

# Spatial patterns and chemical characteristics of root biomass in ecosystems of the Patagonian Monte disturbed by grazing

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## Abstract

We hypothesized that the reduction in perennial-grass cover induced by grazing in shrublands would be associated with a reduction in fine-root biomass in the upper soil, an increase in the spatial heterogeneity of root biomass, and an increase in N and total phenolics concentrations in fine-root biomass. We analysed the spatial distribution of fine-, intermediate-, and thick-root biomass and the N and total phenolics concentrations in fine roots in sites with different aboveground-plant cover induced by grazing disturbance in the Patagonian Monte. We selected sampling sites varying in the distance to the watering point, the time since sheep grazing exclusion, and historical sheep stocking rates/paddock characteristics. Sites excluded from grazing and those far to the watering point showed the highest perennial-grass cover. Tall- and dwarf-shrub cover did not differ among sites. Fine-, intermediate-, and thick-root biomass and the chemistry of fine roots did not strongly differ among sites. At all sites, N concentration in fine roots was similar to that measured in tall shrubs while total phenolics concentration in fine roots fell within the range of that assessed for perennial grasses and tall shrubs. Results on N concentration would indicate that fine roots of tall shrubs are a main component of the bulk fine-root pool supporting previous evidence that life form shifts resulting from grazing has little effect on the root biomass and chemistry in the upper soil of rangelands.

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*Keywords:* Fine roots; Grazing disturbance; N concentration; Spatial heterogeneity; Total phenolics; Upper soil

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## 1. Introduction

Grazing may have an important impact on the structure and functioning of arid ecosystems (Ludwig and Tongway, 1995; Schlesinger et al., 1990). Most evidence is related to its negative effect on aboveground vegetative and reproductive plant biomass (Hutchings and John, 2003; Milchunas and Lauenroth, 1993), changes in the spatial patterning of plant canopies and soil resources (Adler et al., 2001; Bertiller and Coronato, 1994; Callaway, 1995; Mazzarino et al., 1998; Schlesinger et al., 1996), the reduction of soil seed banks (Bertiller, 1996, 1998; Mayor et al., 2003), the decrease in the availability of safe microsites for plant reestablishment (Bisigato, 2000; Oesterheld and Sala, 1990), and the invasion of woody plants (Milchunas and Lauenroth, 1993; Schlesinger et al., 1990). In contrast, the effect of grazing on the belowground plant community structure and function has been under explored in field studies (Hutchings and John, 2003; McNaughton et al., 1998).

Aboveground defoliation can modify the partitioning of assimilates between belowground and aboveground organs and consequently the root growth of defoliated plants (Belsky, 1986; Richards and Caldwell, 1985; Snyder and Williams, 2003). Water and nutrient acquisition by plants are mainly controlled by the size and shape of fine-root systems which are the most active concerning these processes (Casper and Jackson, 1997; Eissenstat, 1992; Hutchings and John, 2003; Schenk and Jackson, 2002). Changes in species composition induced by grazing disturbance, mainly those related to the reduction of herbaceous- and total-plant cover or the replacement of herbaceous by woody plants, may also result in changes in the horizontal and vertical distribution of root biomass in soil (Greenwood and Hutchinson, 1998; Hutchings and John, 2003; Jackson et al., 2000; Schenk and Jackson, 2002). A reduction in the density and cover of perennial grasses could be associated with a reduction of root biomass and activity in the upper-soil layers since herbaceous species tend to have shallower root systems than woody species (Gill and Burke, 1999; Schenk and Jackson, 2002). Moreover, reduced perennial-grass and total-plant cover could lead to increasing heterogeneity in the horizontal spatial patterning of roots (Hutchings and John, 2003; van der Mareel and Titlyanova, 1989).

There is also evidence that grazing can alter root-tissue chemistry at the community level through the replacement of herbaceous plants by woody plants or through changes in root growth and increments in the proportion of fine roots (Johnson and Matchett, 2001). Fine roots usually have higher concentration of N than thick roots (Gordon and Jackson, 2000). Roots of many woody plants could have higher concentrations of phenolic compounds (Hyder et al., 2002) and, in some cases, fine roots of this life form tend to have higher N concentration than those of perennial grasses (Gordon and Jackson, 2000). Changes in root chemistry and spatial distribution can also result in changes in the rates of ecosystem processes such as decomposition, mineralization and nutrient cycling (Milchunas and Lauenroth, 1989; Rodríguez et al., 1995; Gill and Burke, 1999; Jackson et al., 2000; Johnson and Matchett, 2001).

We analysed the spatial structure of root biomass by diameter classes and N and total phenolics concentrations in fine roots in the upper soil (0–50 cm) at sites differing in the distance to the watering point, the time since grazing exclusion, and historical sheep stocking rates/paddock characteristics. We hypothesized that the reduction in perennial-grass cover induced by grazing in shrublands would be associated with a reduction in fine-root biomass in the upper soil, an increase in the spatial heterogeneity of root biomass, and an increase in N and total phenolics concentrations in fine-root biomass.

