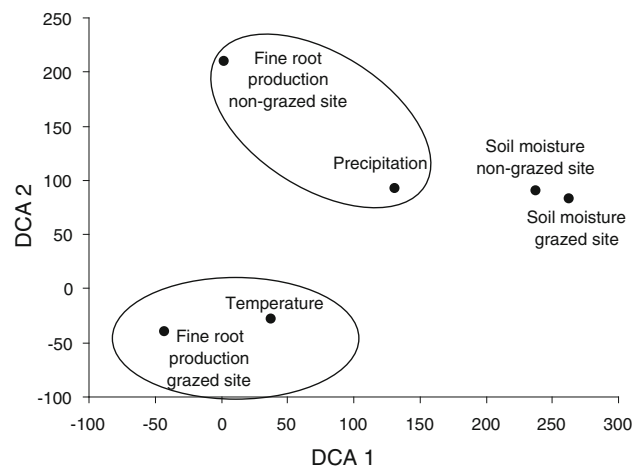

Fig. 7 Detrended correspondence analysis including seasonal values of precipitation, temperature, gravimetric soil moisture and fine root production at the non-grazed and grazed site

biomass in the grazed than in the non-grazed site during the 2-year observation period except for late spring (December) of the second year when the non-grazed site showed larger fine root biomass than the grazed site, in relation to an extraordinary precipitation event. These results are partially consistent with those reported in other studies indicating that fine root biomass is not reduced by grazing (Milchunas and Lauenroth 1989; Pucheta et al. 2004; Rodríguez et al. 2007a). Probably, our findings are associated with the ability of shrubs to develop opportunistic dimorphic-root systems that could eventually occupy the upper soil spaces freed by fine roots of perennial grasses at the grazed site (Peláez et al. 1994; Gebauer et al. 2002; Rodríguez et al. 2007a, b). Moreover, fine root biomass could be promoted by the input of nutrients through dung and urine at the grazed site (McNaughton et al. 1998; Johnson and Matchett 2001).

Our results on differences in the timing of shallow fine root production between sites could also support the

idea of differential fine root contribution of shrubs and perennial grasses to the upper soil under different disturbance regimes. Shrubs and perennial grasses show aboveground phenological asynchrony (Bertiller et al. 1991; Campanella and Bertiller 2008). Previous studies reported that shrubs may develop vegetative growth independently from water inputs during spring-summer or throughout the year. This was related to the fact that deep roots of shrubs with dimorphic systems could reach depths of more than 300 cm and take up water from more stable deep soil sources than perennial grasses with shallow root systems (Bertiller et al. 1991; Campanella and Bertiller 2008). Thus, shrubs may be able to produce shallow fine roots during summer periods coupled with aboveground vegetative activity and the occurrence of high temperatures and small precipitation events wetting the upper soil (Pregitzer et al. 2000; Huang et al. 2008; Zewdie et al. 2008). This is consistent with the high correlation found between fine root production and temperature at the grazed site. In contrast, perennial grasses with shallow root systems and aboveground inactivity during summer may not be able to use small precipitation events and to produce shallow fine roots during this dry season (Ehleringer et al. 1991; Dawson and Pate 1996; Casper and Jackson 1997; Rodríguez et al. 2007b). Our findings of higher fine root production at the non-grazed than at the grazed site during spring of the wettest year (year 2) could further support the idea that perennial grasses may use water pulses to produce fine roots only during the period of aboveground vegetative activity (Bertiller et al. 1991; Campanella and Bertiller 2008). This is in agreement with the high correlation between fine root production and precipitation found at the non-grazed site. The predominance of fine root growth of perennial grasses at the non-grazed site during spring could also be partially supported by lower values of N concentration in fine roots at this site than at the grazed site (Rodríguez et al. 2007a). These results provide some evidence of the effect of grazing on fine root tissue chemistry through the replacement of herbaceous by woody plants with eventual consequences on the rates of ecosystem processes such as decomposition, mineralization, and nutrient cycling as has been reported for other rangeland ecosystems (Jackson et al. 2000; Johnson and Matchett 2001).

