Journal of Vegetation Science ■■ (2017)

Fine-scale root community structure and below-ground responses to grazing show independence from above-ground patterns

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Keywords
Arid rangelands; Below-ground richness; Domestic livestock; Grazing intensification; Patagonia; Root systems; Sheep; Specific root biomass

Received 11 January 2017
Accepted 12 July 2017
Co-ordinating Editor: Sándor Bartha

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Abstract

Question: Root biomass distribution and below-ground processes are the main drivers of plant community structure and dynamics in arid rangelands. However, despite their relevance, below-ground plant responses to disturbance regimes remain poorly understood. This knowledge is a pressing issue since most of our ideas derive from extrapolating above-ground ecological theory and data. Here, we asked how domestic grazing management changes (intensification and abandonment) impact on both below-ground species co-occurrence at microsite level (point-richness) in relation to above-ground patterns and below-ground biomass distribution of dominant graminoid species across different soil layers.

Location: Patagonian steppe, Argentina.

Methods: We sampled and compared ungrazed, moderately grazed and intensively grazed steppes. We evaluated below- and above-ground point-richness (microsite level: 6-cm diameter), as well as total and specific root biomass in the top 20 cm of soil along 50-m transects in commercial paddocks.

Results: We found independence between fine-scale below- and above-ground responses. Below-ground point-richness was at least three times higher than above-ground point-richness. Besides, below-ground point-richness decreased from 4.2 species in ungrazed sites to 3.4 species in intensively grazed ones. Neither grazing intensification nor abandonment changed total root biomass, although intensification changed the root biomass composition, reducing preferred and increasing non-preferred grass species. Strikingly, below-ground point-richness and total root biomass did not differ between microsites covered and not covered by vegetation. This pattern was not affected by grazing.

Conclusions: Our findings showed a higher degree of fine-scale below-ground species co-occurrence than above-ground in this Patagonian steppe. The intensification of grazing slightly decreased below-ground species co-occurrence and changed root composition (species abundance), although grazing management did not modify the high degree of independence between below- and above-ground structure. Even though intensive grazing markedly decreases above-ground biomass, total below-ground biomass does not vary along a wide range of grazing conditions. In general, most of our knowledge about vegetation responses to grazing is based on above-ground information, assuming that below-ground patterns and processes are analogous to those above-ground. This study suggests that below- and above-ground community structure at fine-scale are not strongly correlated and they can be differentially affected by grazing.

Doi: 10.1111/jvs.12571 © 2017 International Association for Vegetation Science

Introduction

Below-ground processes are the main drivers of plant community structure and dynamics in arid and semi-arid rangelands. As aridity rises, both spatial structure of plant root systems and below-ground interactions become more relevant in relation to those above-ground (Lauenroth & Coffin 1992; Lauenroth & Burke 1995; Sun et al. 1997; Burke et al. 1998; Pecháčková et al. 1999; Johnson & Matchett 2001; Wildová 2004). This occurs because in water-limited ecosystems, where soil resources are both highly limited and distributed in patches (cf. Burke et al. 1998), the main form of plant competition is below-ground (Orians & Solbrig 1977; Fowler 1986; Casper & Jackson 1997; Saint Pierre et al. 2002). However, despite their relevance, below-ground responses to changes in disturbance regimes remain poorly studied and most of our ideas derive from extrapolating above-ground ecological theory and data. In particular, the effect of large herbivore grazing on below-ground biomass distribution at species level is still unknown (Frank et al. 2010). Changes in above-ground species composition, induced by grazing intensification, may result in modifications of the vertical stratification of root biomass in the soil (Greenwood & Hutchinson 1998; Jackson et al. 2000; Schenk & Jackson 2002; Rodríguez et al. 2007). For example, reduction of perennial grass cover could be associated with a root biomass decrease in upper soil layers, because grasses have shallower root systems than forbs and woody species (Sala et al. 1989; Schenk & Jackson 2002). Furthermore, herbivory can also modify the composition and abundance of below-ground biomass, since defoliation of plant above-ground portion usually changes assimilates distribution between above- and below-ground organs, affecting the root growth of defoliated plants (Belsky 1986).