## 2. Material and methods

### 2.1. Study area

The Patagonian Monte (southern portion of the Monte Phytogeographic Province) occupies an area of about 42 000 km<sup>2</sup> in northeastern Chubut Province, Argentina between 42–44°20'S and 64–68°W (Soriano, 1950; León and Aguiar, 1985). Sheep were introduced at the beginning of the last century (Ares et al., 1990; Soriano and Sala, 1983) and presently, they are the predominant herbivores in the area (Baldi et al., 2001). Bisigato and Bertiller (1997) reported that sheep grazing disturbance in this area led to the reduction of total-plant and grass cover, species replacement, and the gradual shift of large grass–shrub patches to shrub or dwarf-shrub patches. The study was conducted in an area representative of the sclerophyllous shrubland of *Larrea divaricata* and *Stipa* spp., characteristic of the Patagonian Monte (León and Aguiar, 1985; Soriano, 1950). The mean annual precipitation is 235.9 mm with high inter-annual variation (coefficient of variation = 40.3%) (data series from the period 1982 to 2001; [www.centropatagonico.com](http://www.centropatagonico.com)). Precipitation events are distributed throughout the year with a slight maximum in autumn–winter (Coronato and Bertiller, 1997). Soils are a complex of Typical Petrocalcids–Typical Haplocalcids (Soil Survey Staff, 1998) with a more or less compact caliche layer at ca. 50 cm below the soil surface (del Valle, 1998). Vegetation covers between 25% and 60% of the soil, depending on grazing disturbance, and presents a random patchy structure formed by shrubs clumps within a matrix of perennial grasses and bare soil (Bisigato and Bertiller, 1997). The tall shrubs *L. divaricata* Cav., *Chuquiraga hystrix* D. Don, *Lycium chilense* Miers ex Bert., *Schinus johnstonii* F.A. Barkey, and *Atriplex lampa* Gill, ex Moq. dominate the upper shrub layer (1.0–2.0 m), while the lower layer (0.1–0.5 m) is composed by perennial bunchgrasses *Stipa speciosa* Phil, *Stipa tenuis* Trin. and Rupr., *Stipa humilis* Cav. and *Poa ligularis* Nees ex Steud and dwarf shrubs *Nassauvia fuegiana* Speg. Cabrera, *Acantholippia seriphioides* (A. Gray) Moldenke, *Junellia seriphioides* (Gillies and Hook) Moldenke. At this area, we selected six sampling sites (Table 1) varying in the distance to the watering point (distance), the time since grazing exclusion (time), and historical stocking rates/paddock characteristics (paddock). As

Table 1

Description of the six sampling sites located at ER: Estancia “El Ranchito” (42°49'S, 65°36'W) and SL: Estancia “San Luis” (42°39'S, 65°23'W)

Site attributes	Site					
	ER 1	ER 2	ER 3	SL 1	SL 2	SL 3
Distance to the watering point (m) <sup>a</sup>	300	3000	3000	300	3000	300
Time since grazing exclusion (yr) <sup>b</sup>	0	0	2	0	0	10
Stocking rate (sheep/ha) <sup>c</sup>	0.10	0.10	0.10	0.14	0.14	0.14

<sup>a</sup>For each “Estancia”, sites correspond to the same paddock (ca. 2500 ha) with a single watering point at a corner.

<sup>b</sup>Years without sheep grazing. An entry of 0 indicates that the site was continuously exposed to sheep grazing.

<sup>c</sup>Stocking rate in the last 10 years based on historical registers (Ares et al., 2003a; Bertiller et al., 2002). Both paddocks at Estancia “El Ranchito” and Estancia “San Luis” have been exposed to continuous grazing for at least the last 50 years.

previously reported for the study area (Ares et al., 2003a, b; Bertiller et al., 2002; Bisigato, 2000; Bisigato and Bertiller, 1997) and for other rangelands (Hunt, 2001; Jeltsch et al., 1997), the watering point induces gradients of grazing pressure in the paddocks.

## 2.2. Field sampling

Sampling was conducted from April to June of 2001 during the moist season (autumn) when dominant life forms (perennial grasses, dwarf shrubs, and tall shrubs) exhibit root growth (Bertiller et al., 1991). Annual precipitation (January–December 31) was 278 mm in the sampling year (2001) and 208 mm in the year previous to sampling (2000).

### 2.2.1. Transect sampling

At each sampling site, we randomly selected one 10 m-linear transect. At 1 m intervals on each transect, we centred a plot of 1 × 1 m (with a 10 × 10 cm grid) located at the top of the canopy, and we visually estimated the plant cover by life form. We extracted one cylindrical soil core (50 cm height, and 6 cm diameter) at the centre of each plot on each linear transect ( $n = 10$  cores per transect) either under shrub, grass or mixed canopies or in open bare soil spaces. After extraction, soil cores were divided into five layers of 10 cm each. Roots were separated from the soil by sieving through 2000, 1000, 600 and 300  $\mu\text{m}$  mesh and classified in three diameter classes: fine roots ( $\leq 1.4$  mm), intermediate roots (from  $> 1.4$  to 4 mm) and thick roots ( $> 4$  mm). Roots were washed, dried at 70 °C during 48 h, and weighed (Böhm, 1979). Root biomass was expressed as  $\text{g (dry weight)} \text{m}^{-2}$ .

### 2.2.2. Species-specific sampling

For the assessment of reference values of N and total phenolics concentrations in fine roots of dominant species of the three dominant plant life forms in the study area, we collected fine roots, in the soil depth between 0 and 40 cm at “Estancia San Luis”. We randomly selected three adult individuals of each dominant perennial-grass species (*S. tenuis*, *S. speciosa*, *P. ligularis*), dwarf-shrub species (*A. seriphioides*, *J. seriphioides*, *N. fuegiana*), and tall-shrub species (*L. divaricata*, *C. hystrix*, *A. lampa*, *L. chilense*). We excavated the root system in the soil volume close to the basal area of each individual and carefully removed fine roots which were subsequently washed, and dried at 70 °C for 48 h.

## 2.3. Chemical analyses of roots

For transect samples, we pooled the fine roots of three consecutive soil cores at each linear transect per soil depth in order to obtain enough fine-root biomass for the chemical analysis ( $n = 3$  per site and soil depth). Fine-root biomass at 41–50 cm depth was not analysed due to the low biomass collected. For species-specific samples, we used fine-root biomass of single individuals ( $n = 3$  per specie) as described above. We analysed the fine-root biomass from transect samples and from species-specific samples for N concentration by semi-micro Kjeldahl (Coombes et al., 1985), and concentration of total phenolics by Folin–Ciocalteu technique (extractions in methanol, 12 h, standard: tannic acid; Waterman and Mole, 1994). Values of N concentration were expressed as mg of N per gram dry mass of fine roots and total phenolics concentration as mg of tannic acid per gram dry mass of fine roots.