However, our results could not explain why the production of fine roots during summer was lower in the non-grazed than in the grazed site despite a higher absolute cover of shrubs in the former. Probably, high perennial grass aboveground cover in the non-grazed site was associated with high occupancy of the upper soil by fine roots of perennial grasses preventing the proliferation of fine roots of shrubs in the upper soil. This would indicate some limited fine root carrying capacity of the upper soil as proposed by Rodríguez et al. (2007b) and also some spatial segregation of fine roots of different life forms as reported for plants growing in other arid and semiarid environments and/or in those ecosystems with low concentration of nutrient resources

(Schenk et al. 1999). Additionally, nutrient inputs through dung and urine could partially explain larger proliferation of shallow fine roots of shrubs in the grazed than in the non-grazed site (McNaughton et al. 1998; Nadelhoffer 2000; Johnson and Matchett 2001). These results highlighted that grazing led to a shifting in the main climatic controls of fine root production since, at the non-grazed site, precipitation is a main control in contrast to temperature in the grazed one. This is a relevant issue considering that intra- and interannual variation in precipitation is high in arid ecosystems and more variable than air temperature (Coronato and Bertiller 1997). Accordingly, intra- and interannual variation in fine root production in the non-grazed site could be higher than that at the grazed one.

Annual turnover rates of fine roots

In contrast to our second prediction, we did not find differences in annual fine root turnover between sites in spite of the expected differences in fine root chemistry due to the eventual differential contribution of fine roots of shrubs and perennial grasses (Rodríguez et al. 2007a, b; Carrera et al. 2008). Annual fine root decay equaled fine root production at both sites, and in general, an event of production was followed by another of decay. The lack of differences in annual fine root turnover between sites could be attributable to the prevalence of soil over root chemistry controls on fine root decay rates in the upper soil as found in other studies (Eissenstat and Yanai 1997; Pregitzer et al. 2000). In this sense, we did not find differences in soil moisture between sites, and the upper soil was submitted to a strong desiccation in summer of both years as reported for other areas of the Patagonian Monte (Coronato and Bertiller 1997). Accordingly, we suggest that the most probable control of turnover rates of fine roots in the upper soil at both sites was the strong soil desiccation. Annual turnover rates of fine roots in our study were around one (non-grazed site: 1.04 and grazed site: 1.49 $year^{-1}$) showing that shallow fine roots are highly ephemeral in the upper soil of both sites. These values were within the range of values reported for other shrublands (0.02–1.92 $year^{-1}$, Gill and Jackson 2000; Huang et al. 2008). However, it should be noted that there are few studies reporting rates of fine root turnover in arid shrublands, despite the importance of this process as a major pathway for C and nutrient return to the soil in terrestrial ecosystems (Gill and Jackson 2000; Norby and Jackson 2000; Jha and Mohapatra 2010).

Conclusion

Our findings partially support our predictions since grazing led to an increase in shallow fine root production

in summer but did not affect fine root turnover. As we hypothesized, increased fine root production under grazing in summer could be associated with enhanced root activity of shrubs maintaining leafing activity during the dry period with high temperatures. But this seems to be possible only in those soil spaces freed by fine roots of perennial grasses. Extraordinary high water inputs in spring promoted fine root production only under conditions of high cover of perennial grasses (non-grazed site). This is probably due to higher root growth of perennial grasses during the period of high aboveground vegetative activity of this life form and low root growth of shrubs when upper soil water is not limiting. These results highlighted that grazing led to a shifting in the seasonality (late spring in non-grazed vs. summer in grazed sites) and main climatic controls of fine root production (precipitation in non-grazed vs. temperature in grazed sites). Further, our results highlight that desiccation cycles in the upper soil could be more important than the chemistry of fine roots in relation to fine root turnover. These results have consequences for the conservation, dynamics, and management of these rangelands. Intra- and interannual variation in fine root production in the non-grazed site could be higher than that in the grazed one, and no differences in annual fine root turnover rates between sites would imply larger aboveground than belowground effects of changes induced by grazing on the input of organic matter and nutrients to soil. However, the consequences of the changes in the absolute or relative contribution of shrubs and perennial grasses to fine roots in the upper soil on ecosystem processes should be further explored.