In most ecological studies of rangelands, while the structure of above-ground compartments has been described in great detail, estimating both species abundance and biomass, below-ground biomass is generally grouped into a single category expressed in $g \cdot m^{-2}$, resulting in a "black box" perspective (Leva et al. 2009). This state of the art is mainly the result of methodological problems, such as the difficulty in identifying roots at species level and the need for destructive techniques to obtain data (Pecháčková et al. 1999; Frank et al. 2010). In grasslands, even though root biomass decreases as distance from the plant crown increases, above-ground coverage may not be a good estimator of root distribution patterns (Hook et al.1994; Burke et al. 1998). There are relatively few studies that have resolved the difficulty of identifying species through their roots (using molecular techniques or noticeable root traits). They found that different species share the same soil volume (Pecháčková et al. 1999; de Kronn & Mommer 2006; Mommer et al. 2008, 2010; Leva et al. 2009; Frank et al. 2010, 2015; Hiiesalu et al. 2012; de Kronn et al. 2012; Price et al. 2012; Reyes & Aguiar 2017). In general, it is accepted that plant species co-existence results from root system segregation in space at very fine scales (Schenk 2006). Nevertheless, some empirical results indicate that spatial below-ground segregation of species probably plays a minor role in promoting resource partitioning in grasslands. This is shown by the numerous species co-occurring below-ground in small soil volumes (Frank et al. 2010, 2015; Mommer et al. 2010; Hiiesalu et al. 2012; Price et al. 2012). Besides, in these ecosystems, grazing may be one of the main drivers of below-ground assembly (Frank et al. 2010), although this fact was not verified in the latter studies, thus remaining unknown. In arid rangelands, grazing tends to open the canopy and plants become spatially segregated above-ground. If the current paradigm is correct, species fine-scale spatial co-occurrence below-ground (here also called point-richness) may decrease as grazing intensity rises.

The objective of this work was to evaluate the impact of domestic grazing management on: (1) below-ground co-occurrence of different species at fine spatial scale, relating them to the above-ground patterns and (2) below-ground biomass distribution of individual species. The study was performed in grass–shrub Patagonian steppes. In particular, effects of sheep historical stocking rate (from ungrazed to intensively grazed paddocks), with a focus on dominant perennial graminoid species, were evaluated. Graminoids have greater relevance than shrubs in native and domestic herbivore diet and there is evidence of their higher sensitivity to sheep grazing (Golluscio et al. 1998; Pelliza et al. 2001; Oñatibia et al. 2015; Oñatibia & Aguiar 2016). Our first hypothesis states that increasing grazing pressure from exclusion to high sheep density decreases below-ground co-occurrence of different species at microsite level (small soil volume). This results from the fact that grazing generally increases bare soil area, opening canopies and markedly decreasing most preferred (palatable) species biomass. This process raises preferred species mortality and even promotes their local (stand-level) extinction (Golluscio et al. 1998). Thus, we predict that in response to increasing grazing intensity, the number of species co-occurring below-ground at microsite level (point-richness) decreases. The second hypothesis states that grazing reduces preferred species root biomass because these species are highly defoliated and use their below-ground reserves to produce new shoots after defoliation. However, below-ground biomass reduction is lower than that above-ground, which suffers direct removal by domestic herbivores. Depending on grazing intensity and less preferred species response (i.e. to increase or to maintain their growth), total root biomass of grasses can compensate for the biomass reduction of

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defoliated species. We predict that increasing grazing intensity decreases root biomass of preferred species compared to moderately grazed and ungrazed sites.

Methods

Study site description

We worked in a grass–shrub steppe of 300 km^2 in South Central Patagonia, Chubut province, Argentina. Ungrazed and moderately grazed paddocks were inside the Río Mayo INTA Experimental Station, and intensively grazed paddocks were located in privately owned neighbouring rangelands (45°24′ S, 70°15″ W). This area has been grazed with sheep for more than 100 yr. Mean monthly temperature varies between 2 °C in July and 14 °C in January. Average annual precipitation is 154 ± 44 mm and most rainfall occurs between May and September (Jobbágy et al. 1995). Soils present a coarse texture (sandy), with a high content of pebbles of varying diameter (Paruelo et al. 1988). Plant community richness and equitability is low. Few dominant perennial grasses and shrubs contribute to 96% of total biomass (Fernández et al. 1991; Oñatibia & Aguiar 2016) and mean above-ground net primary production is 56 $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, half of which corresponds to grasses and half to shrubs (Jobbágy & Sala 2000). Grass roots are found in the top 20–30 cm of the soil profile, while shrub roots explore deeper layers (Fernández & Paruelo 1988; Sala et al. 1989). The dominant grass species are *Pappostipa speciosa* Trin. et Rupr., *Pappostipa humilis* Cav., *Poa ligularis* Nees ap. Steud and *Bromus pictus* Hook. The dominant shrub species are *Mulinum spinosum* (Cav.) Pers, *Adesmia volckmannii* Philippi and *Senecio filaginoides* De Candolle. Among grasses, *Poa ligularis* and *Bromus pictus* are the most preferred species for sheep. *Pappostipa speciosa* is a species of intermediate preference and *Pappostipa humilis* is a non-preferred species (Soriano 1956; Bonvissuto et al. 1983; Oñatibia & Aguiar 2016).

