

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

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Abstract We tested whether both shrubs and grasses are able to develop similar active fine-root systems in the upper soil layer of the arid Patagonian Monte ecosystem with non-seasonal precipitation. We selected in the field shrub patches consisting of one isolated modal plant of the dominant shrub *Larrea divaricata* Cav., grass patches formed by one or more bunches of the dominant grass *Stipa tenuis* Phil. (15 cm diameter), and mixed patches consisting of one individual of *L. divaricata* with bunches of *S. tenuis* under its canopy. We assessed the biomass, regrowth, and activity of fine roots (diameter <1.4 mm) of each species in the upper soil (50 cm depth) of each patch type at 3-month intervals. We also measured the N concentration in fine roots to estimate the relative contribution of each species to fine-root biomass of mixed patches. We injected Li^+ in the soil as a chemical tracer to detect fine-root activity of each species in the upper soil. Fine-root biomass was higher in mixed patches than in grass patches while fine-root biomass in shrub patches did not differ from the two former. We did not find differences in fine-root regrowth among patch types. Li^+ injection provided evidence of active fine roots of both species in the upper soil when it was wet. N concentration in fine roots suggested the prevalence of

fine roots of *L. divaricata* in the upper soil of mixed patches. Our results support evidence of the ability of fine roots of both the shrub and the grass species to occupy the upper soil. These findings did not support the two-layer model (H Walter, *Ecology of tropical and subtropical vegetation*, Oliver and Boyd, Edinburgh, 1971) and provide evidence of this model would be less applicable to arid ecosystems with non-seasonal precipitation. Further, our results highlighted some issues deserving more research such as the outcome of belowground competition between neighboring plants of both contrasting life forms, the eventual limited fine-root carrying capacity of the upper soil, and differences in fine-root lifespan between species of both contrasting life form.

Keywords Fine-root competition · *Larrea divaricata* · N in fine roots · Root activity · *Stipa tenuis* · Two-layer model

Abbreviations

L *Larrea divaricata* patches
S *Stipa tenuis* patches
LS *L. divaricata* and *S. tenuis* patches

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Introduction

In arid ecosystems, vegetation is heterogeneously distributed resulting in a pattern of dense plant patches alternating with areas of bare soil or sparse

vegetation (Noy-Meir 1973). Shrubs and perennial grasses usually are the dominant life forms in plant patches (Sala et al. 1989; Bertiller et al. 1991; Reynolds et al. 1997). The coexistence of woody and herbaceous plants was explained by the two-layer hypothesis (Walter 1971). This hypothesis postulates that woody and herbaceous plants have different rooting depths allowing them the use of the water stored in different soil layers (Walter 1971). Accordingly, shrubs with deep-root systems would use more stable water resources stored in the deep soil while perennial grasses with shallow-root systems would tap erratic and discontinuous water sources from the upper soil layers (Noy Meir 1973; Sala et al. 1989; Canadell et al. 1996; Jackson et al. 1996; Casper and Jackson 1997; Coronato and Bertiller 1997; Sun et al. 1997; Hipodonka et al. 2003). However, recent studies indicated that these assumptions are not consistently supported by field data (Reynolds et al. 2000, 2004). Knoop and Walker (1985) found that some grasses could use water from deep soil layers. Other studies (Peláez et al. 1994; Montaña et al. 1995; Gibbens and Lenz 2001; Wilcox et al. 2004) showed that shrubs could have shallow- or dimorphic-root systems allowing them to tap water from upper soil layers. The ability of shrubs to use water from the upper soil layers was associated with phenotypic plasticity in rooting habits in relation to plant phenology and the presence of neighbors (Ogle and Reynolds 2004; Callaway et al. 2003; Pigliucci 2001).

Schenk and Jackson (2002) proposed that the two-layer model is more applicable to arid ecosystems with winter precipitation than to arid ecosystems with summer or non-seasonal precipitation. Accordingly, deep-rooting shrub species would be more abundant in the former with low evaporative losses during the moist season and large water recharge of deep soil layers. In contrast, shrub species with shallow-rooting depths would be more frequent in ecosystems with summer precipitation coupled with high temperatures and high evaporative demand and consequently limited water recharging of deep soil layers. However, field studies and experimental evidence within a broad context are still scarce to support this hypothesis.