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

Aguiar MR, Sala OE (1999) Patch structure, dynamics and implications for the functioning of arid ecosystems. TREE 14:273–277

Ares JO, Beeskow AM, Bertiller MB, Rostagno CM, Irisarri M, Anchorena J, Defossé G, Merino C (1990) Structural and dynamic characteristics of overgrazed lands of northern Patagonia, Argentina. In: Breymeyer A (ed) Managed grasslands. Elsevier Science, Amsterdam, pp 149–175

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

Asner GP, Beatty SW (1996) Effects of an African grass invasion on Hawaiian shrubland nitrogen biogeochemistry. Plant Soil 186:205–211

BassiriRad H, Tremmel DC, Virginia RA, Reynolds JF, de Soyza AG, Brunell MH (1999) Short-term patterns in water and nitrogen acquisition by two desert shrubs following a simulated summer rain. Plant Ecol 145:27–36

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

Bertiller MB, Beeskow AM, Coronato F (1991) Seasonal environmental variation and plant phenology in arid Patagonia (Argentina). J Arid Environ 21:1–11

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

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

Bloom AJ, Chapin SF III, Mooney HA (1985) Resource limitation in plants: an economic analogy. Annu Rev Ecol Syst 16:363–392

Cabrera AL (1976) Las regiones fitogeográficas Argentinas. Enciclopedia Argentina de agricultura y jardinería. 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, Bertiller MB, Larreguy C (2008) Leaf litterfall, fine-root production, and decomposition in shrublands with different canopy structure induced by grazing in the Patagonian Monte, Argentina. Plant Soil 311:39–50

Casper B, Jackson RB (1997) Plant competition underground. Annu Rev Ecol Syst 28:545–570

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

Coronato FR, Bertiller MB (1997) Climatic controls of soil moisture dynamics in an arid steppe of northern Patagonia, Argentina. Arid Soil Res Rehabil 11:277–288

Corre-Hellou G, Crozat Y (2005) Assessment of root system dynamics of species grown in mixtures under field conditions using herbicide injection and N15 natural abundance methods: a case study with pea, barley and mustard. Plant Soil 276:177–192

Dawson TE, Pate JS (1996) Seasonal water uptake and movement in root systems of Australian phraeatophytic plants of dimorphic root morphology: a stable isotope investigation. Oecologia 107:13–20

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

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

Dornbush ME, Isenhart TM, Raich JW (2002) Quantifying fine-root decomposition: an alternative to buried litterbags. Ecology 83:2985–2990

Ehleringer JR, Phillips SL, Schuste WFS, Sandquist DR (1991) Differential utilization of summer rains by desert plants: implications for competition and climate change. Oecologia 88:430–434

Eissenstat DM, Yanai RD (1997) The ecology of root lifespan. Adv Ecol Res 27:2–60

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

Gebauer RLE, Schwinning S, Ehleringer JR (2002) Interspecific competition and resource pulse utilization in cold desert community. Ecology 83:2602–2616

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

Gill R, Burke IC, Milchunas DG, Lauenroth WK (1999) Relationship between root biomass and soil organic matter pools in the shortgrass steppe of eastern Colorado. Ecosystems 2:226–236

Gordon WS, Robert BJ (2000) Nutrient concentration in fine roots. Ecology 81:275–280

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. Palaeontol Electron 4:9. http://palaeo-lectronica.org/2001_1/past/issue1_01.htm

Huang G, Zhao X, Su Y, Zhao H, Zhang T (2008) Vertical distribution, biomass, production and turnover of fine root along a topographical gradient in a sandy shrubland. Plant Soil 308:201–212

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

Jackson RB, Schenk HJ, Jobbagy EG, Canadell J, Colello GD, Dickinson RE, Field CB, Friedlingstein P, Heimann M, Hibbard K, Kicklighter DW, Kleidon A, Neilson RP, Parton WJ, Sala OE, Sykes MT (2000) Belowground consequences of vegetation change and their treatment in models. Ecol Appl 10:470–483

Jha P, Mohapatra KP (2010) Leaf litterfall, fine root production and turnover in four major tree species of the semi-arid region of India. Plant Soil 326:481–491

Johnson LC, Matchett JR (2001) Fire and grazing regulate below-ground processes in tallgrass prairie. Ecology 82:3377–3389

Kemp PR, Reynolds JF, Virginia RA, Whitford WG (2003) Decomposition of leaf and root litter of Chihuahuan desert shrubs: effects of three years of summer drought. J Arid Environ 53:51–59