Estimation of grazing effects on root biomass and on below- and above-ground richness

We sampled in fields with three grazing managements: ungrazed (exclosure >18 yr), moderately grazed and intensively grazed. Each management had four replicates (different paddocks or fields; Oñatibia et al. 2015). To assess the ungrazed management we used four exclosures of different ages, respectively, installed in 1972, 1983, 1994 and 1998. The moderately grazed replicates were paddocks managed with a stocking rate of ~0.2 $\text{sheep}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, during the last 20 yr. The intensively grazed replicates corresponded to paddocks that have been historically managed with ~0.4 $\text{sheep}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (Cipriotti & Aguiar 2005). All study sites are located in a homogeneous plateau (same soil type and topographic position) and they correspond to the same plant community. Therefore, we assumed that differences in the response variables among treatments could be attributed to grazing effects (Cipriotti & Aguiar 2005; Graff et al. 2007; Oñatibia et al. 2015). These three levels of grazing intensity result in different ecosystem structure and functioning. For example, total stock of grass above-ground biomass is lower under intensively grazed conditions compared to those ungrazed and moderately grazed, while grass above-ground production is twice as high in moderately grazed paddocks as in those without grazing and intensively grazed pastures (Oñatibia & Aguiar 2016). Preferred and non-preferred species abundance and spatial distribution are markedly affected mainly under intensively grazed sites (Cipriotti & Aguiar 2005; Graff et al. 2007, 2013; Golluscio et al. 2009; Oñatibia & Aguiar 2016). Also, soil organic C and N stocks may decrease with grazing intensity (Golluscio et al. 2009) and forage provision and C and N stocks in plant biomass are maximized in moderately grazed areas (Oñatibia et al. 2015).

In each paddock, we selected a representative area of its general condition and we randomly located a starting point and a direction of a 50-m transect. In grazed paddocks we avoided areas near watering points or fences where sheep usually overgraze. Every 2 m along the transect we sampled vegetation and soil. In this way, 25 subsamples were obtained in each field (300 in total). We harvested all above-ground biomass within a circular frame of 6 cm in diameter (rooting in that area or not), and using a cylinder (soil corer) of the same diameter, we extracted a 20-cm deep sample of soil and all root biomass (two layers of different depths: 0–10 and 10–20 cm). Samples were individually bagged, labelled and taken to the laboratory in order to sort above-ground and root biomass by species. Roots were identified to species using a key proposed by Leva et al. (2009). This key uses root morphological traits that differ among species, such as diameter, colour and branching. This method is >90% precise (Reyes & Aguiar 2017). The sandy soil texture facilitated root separation, because soil particles are easily detached from roots (Leva et al. 2009). The root biomass cleaning was carefully performed to avoid breaking and detaching fine roots. Specific root biomass was oven-dried at 65 °C for 72 h and weighed. Richness at microsite level in below- and above-ground biomass was estimated as the number of species found in the samples (point-richness).

Data analysis

To evaluate the effect of grazing on the point-richness of below- and above-ground portions, we performed a one-way ANOVA among the three grazing levels for each portion ($n = 4$). We also analysed grazing effects on total root biomass, root richness and root diversity (Simpson index estimated with species biomass), separating and comparing two subsets of soil samples based on above-ground cover: covered and uncovered by vegetation. These analyses were performed using two-way ANOVA with grazing intensity (ungrazed, moderately and intensively grazed) and above-ground microsite (covered and uncovered soil) as factors. We also performed species accumulation curves (cumulative richness) in order to show richness as a function of sample size and thus display the pattern at larger spatial scales.