## 2.4. Statistical data analyses

The significance of the differences in life-form cover (square-root transformed perennial-grass cover, tall-shrub cover, and logarithmic-transformed dwarf-shrub cover) among sites was evaluated by two-way ANCOVA (factors: paddock and distance) using time as covariate. To test distance-dependent autocorrelation within transects, we performed autocorrelation analyses between fine-intermediate- and thick-root biomass in cores within transects ( $n = 10$ ) at lags from 1 to 8 for each 10 cm-soil layer and total soil depth (0–50 cm) at the six sites. We calculated the coefficient of variation of mean fine-, intermediate-, and thick-root biomass by soil depth at each transect ( $n = 1$ ) as an estimator of the horizontal spatial variation of root biomass (van der Mareel and Titlyanova, 1989; Schlesinger et al., 1990). The significance of the differences among sites in (1) fine-, intermediate-, and thick-root biomass and their coefficients of variation, and (2) total N (logarithmic transformed) and total phenolics concentrations in fine roots from transect samples were evaluated by nested ANCOVA. In this analysis, we included paddock and distance as factors, time as covariate and soil depth as a nested factor within cores to test for depth-dependent autocorrelation. The significance of the differences in concentrations of total N and total phenolics in fine roots among life forms were inspected by multiple comparison tests. We used least significant difference (LSD) test when data were homocedastic (total phenolics) and Tamhane's test when data were non-homocedastic (N concentration) (Day and Quinn, 1989). All statistical analyses were performed with the SPSS Package (Norusis, 1997). The level of significance was  $\alpha = 0.05$  throughout the study.

## 3. Results

### 3.1. Plant cover

The cover of perennial grasses was significantly reduced close (300 m) to the watering point ( $F_{1,60} = 64.59$ ,  $P < 0.001$ ; Fig. 1a and Table 2) and in grazed sites ( $F_{1,60} = 56.80$ ,  $P < 0.001$ ; Fig. 1b and Table 2). We did not find a significant effect of paddock nor interactions among factors and the covariate on the perennial-grass cover. Shrub and dwarf-shrub cover did not significantly vary ( $P > 0.05$ ) among sites (Table 2).

### 3.2. Root biomass

We did not find significant autocorrelations between fine-root biomass in the depth from 0 to 50 cm in cores within transects at any site (Fig. 2a). The analysis of autocorrelation by depth showed that fine-root biomass within transects was not autocorrelated in the depth from 0 to 30 cm (Fig. 2b–d). More in depth, we found autocorrelations in fine-root biomass within transects at some lags in three out of six transects at 31–40 cm depth (Fig. 2e) and at two out of six transects at 41–50 cm depth (Fig. 2f). We did not find significant autocorrelations in intermediate and thick roots within transects for the whole depth (0–50 cm) or at each soil layer (data not shown).

The biomass of fine roots decreased significantly with soil depth ( $F_{4,60} = 21.59$ ,  $P < 0.001$ ) and was significantly higher than the biomass of intermediate and thick roots at all sites (Table 3a–c). We found higher fine-root biomass close than far (3000 m) to the

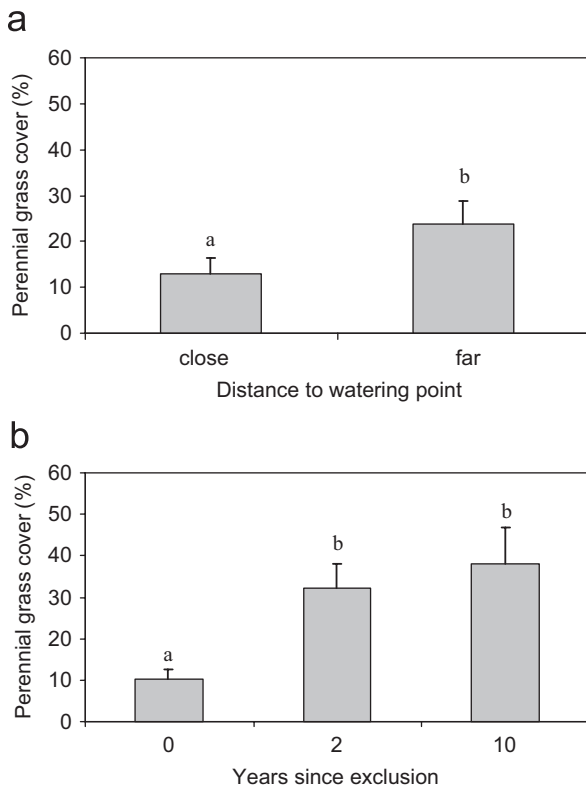


Fig. 1. Mean perennial-grass cover at sites (a) close (300m) and far (3000m) to the watering point,  $n = 60$ , and (b) with different time since grazing exclusion (0, 2 and 10 years),  $n = 60$ . Vertical bars represent one standard error. Lowercase letters indicate significant differences among mean values of perennial-grass cover.