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

Ludwig JA, Tongway DJ (1995) Desertification in Australia: an eye to grass roots and landscapes. Environ Monit Assess 37:231–237

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

McNaughton SJ, Banyikwa FF, McNaughton MM (1998) Root biomass and productivity in a grazing ecosystem: the Serengeti. Ecology 79:587–592

Milchunas DG, Lauenroth WK (1989) Three dimensional distribution of plant biomass in relation to grazing and topography in the shortgrass steppe. Oikos 55:82–86

Moretto AS, Distel RA (2003) Decomposition of and nutrient dynamics in leaf litter and roots of *Poa ligularis* and *Stipa gynerioides*. J Arid Environ 55:502–514

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

Nadelhoffer KJ (2000) The potential effects of nitrogen deposition on fine-root production in forest ecosystems. New Phytol 147:131–139

Norby RJ, Jackson RB (2000) Root dynamics and global change: seeking an ecosystem perspective. New Phytol 147:3–12

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

Peek MS, Leffler AJ, Ivans CY, Ryel RJ, Caldwell MM (2004) Fine root distribution and persistence under field conditions of three co-occurring Great Basin species of different life form. New Phytol 165:171–180

Peláez DV, Distel RA, Boó RM, Elia OR, Mayor MD (1994) Water relations between shrubs and grasses in semi-arid Argentina. J Arid Environ 27:71–78

Pregitzer KS, King JS, Burton AJ, Brown SE (2000) Responses of tree fine roots to temperature. New Phytol 147:105–115

Pucheta E, Bonamici I, Cabido M, Díaz S (2004) Below-ground biomass and productivity of a grazed site and a neighbouring ungrazed exclosure in a grassland in central Argentina. Austral Ecol 29:201–208

Rao IM, Plazas C, Ricaurte J (2001) Root turnover and nutrient cycling in native and introduced pastures in tropical savannas. In: Horst W, Schenk MK, Bürkert A, Claassen N, Flessa H, Frommer WB, Goldbach HE, Olfs HW, Römheld V, Sattelmacher B, Schmidhalter U, Schubert S, von Wirén N, Wittenmayer L (eds) Plant nutrition: food security and sustainability of agro-ecosystems. Springer, New York, pp 976–977

Rodríguez MV, Bertiller MB, Sain CL (2007a) Spatial patterns and chemical characteristic 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 case study in the arid Patagonian Monte with non-seasonal precipitation. Plant Soil 300:281–288

Roumet C, Urcelay C, Díaz S (2006) Suites of root traits differ between annual and perennial species growing in the field. New Phytol 170:357–368

Sala OE, Golluscio RA, Lauenroth WK, Soriano A (1989) Resource partitioning between shrubs and grasses in the Patagonian steppe. Oecologia 81:501–505

Schenk HJ, Callaway RM, Mahall BE (1999) Spatial root segregation: are plants territorial? Adv Ecol Res 28:146–180

Silva JS, Rego FC (2003) Root distribution of a Mediterranean shrubland in Portugal. Plant Soil 255:529–540

Snyder KA, Tartowski SL (2006) Multi-scale temporal variation in water availability: implications for vegetation dynamics in arid and semi-arid ecosystems. J Arid Environ 65:219–234

Snyman HA (2009) Root studies on grass species in a semi-arid South Africa along a degradation gradient. Agric Ecosyst Environ 130:100–108

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

Sokal RR, Rohlf FJ (1981) Biometry. Freeman, San Francisco

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

Tongway D, Ludwig JA (2005) Heterogeneity in arid and semiarid lands. In: Lovett GM, Jones CG, Turner MG, Weathers KC (eds) Ecosystem function in heterogeneous landscapes. Springer, New York, pp 189–205

Valverde-Barrantes OJ, Raich JW, Russell AE (2007) Fine-root mass, growth and nitrogen content for six tropical tree species. Plant Soil 290:357–370

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

Zewdie S, Fetene M, Olsson M (2008) Fine root vertical distribution and temporal dynamics in mature stands of two enset (*Ensete ventricosum* Welw Cheesman) clones. Plant Soil 305:227–236

Zhao W, Chen SP, Han XG, Lin GH (2009) Effects of long-term grazing on the morphological and functional traits of *Leymus chinensis* in the semiarid grassland of Inner Mongolia, China. Ecol Res 24:99–108