The Patagonian Monte shares plant and climate attributes from the Patagonian and Monte Phytogeographical Provinces and precipitation occurs without a

marked seasonal pattern (Cabrera 1976). Accordingly, this is an interesting area to test the Schenk and Jackson (2002) suggestion indicating the lack of a strict spatial partition of fine roots in the soil between shrubs and grasses in ecosystems with summer or non-seasonal precipitation. In our study, we tested whether both shrubs and grasses are able to develop similar active fine root systems in the upper soil layer. We predicted that grasses have larger ability than shrubs to develop fine-root systems (in terms of biomass, regrowth and activity) in the shallow soil. For this purpose, we assessed the biomass, regrowth, N concentration, and activity of fine roots (diameter <1.4 mm) of a dominant evergreen shrub and a dominant perennial grass in the upper soil (50 cm depth) at field areas of the arid Patagonian Monte.

Material and methods

Study site

The study was carried out at representative sites of the Patagonian Monte (southern portion of the Monte Phytogeographic Province) which occupies an area of about 42,000 km² in north-eastern Chubut Province, Argentina between 42°–44°20'S and 64°–68°W (Soriano 1950; León et al. 1998). Vegetation is represented by the steppe of *Larrea divaricata* Cav. and *Stipa* spp. (Soriano 1950, Morello 1958; León et al. 1998; Kropfl et al. 2002) covering 40–60% of the soil in a random patchy structure formed by shrubs clumps encircled by grasses, grass patches, and shrub patches on a matrix of bare soil (Bisigato and Bertiller 1997). The mean annual precipitation is 236 mm with high mean inter-annual variation (coefficient of variation=40.3%; data series from the period 1982–2001; www.cenpat.edu.ar). 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 (del Valle 1998; Soil Survey Staff 1998) with a calcium carbonate layer in the depth from 0.45 to 1 m. This layer is hard when is dry but it is not compacted and has abundant interstitial pores which are penetrated by fine roots (Bertiller et al. 1991; Súnico 1996).

Experimental design

We selected five sampling sites (1 ha each) at plane areas representative of the steppe of *Larrea divaricata* and *Stipa* spp., which were separated from each other by at least 3 km. The sites were exposed to low grazing intensities of large native and domestic herbivores (ca. 0.1 sheep per hectare; Baldi et al. 2001; Bertiller et al. 2002). At each sampling site ($n=5$), we selected three types of modal plant patches formed by: (1) isolated plants (ca. 100 cm diameter) of *L. divaricata* (L), (2) one or more bunches (ca. 15 cm diameter) of *S. tenuis* Phil. (S), and (3) one individual of *L. divaricata* (ca. 100 cm diameter) with bunches of *S. tenuis* under its canopy (LS). These patch types are the most frequent among shrub and perennial grass patches in the five sampling sites (Bisigato and Bertiller 1997). We selected eight patches of each type separated at least 100 cm from the surrounding vegetation by bare soil. Further, we recorded monthly precipitation and mean monthly air temperature by a weather station located at 40 km from the sampling sites (data series from the period 2004 to 2005; www.cenpat.edu.ar).

Larrea divaricata and *Stipa tenuis* are the dominant evergreen-shrub and perennial-grass species, respectively, in areas with variable intensity of grazing disturbance (Bisigato and Bertiller 1997). *Larrea divaricata* is a tall shrub (1.0–3.0 m), which grows vegetatively all year round and displays reproductive growth from October to February (spring–mid summer, Bertiller et al. 1991). As in other ecosystems of the Monte of Argentina (Kropfl et al. 2002), *L. divaricata* has a deep-root system (more than 3 m) with high horizontal development in the study area (Bertiller et al. 1991). This species is not grazed by native and domestic large herbivores (Baldi et al. 2004). The perennial grass *Stipa tenuis* develops vegetative–reproductive growth from July to November with an aboveground resting period in summer (Bertiller et al. 1991). The root system of *S. tenuis* reaches up to 40–50 cm in depth (Bertiller et al. 1991; Becker et al. 1997). This is one of the preferred species by large native and domestic herbivores (Baldi et al. 2004).

Fine-root biomass and regrowth

Sampling of fine-root biomass and regrowth was carried out at 3-month intervals from December 2003

to September 2005. At each sampling date ($n=8$ for biomass and $n=7$ for regrowth), we randomly selected one patch of each type (L, S, LS) per site. We extracted one cylindrical soil core (50 cm height, and 6 cm diameter) at ca. 15 cm from the shrub basal area at L and LS patches and at the center of the patch at S patches. This distance was selected based on a previous sampling indicating a maximum of fine-root biomass of *L. divaricata* in the upper soil at 15–20 cm from the basal stem. At larger distances, decreased the fine-root biomass and increased the probability to extract soil samples with fine roots of other species. Soil samples were subsequently divided into five layers of 10 cm each. Fine roots (diameter < 1.4 mm) were separated from the soil by sieving through 2,000, 1,000, 600 and 300 μm mesh screen, washed, dried at 70°C for 48 h, and weighed (Böhm 1979). Fine-root biomass was expressed as grams (dry weight) per square meter soil.