Table 2

Mean percentage of plant cover of life forms (perennial grasses, tall shrubs, dwarf shrubs) at each site  $\pm$  one standard error

Life form	Site					
	ER 1	ER 2	ER 3	SL 1	SL 2	SL 3
Perennial grasses	1.1 $\pm$ 0.6	19.8 $\pm$ 4.1	32.1 $\pm$ 6.0	0.1 $\pm$ 0.0	19.5 $\pm$ 4.7	38.8 $\pm$ 9.2
Tall shrubs	20 $\pm$ 4.2	17.9 $\pm$ 5.3	26.8 $\pm$ 8.9	10 $\pm$ 4.4	13.8 $\pm$ 4.4	19.4 $\pm$ 7.0
Dwarf shrubs	2.2 $\pm$ 1.9	16.5 $\pm$ 5.1	10.6 $\pm$ 6.9	23.3 $\pm$ 5.9	8.5 $\pm$ 2.6	11.2 $\pm$ 5.8

For description and acronyms of sites see Table 1.

watering point at ER paddock while, at SL paddock, fine-root biomass did not vary between distances to the watering point (significant paddock  $\times$  distance interaction,  $F_{1,60} = 8.03$ ,  $P = 0.006$ ; Fig. 3a and Table 3a). Also, we found higher fine-root biomass at SL paddock than at ER paddock at 41–50 cm depth while at the other soil depths fine-root biomass did not differ between paddocks (significant interaction paddock  $\times$  soil depth,

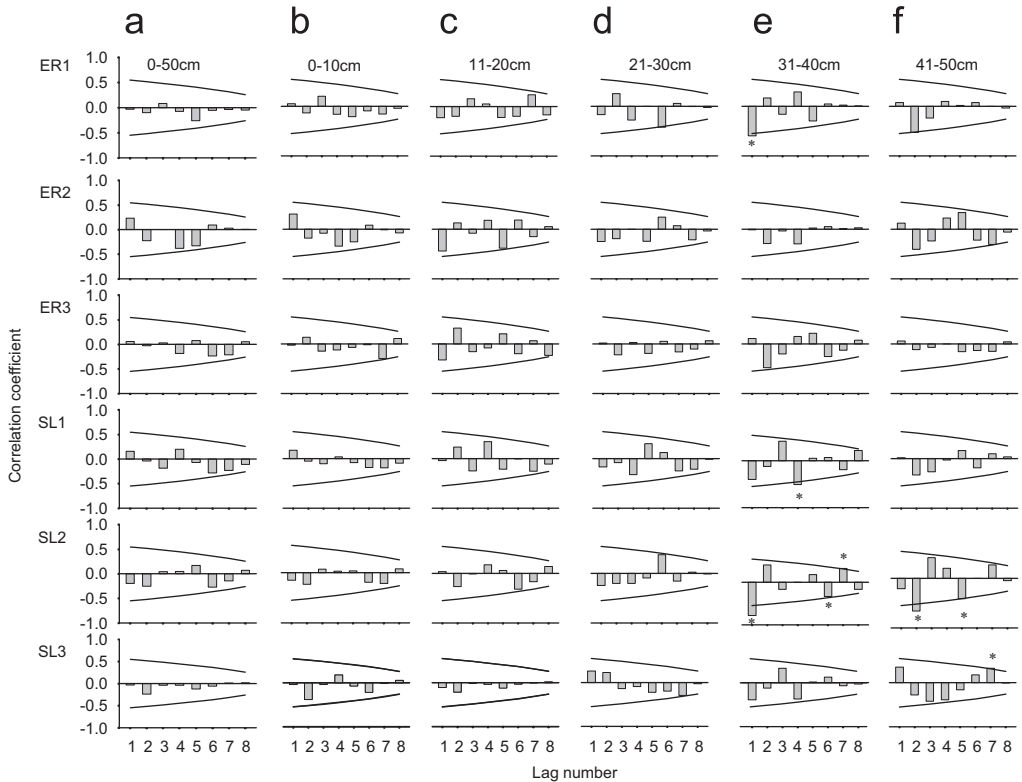


Fig. 2. Autocorrelations between fine-root biomass in cores within transects at lags from 1 to 8 for (a) total soil depth (0–50 cm) and (b)–(f) 10 cm-soil layers and at the six study sites. For site description and acronyms see Table 1. Asterisks indicate significant autocorrelations at  $P \leq 0.05$ . Lines indicate confidence intervals for autocorrelations (bars) at  $P = 0.05$ .

$F_{4,60} = 5.80$ ,  $P < 0.001$ ; Fig. 3b and Table 3a). We did not find significant differences in fine-root biomass related to the time since grazing exclusion.

In the depth from 0 to 10 cm, intermediate root biomass was higher far than close to the watering point while it did not differ among distances to the watering point at the other soil depths (significant soil depth  $\times$  distance interaction,  $F_{4,60} = 3.53$ ,  $P = 0.008$ ; Fig. 3c and Table 3b). Intermediate-root biomass did not vary among paddocks in the depth from 0 to 40 cm but was higher in SL than in ER paddock at 41–50 cm soil depth (significant depth  $\times$  paddock interaction,  $F_{4,60} = 2.83$ ,  $P = 0.026$ ; Fig. 3d and Table 3b). Intermediate-root biomass also was higher in the depth from 41 to 50 cm in the site with 10 years of grazing exclusion in SL than in the other sites. At the other soil depths intermediate-root biomass did not differ among sites with different times since grazing exclusion (significant depth  $\times$  time interaction,  $F_{4,60} = 2.96$ ,  $P = 0.021$ , Fig. 3e and Table 3b). Thick roots did not vary among sites differing in paddock, distance to watering point or time since sheep exclusion (Table 3c). We did not find significant differences in the coefficient of variation of fine-, intermediate-, and thick-root biomass among sites differing in paddock, distance to watering point or time since sheep exclusion at any depth (Table 4).