We used one-way ANOVA to assess the effect of grazing on both total root biomass and each graminoid species root biomass, comparing them at 0–10, 10–20 and 0–20 cm among the three grazing levels. We also compared total root biomass between depths (0–10 and 10–20 cm). Thus, we analysed vertical distribution (vertical structure), while horizontal patterns were not considered. The results of relative biomass of each species according to total graminoid root biomass were analysed with two-way ANOVA using species and grazing level as factors. Concurrently, each species was analysed separately for different grazing intensities. Root vertical stratification (proportion of root biomass in the top 10 cm in relation to that in the top 20 cm of soil) was analysed with two-way ANOVA to determine the effect of species and grazing intensity as factors. This stratification was also compared using one-way ANOVA only among species. These data were transformed to arcsine. In all cases, we controlled data normality and variance homogeneity. Treatment means were compared with a Tukey test *post-hoc* ANOVA. Paddocks were considered as a random factor and subsample data ($n = 25$) were nested in each paddock ($n = 4$). Exclosures were used as replicates of ungrazed treatment after corroborating that time of grazing exclusion had no significant effect on root biomass ($P > 0.05$, resulting from a regression analysis between age of exclusion and biomass). We tested, through a DW test (Durbin & Watson 1951), that our data were not spatially auto-correlated for any response variable (see Appendix S1 as an example for below-ground richness and total below-ground biomass). Analyses were conducted with Statistica 8.0 software (Stat Soft, Tulsa, OK, US) and R software (v 3.2.4, packages vegan and lmtest, functions specaccum, lm, dwtest and acf; R Foundation for Statistical Computing, Vienna, AT).

Results

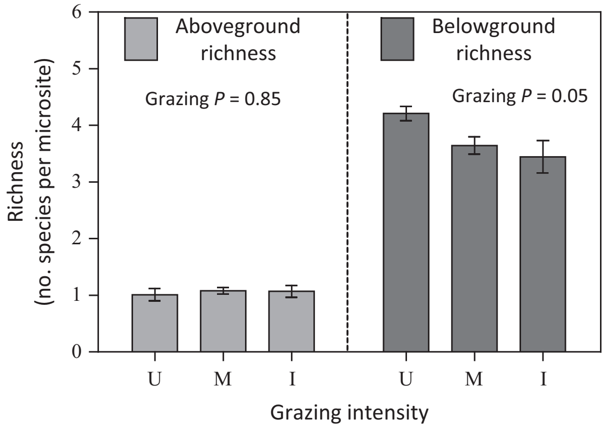

Fig. 1. Above- and below-ground richness of graminoid species at microsite level (point-richness) under three grazing levels: Ungrazed (U), Moderate grazing (M) and Intensive grazing (I). Bars correspond to mean values and vertical lines indicate SE. *P*-value refers to one-way ANOVA among grazing intensities in each vegetation portion (above- and below-ground).

Below- and above-ground plant community structure at microsite level were not strongly correlated. Below-ground point-richness of graminoid species was at least three times higher than that above-ground (Fig. 1). While above-ground richness did not vary among grazing conditions ($P = 0.85$), below-ground richness was higher in ungrazed paddocks than in grazed fields, approximately decreasing from 4.2 species·microsite^{-1} in ungrazed sites to 3.4 species·microsite^{-1} in intensively grazed sites ($P = 0.05$; Fig. 1). In contrast, species accumulation curves showed the same below- and above-ground total richness at larger spatial scales under all grazing conditions (Appendix S2). Taking into account all grazed and ungrazed paddocks, more than 40% of the samples did not present above-ground biomass. Instead, in the below-ground portion, 100% of the samples presented root biomass. Total grass root biomass did not differ between microsites covered by vegetation and not covered. This pattern was similar along the grazing gradient ($P > 0.05$ in all cases; Fig. 2a). Below-ground point-richness did not change between covered and not covered microsites, although it decreased along the grazing gradient in both types of microsite (Fig. 2b). Root diversity showed the same pattern as root biomass and did not vary under any grazing conditions or between microsites ($P > 0.05$ in all cases).

Graminoid roots showed vertical stratification. Biomass values were twice as high in the 0–10 cm portion of soil as in the 10–20 cm portion ($P < 0.05$). However, biomass in each stratum and total root biomass in the top 20 cm of soil did not change along the grazing gradient (0–10 cm, $P = 0.71$; 10–20 cm, $P = 0.29$; 0–20 cm, $P = 0.53$). On average, below-ground biomass in the top 20 cm of soil was 117.4 ± 6.5 g·m^{-2} (mean ± SE of overall grazing conditions).