After the sampling of fine-root biomass, we introduced in each remnant soil hole one cylindrical in-growth core to assess fine-root regrowth (Böhm 1979). Each in-growth core (50 cm height, 4 cm diameter, 2,000 μm mesh) was filled with root-free soil of the five 10-cm layers previously extracted from each hole. After 3 months, in-growth cores were removed and fine roots were separated from the soil by the same procedure used for fine-root biomass. Grass bunches at S and LS patches were protected from grazing by metal cages (1 cm mesh) during the 3-month period that the chambers were in the field. Fine-root regrowth was expressed as gram (dry weight) per square meter per day. We could not separate fine roots of each species in LS samples since they had similar coloration and morphology. Also, we monthly measured the soil moisture at each 10 cm soil layer (water content per 100 g of oven-dried soil, 105°C, 48 h) in one randomly located cylindrical soil core (50 cm height, and 6 cm diameter) per patch and site.

Nitrogen concentration and activity of fine roots

Rodríguez et al. (2007) showed that perennial-grass species had lower N concentration in fine roots than evergreen-shrub species in the study area. Accordingly, we measured N concentration in fine roots to assess the prevalence of shrub or grass fine roots in LS patches. In other studies, root chemistry was also

used in the assessment of root system dynamics of species grown in mixtures under field conditions (Corre-Hellou and Crozat 2005). We measured the N concentration in two samples ($n=2$) of fine-root biomass from each patch type and sampling date by semi-micro Kjeldahl (Coombs et al. 1985). Values of N concentration were expressed as milligram of N per gram dry mass of fine roots.

We used Li^+ as a chemical tracer to detect the presence of active fine roots (Gibson 1988) in the upper soil of L and LS patches. We injected 320 ml of lithium chloride solution (100 g l^{-1}) in the soil at a depth of 15 cm distributed in 16 doses per patch surrounding, at ca. 15 cm, the basal stems of *L. divaricata* plants at three patches of L and at three of LS. Injections were carried out with high soil moisture ($8.2 \pm 0.2\%$) in July 2005 and with low soil moisture ($4.3 \pm 0.2\%$) in March 2006. At this date, we also injected the solution in the soil of three patches of L and three of LS irrigated 1 week before with 5 l of water on a ring of ca. 80 cm^2 surrounding the basal stems of *L. divaricata*. We collected green-leaves of each *L. divaricata* plant at L ($n=3$) and LS ($n=3$) patches, and green leaves of each *S. tenuis* bunch at LS patches ($n=3$), before the application of the solution (control) and 20 days after the injection. We did not collect green leaves of *S. tenuis* in March because of its aboveground rest period. Samples were dried at 60°C and weighted, ashed at 550°C and digested in 25 ml of HCl 5%. The concentration of Li^+ in the extract was measured by atomic absorption spectrometry. Li^+ concentration mostly in leaves of long-lived species may vary between and within species or plants due to differences in plant size, phenology, and heterogeneous activity within above- and belowground parts of the plants (Haase et al. 1995). Accordingly, we expressed the paired values (before and after injection) of Li^+ concentration in green leaves of each plant as a fraction of the mean of both values. This allowed us to highlight contrasts between the Li^+ concentration in green leaves before and after injection irrespective of the variation between and within plant species.

Data analyses

We used three-way analysis of the covariance (ANCOVA) to evaluate the significance of the differences in fine-root biomass and fine-root regrowth due