Table 3

Mean root biomass ( $\text{g m}^{-2}$ )  $\pm$  one standard error by root diameter class, soil depth and site,  $n = 10$ 

Root diameter class	Soil depth (cm)	Site					
		ER 1	ER 2	ER 3	SL 1	SL 2	SL 3
(a) Fine roots (<1.4 mm)	0–10	359.1 $\pm$ 88.5	170.5 $\pm$ 36.9	293.3 $\pm$ 74.3	131.2 $\pm$ 42.8	236.5 $\pm$ 118.8	189.7 $\pm$ 56.7
	11–20	189.6 $\pm$ 18.8	121.0 $\pm$ 17.3	109.6 $\pm$ 16.6	219.3 $\pm$ 104.7	140.0 $\pm$ 20.7	184.9 $\pm$ 44.7
	21–30	138.3 $\pm$ 23.5	57.4 $\pm$ 14.9	103.5 $\pm$ 18.7	76.2 $\pm$ 11.8	149.5 $\pm$ 25.2	92.9 $\pm$ 13.4
	31–40	108.3 $\pm$ 9.7	57.9 $\pm$ 15.9	116.1 $\pm$ 36.5	57.0 $\pm$ 6.4	105.3 $\pm$ 24.4	127.0 $\pm$ 12.8
	41–50	61.2 $\pm$ 13.1	42.8 $\pm$ 15.6	34.9 $\pm$ 7.0	64.2 $\pm$ 13.2	96.5 $\pm$ 15.9	108.0 $\pm$ 19.0
	0–50	856.6 $\pm$ 153.9	449.9 $\pm$ 100.7	657.6 $\pm$ 153.3	548.1 $\pm$ 179.1	728.0 $\pm$ 205.2	702.7 $\pm$ 146.7
(b) Intermediate roots (1.4–4 mm)	0–10	39.1 $\pm$ 17.3	41.3 $\pm$ 11.8	46.2 $\pm$ 12.8	2.2 $\pm$ 2.2	45.7 $\pm$ 20.7	17.2 $\pm$ 8.1
	11–20	31.5 $\pm$ 4.2	43.6 $\pm$ 8.4	39.9 $\pm$ 12.7	49.2 $\pm$ 11.3	49.3 $\pm$ 14.1	24.5 $\pm$ 10.4
	21–30	34.8 $\pm$ 8.2	20.0 $\pm$ 6.6	36.3 $\pm$ 7.9	41.4 $\pm$ 12.8	54.0 $\pm$ 13.1	21.4 $\pm$ 6.3
	31–40	55.5 $\pm$ 10.1	23.9 $\pm$ 7.9	28.3 $\pm$ 5.2	31.4 $\pm$ 7.1	46.6 $\pm$ 17.1	96.0 $\pm$ 59.9
	41–50	28.4 $\pm$ 5.4	21.1 $\pm$ 6.7	17.7 $\pm$ 7.6	46.4 $\pm$ 14.1	39.9 $\pm$ 16.6	73.5 $\pm$ 24.0
	0–50	189.6 $\pm$ 45.4	150.1 $\pm$ 41.5	168.6 $\pm$ 46.4	170.8 $\pm$ 47.5	235.7 $\pm$ 81.8	232.8 $\pm$ 108.9
(c) Thick roots (>4 mm)	0–10	18.9 $\pm$ 18.9	6.5 $\pm$ 6.8	154.4 $\pm$ 142.3	0	8.8 $\pm$ 8.8	14.4 $\pm$ 13.1
	11–20	34.6 $\pm$ 27.6	2.7 $\pm$ 2.8	12.3 $\pm$ 8.3	85.2 $\pm$ 73.1	37.3 $\pm$ 31.3	143.5 $\pm$ 119.6
	21–30	20.5 $\pm$ 15.2	9.6 $\pm$ 10.6	5.8 $\pm$ 4.2	85.4 $\pm$ 55.9	58.9 $\pm$ 38.8	55.1 $\pm$ 25.7
	31–40	11.8 $\pm$ 11.8	21.6 $\pm$ 15.7	23.6 $\pm$ 12.1	5.9 $\pm$ 3.4	15.8 $\pm$ 15.1	76.8 $\pm$ 68.7
	41–50	2.1 $\pm$ 2.1	34.3 $\pm$ 18.0	0	157.5 $\pm$ 93.2	9.3 $\pm$ 9.3	54.1 $\pm$ 24.1
	0–50	88.1 $\pm$ 75.7	74.9 $\pm$ 54.1	196.3 $\pm$ 167.0	334.1 $\pm$ 225.7	130.4 $\pm$ 103.6	344.0 $\pm$ 251.5

For description and acronyms of sites see Table 1.

### 3.3. Total nitrogen and total phenolics concentrations in fine roots

The N concentration in fine roots varied among life forms (Fig. 4a). The N concentration in fine roots of tall shrubs ( $10.8 \text{ mg g}^{-1}$ ) was higher than that in dwarf shrubs and perennial grasses ( $6.5$  and  $5.8 \text{ mg g}^{-1}$ , respectively). N concentration in fine roots was higher far than close to the watering point at ER paddock while the reverse occurred at SL paddock (significant distance  $\times$  paddock interaction,  $F_{1,60} = 15.59$ ,  $P = 0.002$ , Fig. 4b and Table 5). N concentration in fine roots at 31–40 cm soil depth was higher close than far to the watering point while it did not differ between distances relative to the watering point at other soil depths (significant distance  $\times$  depth interaction,  $F_{3,60} = 3.70$ ,  $P = 0.02$ , Fig. 4c). At all sites, N concentration in fine roots fell within the range of those measured for tall shrubs (Table 5 and Fig. 4a).

The concentration of total phenolics in fine roots varied among life forms (Fig. 5). Fine roots of dwarf shrubs showed higher concentration of total phenolic compounds ( $5.4 \text{ mg g}^{-1}$ ) than those of tall shrubs and perennial grasses ( $3.4$  and  $3.5 \text{ mg g}^{-1}$ ). Fine-root biomass at the plant community did not significantly differ in concentration of total phenolics among sites at any soil depth (Table 6). At all sites, total phenolics concentration in fine roots fell within the range of those measured in perennial grasses and tall shrubs (Table 6 and Fig. 5).