Grazing intensification and abandonment changed the below-ground biomass of particular species (Fig. 3). *Poa*

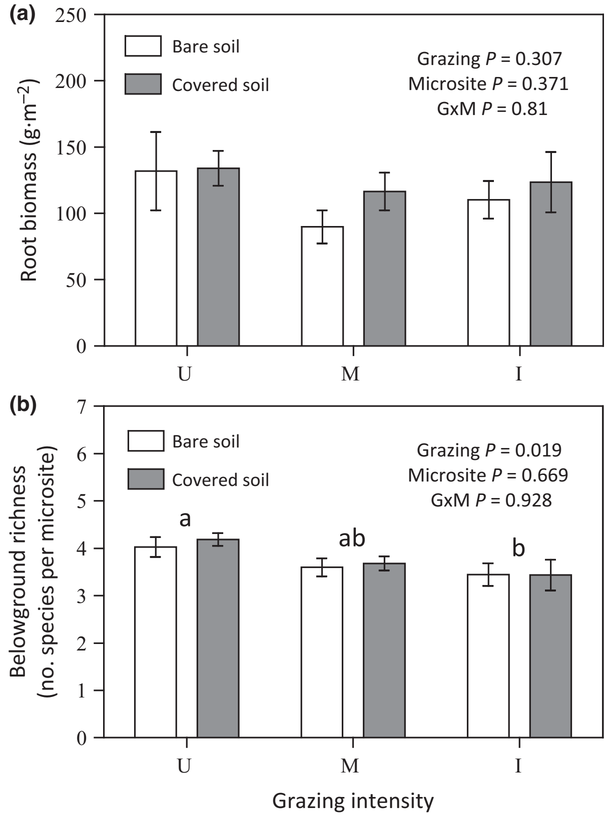

Fig. 2. (**a**) Total root biomass and (**b**) below-ground point-richness under three grazing levels: Ungrazed (U), Moderate grazing (M) and Intensive grazing (I) in two subsets of soil samples: microsites covered by a vegetation patch and not covered. Bars correspond to the mean values and vertical lines indicate SE. *P*-values refer to two-way ANOVA between grazing intensity and microsite as factors. Different letters indicate significant differences ($P < 0.05$) among grazing intensities (Tukey test).

ligularis and *B. pictus* decreased in response to increasing grazing intensity, although their response patterns were different. The root biomass of *P. ligularis* was maximal in ungrazed sites and decreased significantly ($P < 0.05$) only in intensive grazing paddocks, being intermediate in those moderately grazed (Fig. 3a). *Bromus pictus* biomass was four times higher under ungrazed situations than in both grazing intensity paddocks (Fig. 3b). *Pappostipa speciosa* and *Carex* sp. did not exhibit changes in below-ground biomass associated with grazing (Fig. 3c,d). Root biomass of *P. humilis* increased with grazing intensity, mainly in the topsoil portion (0–10 cm) and under intensive grazing conditions (Fig. 3e). On average, only 14% of graminoid root biomass (16.5 ± 2.6 g·m^{-2}) could not be classified by species. This fraction did not vary with grazing intensity ($P = 0.64$). Shrub and forb species roots were also found in the soil samples, although their biomass was relatively much less important and did not change with grazing intensity (Fig. 3f).

Under the three grazing conditions, 40% of total root biomass was represented by *P. speciosa* in the top 20 cm of soil (Fig. 4). *Poa ligularis* and *P. humilis* showed inverse patterns. The first one contributed about 20% of the root biomass in exclosures and moderate grazing, but represented <10% of the biomass in intensive grazing. In contrast, *P. humilis* constituted <10% in exclosure areas and moderately grazed areas, and >25% in intensively grazed fields (Fig. 4). *Carex* sp. represented about 5% of the graminoid root biomass in all conditions. Finally, *B. pictus* accounted for nearly 3% of the root biomass in exclosures but did not reach 1% under grazed conditions (Fig. 4).

Graminoid species differed in their below-ground biomass vertical distribution. The proportion of root biomass in the top 10 cm of soil was higher in *P. ligularis*, *P. speciosa* and *P. humilis* than in *B. pictus* and *Carex* sp. The first three species had over 70% of biomass distributed in the top 10 cm of soil (Fig. 5). Grazing intensity did not alter this ratio in any of the graminoid species ($P > 0.05$ in all cases).

Discussion

The rangeland biome is generally characterized by a disturbance regime influenced by aridity and large herbivore grazing (Stebbins 1972, 1981; Raven & Axelrod 1974). Despite the fact that below-ground processes become more important to ecosystem structure and functioning as aridity increases (Lauenroth & Coffin 1992; Lauenroth & Burke 1995; Burke et al. 1998), we still do not know how grazing could affect below-ground structure (i.e. root biomass distribution of individual species) in arid steppes. In particular, knowledge is scarce about the effects of grazing on root biomass composition, below-ground richness and biomass stocks, and if these effects are related to those occurring above-ground (Frank et al. 2010). Our hypotheses were partially supported. Grazing intensification decreased below-ground richness at microsite level and changed the root biomass composition of graminoids, reducing preferred species and increasing non-preferred ones. However, neither grazing intensification nor abandonment changed total root biomass in the top 20 cm of soil. Our results also showed a high degree of independence between the responses found below- and above-ground. The impacts of grazing historical management on below-ground biomass were less pronounced than on above-ground plant biomass (Oñatibia & Aguiar 2016). While selective grazing generally promotes some species and inhibits others, in Patagonian steppes this effect is higher in above- than in below-ground portions, probably because of herbivore direct consumption of above-ground biomass.