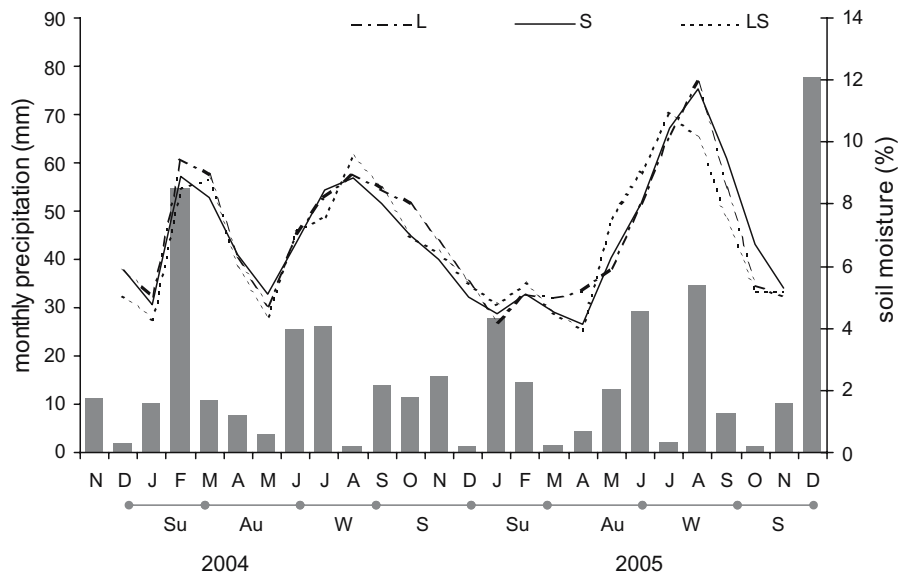
to patch type (L, S, LS) and interactions between patch type and sampling date, year, soil depth and soil moisture. We used a similar ANCOVA to compare fine-root biomass and fine-root regrowth between LS and L+S (the sum of L and S). In these analyses, patch type, sampling date and year were included as main factors, soil depth as a nested factor within cores, and soil moisture (mean values of the 3 months before fine-root sampling) as covariate. Post-hoc differences among plant patches were analyzed by least minimum difference (LSD) multiple comparisons test. In all cases, data were squared-root transformed for the analyses to meet ANCOVA assumptions. The significance of the differences in soil moisture and N concentration due to patch types (L, LS, S) and the interactions between patch type and sampling date, year, and soil depth was evaluated by three-way ANOVA. In this analysis, patch type, sampling date and year were included as main factors and soil depth as nested factor within soil cores. In the former analyses, we did not consider the single effects of other factors than patch type (i.e. sampling date, year, soil depth) or the covariate soil moisture on fine-root biomass and regrowth since the analysis of these effects were out of the scope of this paper. We used ANOVA of repeated measures to evaluate the significance of the differences in relative values of Li^+ concentration before and after Li^+ addition in the leaves of *L. divaricata* in L and LS patches and in the leaves of *S. tenuis* in LS patches. Statistical analyses were performed with the SPSS 7.5 Package (Norusis 1997). The level of significance was $\alpha=0.05$ throughout the study.

Results

Environmental conditions

During the sampling period precipitation was 184 mm in the first and 225 mm in the second year. Precipitation events occurred throughout the year but the largest monthly values occurred both in summer and winter in both years. The mean soil moisture in the depth from 0 to 50 cm varied according to precipitation showing maximum values in summer and winter. Soil moisture did not differ among patch types ($F_{2, 120}=0.63$, $p=0.98$) and we did not find significant interactions among patch type and the other factors (sampling date, year, and soil depth; Fig. 1).

Fig. 1 Monthly precipitation (bars) and soil moisture (lines) underneath plant patches of *Larrea divaricata* (L), *Stipa tenuis* (S) and both species (LS) at the study area during the study period (2004–2005). Su Summer; Au autumn; W winter; S spring



Fine-root biomass and regrowth

Fine-root biomass was higher in LS than in S while L did not differ from the two former plant patches ($F_{2, 120}=3.10, p=0.04$; Table 1). Fine-root biomass in LS was lower than the sum of fine-root biomass in L and S: L+S ($F_{1, 80}=25.44, p<0.01$). We did not find significant interactions among patch type and the other factors (sampling date, year, and soil depth) or the covariate (soil moisture) on fine-root biomass. The lack of patch type \times sampling date interactions

indicated that differences in fine-root biomass among patch types followed the same trend at all dates.