## 4. Discussion

In the Patagonian Monte, as in other arid and semi-arid shrublands of the world, the impact of grazers on vegetation is heterogeneous within paddocks. A number of



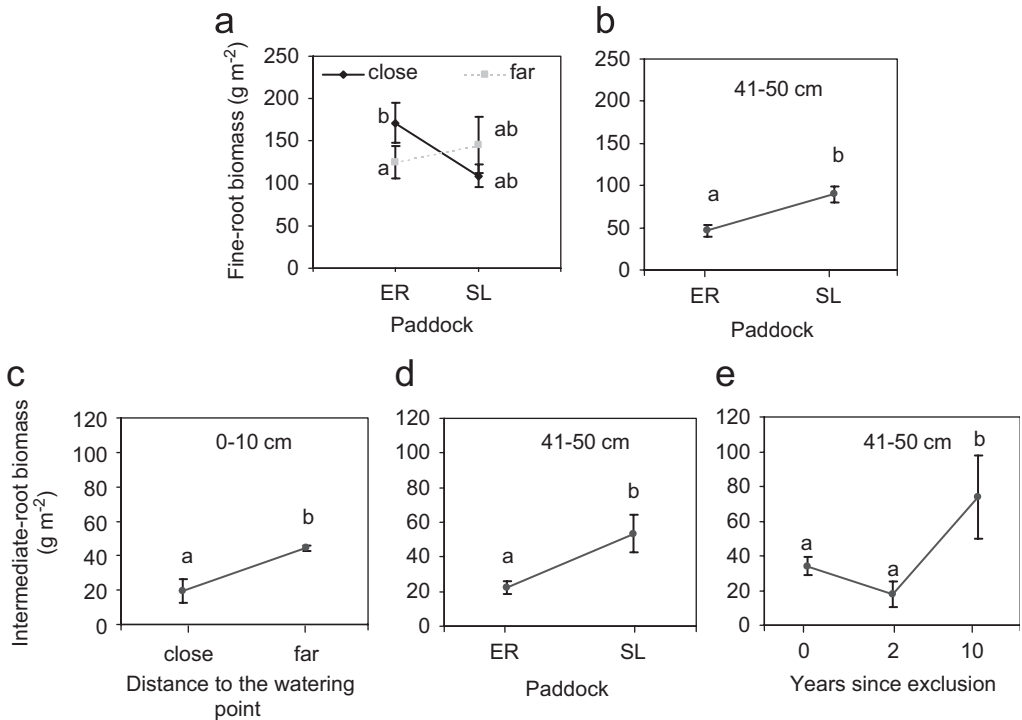


Fig. 3. (a) Mean fine-root biomass at sites close (300 m) and far (3000 m) to the watering point at ER and SL; (b) mean fine-root biomass at 41–50 cm soil depth at ER, and SL; (c) mean intermediate-root biomass at 0–10 cm soil depth at sites close (300 m), and far (3000 m) to the watering point; (d) mean intermediate-root biomass at 41–50 cm soil depth at ER, and SL; and (e) mean intermediate-root biomass at sites with 0, 2 and 10 years since sheep grazing exclusion;  $n = 60$ . Different lowercase letters indicate significant differences among root-biomass data. For site description and acronyms see Table 1.

environmental factors influence the spatial distribution of sheep grazing in the Patagonian Monte, but the location of water is particularly important (Ares et al., 2003a; Bertiller et al., 2002; Bisigato and Bertiller, 1997). Sources of water usually concentrate grazing activity, resulting in a gradient of attenuated grazing impact (a piosphere) from the watering point (Hunt, 2001; Jeltsch et al., 1997; Lange, 1969; Pringle and Landsberg, 2004). Accordingly in our study, the grazed sampling sites close to watering points exhibited signs of grazing disturbance like lower perennial-grass cover than those far to watering points or excluded from grazing.

The reduction in the perennial-grass cover was not reflected in corresponding changes in the fine-root biomass in contrast to our hypothesis. This evidence together with the chemistry of fine roots, that was characteristic of tall shrubs (mainly N concentration), would indicate an apparent predominance of fine-root biomass of tall shrubs over that of perennial grasses or dwarf shrubs at all sites. This occurred even at sites excluded from grazing or at grazed sites far to the watering point where the perennial-grass cover was higher or equal to that of tall shrubs. Since our study only analysed fine roots in the depth from 0 to 50 cm, we could have overlooked eventual differences in vertical-root distribution among sites below this depth and/or underestimated the total fine-root

Table 4

Mean coefficient of variation ((standard deviation/mean) × 100) by diameter class, soil depth and sampling site

Root diameter class	Soil depth (cm)	Site					
		ER 1	ER 2	ER 3	SL 1	SL 2	SL 3
(a) Fine roots (<1.4 mm)	0–10	78.0	169.0	96.3	222.5	128.5	162.0
	11–20	31.5	52.2	68.7	33.6	55.8	41.8
	21–30	53.9	143.1	81.2	99.2	52.3	76.6
	31–40	28.6	69.2	35.4	64.5	41.4	35.9
	41–50	68.1	95.5	117.9	65.0	34.9	31.9
	0–50	260.0	528.9	399.6	485.0	312.9	348.1
(b) Intermediate roots (1.4 to 4 mm)	0–10	140.2	129.8	119.9	2432.1	120.3	326.8
	11–20	42.1	31.4	44.8	38.3	37.3	59.8
	21–30	74.8	134.4	74.6	54.2	41.9	120.6
	31–40	57.9	145.7	115.3	108.4	79.4	31.0
	41–50	60.5	85.7	119.4	45.1	51.4	28.0
	0–50	375.5	527.0	473.9	2678.2	330.3	566.2
(c) Thick roots (>4 mm)	0–10	316.2	918.1	38.9	0.0	676.4	415.9
	11–20	252.1	3193.4	706.6	102.4	233.6	60.9
	21–30	233.9	499.9	817.7	56.4	31.5	33.7
	31–40	316.2	173.0	158.4	632.3	235.6	48.7
	41–50	316.2	0.0	0.0	0.0	141.8	24.6
	0–50	1434.7	4784.4	1721.6	791.1	1318.9	583.7

For description and acronyms of sites see Table 1.

biomass. However, previous studies reported shallow distributions of fine-root biomass in sclerophyllous-shrub communities (more than 79% of the fine-root biomass is located in the upper 30 cm soil, Jackson et al., 1997) as well as reduced effective soil depth for root exploration due to the presence of caliche layers, such as those in our study sites (Brisson and Reynolds, 1994).