Above-ground richness that we measured in our samples (a few cm^2 of area) was one species on average and

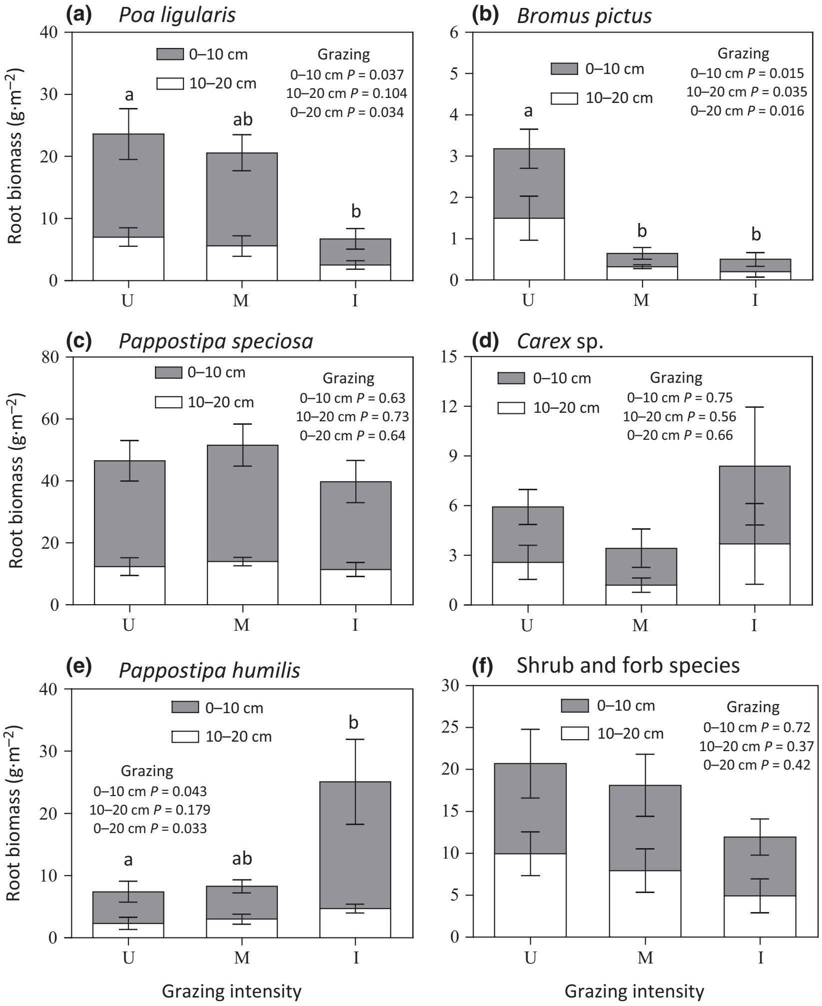

Fig. 3. Root biomass of (**a**) *Poa ligularis*, (**b**) *Bromus pictus*, (**c**) *Pappostipa speciosa*, (**d**) *Carex* sp., (**e**) *Pappostipa humilis* and (**f**) shrub and forb species in the top 20 cm of soil in three grazing intensities: Ungrazed (U), Moderate grazing (M) and Intensive grazing (I). Biomass values were separated into two fractions (0–10 and 10–20 cm). Bars correspond to mean values and vertical lines indicate SE. *P*-values refer to ANOVA among grazing intensities for each fraction and each species. Different letters indicate significant differences ($P < 0.05$) for total root biomass (0–20 cm) resulting from a one-way ANOVA among grazing intensities for each species (Tukey test). *y*-axes have different ranges of values in order to highlight the differences among treatments and fractions in each species.

did not change among grazing intensities. This indicates that overlapping of different species' canopies is very low, regardless of the historical grazing management. Instead, below-ground point-richness was in all cases more than three times that of above-ground one and, surprisingly, did not decrease in not covered microsites (bare soil). These patterns demonstrate that, at microsite level, the above-ground portion of vegetation is more territorial, while the below-ground portion is considerably intermingled or mixed (lack of root system segregation; Leva et al. 2009; Reyes & Aguiar 2017). Similar patterns were found in other grasslands, where below-ground fine-scale richness was up to two times larger than above-ground richness, indicating that conventional above-ground studies of plant richness may overlook many co-existing species (Hiiesalu et al. 2012; Price et al. 2012). Besides, in this study, grazing decreased the below-ground co-occurrence, probably due to the fact that root biomass of preferred species was reduced so that in some areas grazing could promote local extinction (Golluscio et al. 1998; Oñatibia et al. 2015; Oñatibia & Aguiar 2016).