We did not find differences in fine-root regrowth among plant patches ($F_{2, 105}=0.42, p=0.65$) nor significant interactions among patch type and the other factors (sampling date, year, and soil depth) or the covariate (soil moisture; Table 1). Fine-root regrowth in LS was lower than the sum of fine-root regrowth in L and S: L+S ($F_{1, 70}=18.63, p<0.01$) and we did not find significant interactions among patch type and the other factors (sampling date, year, and

Table 1 Fine-root biomass (g m^{-2}) \pm one standard error, fine-root regrowth ($\text{g m}^{-2} \text{day}^{-1}$) \pm one standard error and fine-root N concentration (mg g^{-1}) \pm one standard error at plant patch types

(L, S, LS) at each sampling date and during the whole observation period (December 2004–September 2005), $n=120$

Date	Fine-root biomass			Fine-root regrowth			Fine-root N concentration			
	Patch type			Patch type			Patch type			
	L	S	LS	L	S	LS	L	S	LS	
2004	December	485 \pm 82	446 \pm 127	525 \pm 99	–	–	–	9.3 \pm 1.7	7.8 \pm 1.3	8.7 \pm 0.5
	March	350 \pm 80	270 \pm 51	476 \pm 40	0.34 \pm 0.11	0.18 \pm 0.09	0.27 \pm 0.10	9.1 \pm 0.4	8.0 \pm 0.1	8.5 \pm 1.6
	June	124 \pm 23	225 \pm 97	125 \pm 36	0.08 \pm 0.02	0.14 \pm 0.04	0.01 \pm 0.03	10.5 \pm 0.8	7.9 \pm 0.2	10.7 \pm 0.1
	September	382 \pm 66	284 \pm 85	487 \pm 99	0.26 \pm 0.04	0.30 \pm 0.08	0.13 \pm 0.03	9.3 \pm 1.0	7.9 \pm 0.1	10.1 \pm 0.7
2005	December	461 \pm 81	405 \pm 56	331 \pm 80	0.07 \pm 0.01	0.08 \pm 0.01	0.10 \pm 0.02	8.7 \pm 0.2	6.5 \pm 0.6	10.5 \pm 2.0
	March	224 \pm 11	242 \pm 58	295 \pm 77	0.12 \pm 0.04	0.13 \pm 0.04	0.16 \pm 0.06	10.1 \pm 1.3	6.5 \pm 0.5	9.9 \pm 0.8
	June	191 \pm 44	77 \pm 14	200 \pm 32	0.10 \pm 0.04	0.10 \pm 0.04	0.10 \pm 0.03	11.9 \pm 0.6	7.9 \pm 1.7	8.5 \pm 0.8
	September	313 \pm 48	201 \pm 25	452 \pm 122	0.62 \pm 0.18	0.34 \pm 0.11	0.35 \pm 0.10	9.4 \pm 1.8	8.7 \pm 1.3	9.4 \pm 0.9
2004–2005	mean	316 \pm 27 ab	270 \pm 29 a	361 \pm 34 b	0.22 \pm 0.04 a	0.18 \pm 0.03 a	0.17 \pm 0.03 a	9.8 \pm 0.4 b	7.6 \pm 0.3 a	9.5 \pm 0.3 b

Different lowercase indicate significant differences for each variable for the whole observation period among patch types.

soil depth) or the covariate (soil moisture) on fine-root regrowth. The lack of patch type \times sampling date interactions indicated that differences in fine-root regrowth among patch types followed the same trend at all dates.

N concentration and activity in fine roots

N concentration in fine roots was significantly lower in S than in L and LS patches ($F_{2, 48}=10.77, p<0.01$). Fine roots of L and LS did not differ in N concentration between them (Table 1). We did not find significant interactions among patch type and the other factors (sampling date, year, and soil depth) or the covariate (soil moisture) on N concentration in fine roots. The lack of patch type \times sampling date interactions indicated that differences in N concentration in fine roots among patch types followed the same trend at all dates.

The relative Li^+ concentration in green leaves of *L. divaricata* in L and LS and in those of *S. tenuis* in LS was significantly higher after than before injection both in July and after irrigation in March ($F_{1, 14}=23.84, p<0.01$; Table 2). We did not find significant differences in the relative Li^+ concentration in green leaves of *L. divaricata* before and after injection in the patches without irrigation in March.

Discussion

Our results showed that both the shrub and the perennial grass growing in monospecific patches occupied with a similar fine-root biomass and vertical distribution the upper soil (0–50 cm). This result is consistent with field observations at the same community reporting no changes in total fine-root