Contrarily to the two-layer hypothesis of Walter (1971) predicting the dominance of roots of herbaceous plants in the upper-soil layers, we found evidence of the ability of shrub roots to occupy shallow-soil layers and eventually soil spaces freed by perennial grasses. These have also been observed in other arid ecosystems of the world (Casper and Jackson, 1997; Fernández and Paruelo, 1988; Jackson and Caldwell, 1993; Lee and Lauenroth 1994; Montaña et al., 1995; Weltzin and McPherson, 1997; Wilcox et al., 2004). These findings seem to be consistent with the development of opportunistic dimorphic-root systems in shrubs as indicated for other arid and semi-arid shrublands of the world (Gebauer et al., 2002; Gibbens and Lenz, 2001; Montaña et al., 1995; Peláez et al., 1994; Snyder and Williams, 2003). A previous study in the area indicated that root systems of most shrub species reach deep soil layers (Bertiller et al. 1991). However, concluding about the existence of dimorphic shrub-root systems in the Patagonian Monte should be based on studies at still deeper depths (> 50 cm) than in this study.

Our results suggest that changes in the aboveground cover induced by grazing may not affect the belowground biomass at the community level as found in other studies (Cargill and Jefferies, 1984; McNaughton et al., 1998; Milchunas and Lauenroth, 1989). This also

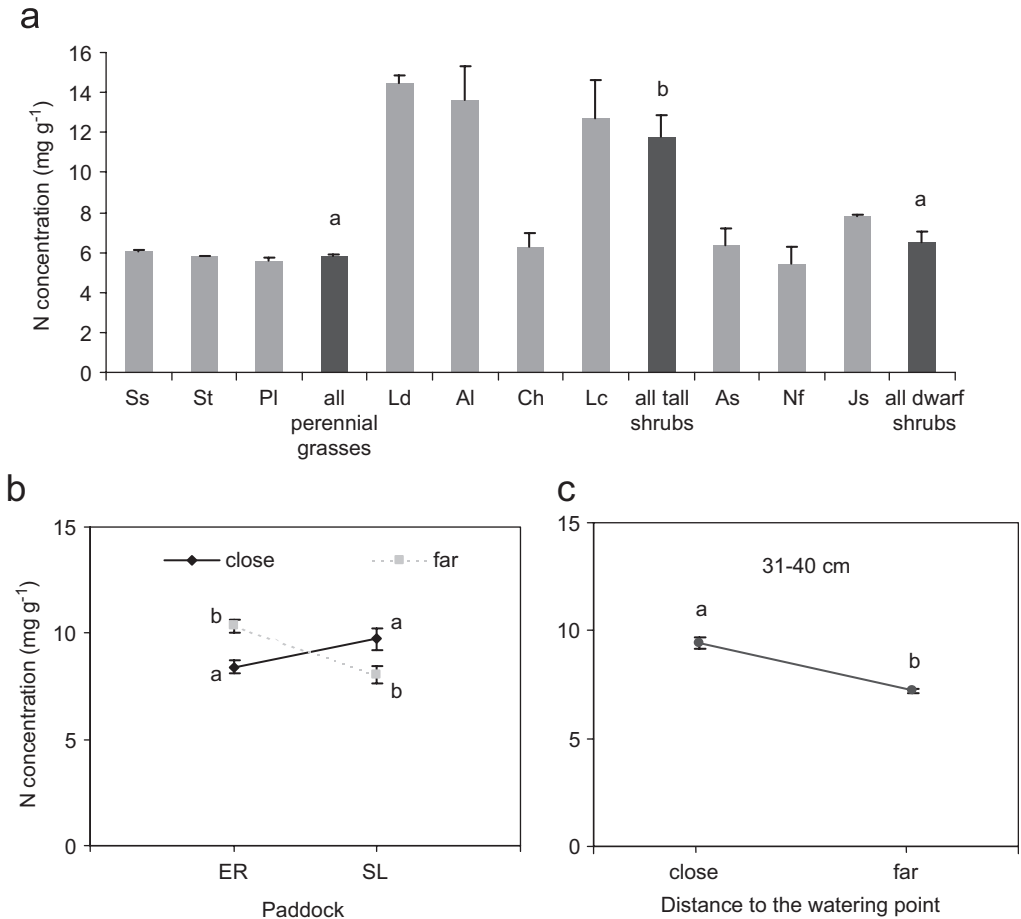


Fig. 4. Mean N concentration in fine roots (a) in dominant species and life forms ( $n = 3$  per species). Perennial grasses: Ss (*Stipa speciosa*), St (*Stipa tenuis*), PI (*Poa ligularis*); tall shrubs: Ld (*Larrea divaricata*), Al (*Atriplex lampa*), Ch (*C. hystrix*), Lc (*Lycium chilense*); dwarf shrubs: As (*Acantholippia seriphioides*), Nf (*Nassauvia fuegiana*), Js (*Junellia seriphioides*); (b) at sites close (300 m) and far (3000 m) to the watering point at ER and SL; (c) at 31–40 cm soil depth at sites close (300 m) and far (3000 m) to the watering point,  $n = 60$ . Different lowercase letters indicate significant differences among life forms or sites. Vertical bars represent one standard error.