Previous studies on total root biomass in grazed fields allow us to put our results into context. The absence of grazing effects on total root biomass was consistent with some field studies in other rangelands (Cargill & Jefferies 1984a,b; Milchunas & Lauenroth 1989; Pucheta et al. 2004). However, grazing has been found to increase, decrease or retain root biomass, above-ground biomass

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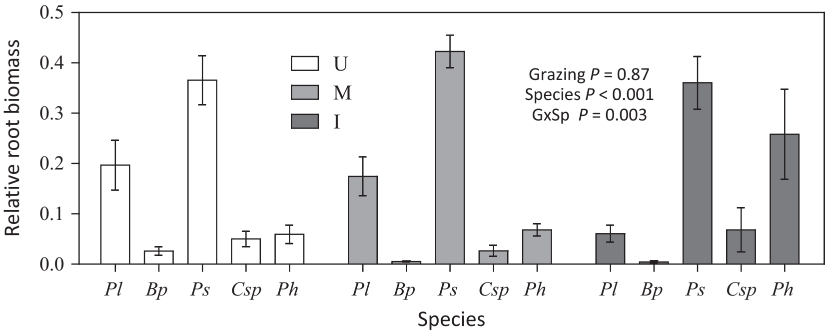

Fig. 4. Root relative biomass of each dominant graminoid species (*Pl: Poa ligularis*, *Bp: Bromus pictus*, *Ps: Pappostipa speciosa*, *Csp: Carex* sp., *Ph: Pappostipa humilis*) in relation to total root biomass in the top 20 cm of soil in three communities with different grazing intensities: Ungrazed (U), Moderate grazing (M) and Intensive grazing (I). Bars correspond to mean values and vertical lines indicate SE. *P*-values refer to a two-way ANOVA between grazing intensity and species as factors.

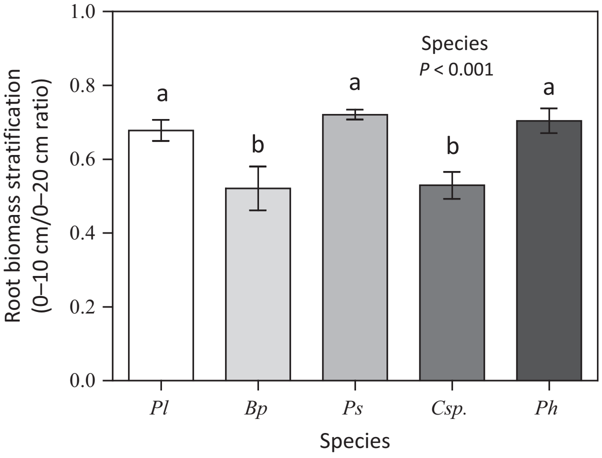

Fig. 5. Root biomass proportion in the top 10 cm in relation to root biomass in the top 20 cm of soil (stratification) for graminoid species; *Pl: Poa ligularis*, *Bp: Bromus pictus*, *Ps: Pappostipa speciosa*, *Csp: Carex* sp., *Ph: Pappostipa humilis.* Bars correspond to the mean values and vertical lines indicate SE. *P*-value refers to one-way ANOVA. Different letters indicate significant differences among species ($P < 0.05$) (Tukey test).

and their relationship unchanged (Derner et al. 2006). In their global review, Milchunas & Lauenroth (1993) showed that root biomass positively responded to defoliation in most studies included in their review for grazed and ungrazed grasslands ($n = 29$). In general, field studies are scarce, contradictory and tend to indicate that grazing has little effect on rangeland below-ground production. This is probably because grazing does not necessarily reduce root growth to restore the above-ground portion after defoliation (McNaughton et al. 1998; Rodríguez et al. 2007). In this Patagonian steppe, below-ground biomass did not change along a wide range of grazing intensities, even while above-ground biomass markedly decreased (Oñatibia & Aguiar 2016). Inner Mongolian steppes showed similar results since, as grazing pressure increases, above-ground biomass markedly decreases and root biomass only substantially decreases under very high grazing conditions (Zhao et al. 2005). This pattern may occur due to the fact that plants adapted to poor habitats preferentially assign C below-ground, being relatively inflexible in their C allocation patterns to below- and above-ground portions compared with plants adapted to productive habitats (Chapin 1980). These plant traits determine their ability to produce new leaves after defoliation without substantially changing root growth (Chapin & Slack 1979). In addition, our work provides data about different (compensatory) species responses to grazing, which further explains the relative constancy of total root biomass. These data showed that the decrease of preferred grass species root biomass (which suffers defoliation under grazed conditions) was compensated by the increase in non-preferred grass species and by the unchanged root biomass of the below-ground dominant species.