biomass in the upper soil (0–50 cm) when grass cover was reduced by grazing (Rodríguez 2002; Rodríguez et al. 2007), and suggesting that fine roots of shrubs are able to occupy the upper soil freed by grasses. We did not associated the occupancy of the shallow soil by fine roots of shrubs with the presence of a calcium carbonate layer in the soil of the study area since this layer is porous and fine roots of both plant life forms may penetrate it (Bertiller et al. 1991; Súnico 1996). Our findings are consistent with studies indicating that shrubs could have shallow- or dimorphic-root systems using water and nutrients available in the upper soil (Peláez et al. 1994; Montaña et al. 1995; Gibbens and Lenz 2001; Reynolds et al. 2000, 2004; Wilcox et al. 2004). The root system of *L. divaricata* could be described as a dimorphic-root system (Casper and Jackson 1997; Ogle et al. 2004) with fine roots in the upper soil along with deep roots reaching more than 300 cm soil depth (Bertiller et al. 1991). However, *L. divaricata* was not able to maintain active fine roots in the upper soil at least during some drought periods developing an opportunistic active shallow-fine root system after water pulses (irrigation in our experiment) as shrubs of other arid ecosystems (Schwinning et al. 2002). These findings did not support the two-layer model (Walter 1971) and provide evidence on the Schenk and Jackson (2002) proposal that the two-layer model would be less applicable to arid ecosystems with summer or non-seasonal precipitation. We could not assess by visual observation the relative contribution of fine roots of each species in the upper soil of mixed patches but we identified active fine roots of both species when the soil at this layer was wet. In contrast to our prediction, N concentration in fine roots could indicate the prevalence of fine roots of *L. divaricata* in the upper soil of mixed patches. These results could denote higher potential capacity of fine roots of *L.*

Table 2 Relative values of Li^+ concentration (ppm ppm^{-1}) \pm one standard error in green leaves of *Larrea divaricata* and *Stipa tenuis* growing in L and LS patches before and after Li^+ injection in July (soil moisture $8.2\pm 0.2\%$) and in March (soil moisture $4.3\pm 0.2\%$) with irrigation, $n=3$

Date	Patch type	<i>Larrea divaricata</i>		<i>Stipa tenuis</i>	
		Before	After	Before	After
July 2005	L	0.95 \pm 0.02	1.05 \pm 0.02	–	–
	LS	0.04 \pm 0.09	1.96 \pm 0.09	0.38 \pm 0.07	1.62 \pm 0.07
March 2006 (irrigated)	L	0.73 \pm 0.02	1.27 \pm 0.02	–	–
	LS	0.65 \pm 0.14	1.35 \pm 0.14	Nd	Nd

Nd No data due to aboveground rest period

divaricata relative to those of *S. tenuis* to occupy upper soil volumes or the outcome of competition between fine roots of neighboring plants of both life forms in the upper soil of mixed patches. However, the lack of differences in fine-root regrowth among species at the different patch types did not support these assertions. In addition, some desert plants induce the formation of rhizoplanes, which provide an ideal habitat for free-living N-fixer soil microorganisms (Whitford 2002). Also, mycorrhizal-fungi in N-limited environments may increase the efficiency of P and N uptake (Lambers et al. 1998; Whitford 2002). Accordingly, differences between species in N concentration of fine roots could be masked or enhanced by different grades of free living N-fixers on fine roots or mycorrhizal fungi infection. Alternatively, our findings could provide evidence of higher lifespan of fine roots of *L. divaricata* relative to those of *S. tenuis*, probably induced by high concentration of soluble phenolics (Rodríguez et al. 2007). Many studies reported increased fine-root lifespan associated with increased concentration of soluble phenolics (Ryser and Lambers 1995; Van der Krikt and Berendse 2002; Peek et al. 2005). Additionally, lower fine-root biomass in mixed patches than the sum of the fine-root biomass in both *L. divaricata* and *S. tenuis* patches could indicate a limited fine-root carrying capacity of the upper soil.

In summary, our results support the evidence of the ability of fine roots of both the shrub *L. divaricata* and the grass *S. tenuis* to occupy with a similar fine-root biomass and vertical distribution the upper soil layer and of the eventual prevalence of fine roots of shrubs over those of grasses in the shallow soil of arid Patagonian Monte ecosystems with non-seasonal precipitation. However, the low number of samples taken in our study could have masked differences between shrub and grass fine roots due to the high spatial variability in root distribution in arid ecosystems. Also, the sampling interval of 3 months selected in our study might have been too long relative to the lifetime of fine roots. Moreover, rainfall conditions during the study were within the mean values expected for the area (www.cenpat.edu.ar). Larger values of precipitation could bring out differences in the dynamics of fine-root biomass and regrowth of shrubs and grasses. These remarks should be taken into consideration in future studies. In addition, our findings highlighted some issues deserving more research such as the outcome of belowground

competition between neighboring plants of both contrasting life forms, the eventual limited fine-root carrying capacity of the upper soil, and differences in fine-root lifespan between species of both contrasting life form.

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