Table 5  
Mean N concentration ( $\text{mg g}^{-1}$ ) in fine roots  $\pm$  one standard error by soil depth and sampling site

Soil depth (cm)	Site					
	ER 1	ER 2	ER 3	SL 1	SL 2	SL 3
0–10	9.8 $\pm$ 0.3	11.1 $\pm$ 0.2	9.9 $\pm$ 1.5	12.1 $\pm$ 0.4	9.9 $\pm$ 0.9	10.7 $\pm$ 0.4
11–20	7.8 $\pm$ 0.7	11.4 $\pm$ 1.0	10.4 $\pm$ 1.1	10.4 $\pm$ 0.9	8.2 $\pm$ 0.2	9.8 $\pm$ 0.3
21–30	7.5 $\pm$ 0.3	10.1 $\pm$ 1.6	10.0 $\pm$ 1.1	10.4 $\pm$ 0.3	7.2 $\pm$ 0.5	9.7 $\pm$ 0.2
31–40	8.6 $\pm$ 0.2	7.4 $\pm$ 1.7	7.4 $\pm$ 0.4	10.3 $\pm$ 0.4	6.8 $\pm$ 0.4	9.4 $\pm$ 1.2

For description and acronyms of sites see Table 1.

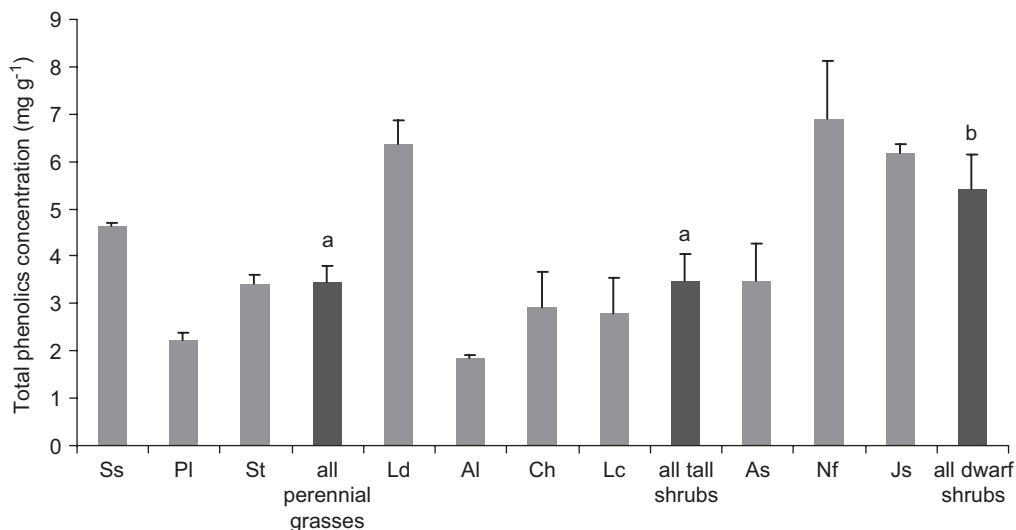


Fig. 5. Mean concentration of total phenolics in fine roots in dominant species ( $n = 3$  per species) and life forms. Acronyms of species as in Fig. 4. Different lowercase letters indicate significant differences among life forms. Vertical bars represent one standard error.

Table 6

Mean total phenolics concentration ( $\text{mg g}^{-1}$ ) in fine roots  $\pm$  one standard error by soil depth and sampling site

Soil depth (cm)	Site					
	ER 1	ER 2	ER 3	SL 1	SL 2	SL 3
0–10	1.2 $\pm$ 0.4	1.7 $\pm$ 0.1	1.1 $\pm$ 0.1	1.2 $\pm$ 0.3	2.1 $\pm$ 0.5	1.2 $\pm$ 0.0
11–20	1.4 $\pm$ 0.3	2.2 $\pm$ 0.3	1.5 $\pm$ 0.3	1.3 $\pm$ 0.2	1.8 $\pm$ 0.1	2.8 $\pm$ 0.0
21–30	0.8 $\pm$ 0.7	3.9 $\pm$ 1.6	1.2 $\pm$ 0.2	1.9 $\pm$ 0.0	3.2 $\pm$ 1.2	1.8 $\pm$ 0.0
31–40	1.9 $\pm$ 1.0	3.7 $\pm$ 0.0	1.7 $\pm$ 0.9	1.3 $\pm$ 0.0	2.6 $\pm$ 0.3	2.2 $\pm$ 0.3

For description and acronyms of sites see Table 1.

matches current hypotheses of a long evolutionary history of grazing of large wild herbivores in Patagonian ecosystems (Adler et al., 2005; Lauenroth, 1998). High grazing selection pressure upon plants might have resulted in adaptations to successfully exploit environments disturbed by grazing. Thus, selection may have led to increasing diversity and abundance of shrub species with grazing resistant fine-root systems with high potential to foraging resources from the upper soil layers.

Moreover, fine roots are an important source and/or sink for nutrients in terrestrial ecosystems (Gordon and Jackson, 2000). Our results indicate that life-form shifts induced by grazing would not affect root chemistry and biomass in shallow-soil layers of these arid ecosystems. This further support recently reported findings on the importance of shrub roots in the activity and function of upper-soil layers (Schenk and Jackson, 2002; Wilcox et al., 2004).

## 5. Conclusions

We concluded that roots of shrubs prevailed at the shallow-soil layers of sites either with high or low perennial-grass cover. We associated this with the ability of shrubs to allocate fine roots to the upper-soil layers supporting previous evidence for more mesic ecosystems indicating that life form shifting in the aboveground vegetation may have little effect on near-surface root systems and associated processes.

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