It is generally accepted that grazing changes the composition of rangeland communities (Milchunas & Lauenroth 1993), although these changes have only been studied in above-ground vegetation. Previous studies on grazing effects on root biomass have shown changes in the below-ground composition of different life forms, such as grasses and shrubs (Rodríguez et al. 2007), but grazing impacts at species level were not documented. Here we found that grazing, especially when it was intensive, changed below-ground composition of root biomass within graminoids. These root biomass responses to grazing intensification and abandonment did not linearly represent what happens in the above-ground portion (Oñatibia & Aguiar 2016), probably because defoliation can modify the stem–root ratio to different degrees depending on species preference (Saint Pierre et al. 2002). Thus, grazing may impact the relative C distribution between below- and above-ground biomass (Briske & Richards 1995; Briske et al. 1996). Furthermore, grazing intensification could alter nutrient cycling because roots of species with increasing abundance have lower N concentration, higher lignin content and lower decomposition rate than decreasing species (Semmartin et al. 2004; Vivanco & Austin 2006; Oñatibia et al. 2015). These changes may have direct consequences for the community of fauna and soil microorganisms, because domestic herbivore intensification modifies richness and species abundance of their food base. Our findings represent vertical root distribution patterns only in the top 20 cm of soil due to the fact that we focused on dominant perennial graminoid species. However, deeper roots (shrubs and forbs) might also respond to grazing management changes, although these life forms are generally less affected by herbivores (Oñatibia et al. 2015; Oñatibia & Aguiar 2016).

Finally, it should be mentioned that our approach assessed some unevaluated aspects in other grassland studies, such as measuring grazing intensity effects on specific root biomass (Frank et al. 2010). Partly this was possible because the study site contains few co-dominant grass species and low total richness. We submit that our findings may be extrapolated only to low diversity ecosystems at the scale we measured (microsite). Pärtel et al. (2012) proposed that, in addition to the disturbance regime (evaluated in this study), relationships between below- and above-ground species richness can vary as a function of the spatial scale, the species pool size and the site productivity. These hypotheses suggest that our study should be replicated along aridity gradients (including wetter and more diverse sites) and measuring at different spatial scales in order to improve our understanding about below-ground ecology of grazing lands. In addition, the results of this study should be interpreted considering that we examined the presence and abundance of roots and not their activity. Nevertheless, our study provides novel knowledge about fine-scale root ecology and its linkage with the above-ground structure under different grazing intensities in arid rangelands. In conclusion, we showed that below-ground species overlap was substantially higher than overlap in above-ground canopies. Besides, the intensification of domestic grazing slightly increased root segregation and changed below-ground species composition, independently of above-ground structure. This impact could cause changes in the use of soil resources, affecting below-ground ecosystem functioning. In general, most of our knowledge about vegetation processes and responses to grazing is inferred from above-ground information, assuming that below-ground patterns and processes are similar to those above-ground. The findings of this study suggest that below-ground structure can be differentially affected by grazing intensification.

Acknowledgements

We thank F. Palottini for assistance in data analysis. We also thank P. Graff and S. Roberts for helping in sample collection and root separation, respectively. R. Golluscio, A. Cingolani and A. Bisigato made helpful comments about early versions of this manuscript. Two anonymous referees have made comments and suggestions that significantly improved the quality of the manuscript. Funding was provided by grants from ANPCyT (PICT 00462 and PICT 2014-2100) and UBA (G032 and 20020130100424BA) to MRA. GRO was sponsored by fellowships from UBA and CONICET. MFR was sponsored by fellowships from ANPCyT and CONICET. MRA is member of CONICET. INTA granted the access to the facilities and experimental field. GRO and MRA designed the research; GRO, MFR and MRA collected the data and conducted the analysis; GRO led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Figures of Durbin-Watson test to evaluate autocorrelation for below-ground richness and total below-ground biomass.

Appendix S2. Figures of below- and above-ground species accumulation curves.

Doi: 10.1111/jvs.12571 © 2017 International Association for Vegetation Science