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Habitat productivity influences root mass vertical distribution in grazed Mediterranean ecosystems

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ABSTRACT

Herbivores are expected to influence grassland ecosystems by modifying root biomass and root spatial distribution of plant communities. Studies in perennial dominated grasslands suggest that grazing intensity and primary productivity may be strong determinants of the vertical distribution of subterranean biomass. However, no studies have addressed this question in annual dominated pastures. In this study we assess the effect of grazing and habitat productivity on the vertical distribution of root mass in an annual dominated Mediterranean pasture grazed by free-ranging sheep and wild rabbits. We evaluate the effects of grazing on total root mass and vertical root distribution (0–4, 4–8 and 8–12 cm depths) in two neighboring topographic sites (uplands and lowlands) with different productivity using a replicated fence experiment which excludes sheep and sheep plus rabbits. We found evidences that grazing affected root biomass and vertical distribution at lowlands (high productivity habitats), where places grazed by sheep plus rabbits exhibit more root mass and a higher concentration of it towards the soil surface than only rabbits and ungrazed places. In contrast, grazing did not affect root biomass and vertical distribution at uplands (low productivity habitats). We suggest that higher nitrogen and organic matter found in lowlands permit a plant adjustment for nitrogen acquisition by increasing biomass allocation to root production which would allow plant regrowth and the quick completion of the annual life cycle. Contrary, soil resources scarcity at uplands do not permit plants modify their root growth patterns in response to grazing. Our study emphasizes the importance of primary productivity in predicting grazing effect on belowground processes in Mediterranean environments dominated by annuals.

1. Introduction

Reviews by Canadell et al. (1996), Jackson et al. (1996) and Schenk and Jackson (2002a) synthesize what is known about root distribution, rooting depths, and belowground biomass for the main terrestrial biomes. Despite many recent advances, these authors highlight the existence of important gaps of knowledge about belowground processes and root attributes, which are particularly significant for the case of herbivore effects on grasslands (see also Lauenroth, 2000; Johnson and Matchett, 2001). The effects of grazing on subterranean biomass structure and root processes are difficult to predict as indicated by the contrasting results yielded by available field studies, which range from positive effects on root biomass productivity (e.g. Frank et al., 2002) to neutral (Milchunas and Lauenroth, 1989; McNaughton et al., 1998; Pucheta et al., 2004) or negative effects (Pandey and Singh, 1992; Beaulieu et al., 1996; Biondini et al., 1998; Engel et al., 1998).

Plant community structure depends on the interaction of many factors, including climate, soil type, water and nutrient availability, and grazing intensity (e.g. Chapin et al., 1987). Biomass allocation between roots and shoots is usually adjusted depending on the availability of essential resources (Bloom et al., 1985; Chapin et al., 1987; Shipley and Meziane, 2002). In general, under productive conditions, plants compete more for light and will tend to allocate more biomass towards the aboveground level, whereas, under less productive conditions, plant growth is more limited by soil resources and allocation to roots will tend to be favoured (e.g. see Brouwer, 1983; Tilman, 1988; Kadmon, 1995; see also Seginer, 2004 and references therein). Defoliation by herbivores has the potential to modify the partitioning of assimilates between roots and shoots, altering root growth in grazed plants (Richards and Caldwell, 1985; Belsky, 1986; Synder and Williams, 2003), which may result in detectable changes of the spatial distribution of both roots (e.g. Milchunas and Lauenroth, 1989; Rodríguez et al., 1995, 1996) and

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subterranean biomass as a whole (e.g. Greenwood and Hutchinson, 1998; Hutchings and John, 2003).

Alterations in root biomass distribution of grazed plants may have large implications for plant–plant competitive interactions as in grasslands the greater proportion of biomass is often belowground (Milchunas and Lauenroth, 1989; Jackson et al., 1996). The effects can even be larger in drier environments where herbaceous plants are expected to have larger root:shoot ratios (Chapin et al., 1993; Schenk and Jackson, 2002a,b). Few community-level studies in water-limited pastures have documented herbivore grazing effects on roots (Van der Maarel and Titlyanova, 1989; Greenwood and Hutchinson, 1998; Zhao et al., 2005) and spatial distribution of belowground biomass (Milchunas and Lauenroth, 1989; Rodríguez et al., 1995). Milchunas and Lauenroth (1989) found that heavy grazing in North American shortgrass steppes had only a small effect on the vertical distribution of roots, but led to a more uniform horizontal distribution of belowground biomass than light grazing. Complementarily, Rodríguez et al. (1995) found well defined but contrasted belowground biomass vertical profiles when comparing intensively grazed mesic and xeric pastures in Northwest Spain. These authors found that reduction of belowground biomass with soil depth was more gradual in xeric than in mesic pastures, which tend to concentrate more biomass towards the uppermost soil layers. Taken together, these results on perennial species-dominated communities suggest that grazing intensity and primary productivity may be strong determinants of the vertical distribution of subterranean biomass in semiarid grasslands. Little is known, however, for the case of semiarid communities dominated by annuals, making it difficult to draw generalisations from the results of these studies. Particularly because, as annual species lack temporal continuity in competitive interaction (Osem et al., 2002), it is possible that perennial and annual communities differ in the response of their belowground components to grazing.

Here we investigate how root biomass and root vertical distribution relates with grazing and habitat productivity in annual dominated semiarid pastures of Spain in which plant growth is usually limited by soil resources. Specifically, we conducted a three-year field experiment in a semiarid environment (locally known as "dehesa", a savannah-like ecosystem) in which annual plants are the major biomass producers, and water and nitrogen the main limiting factors of primary productivity (Savé et al., 1999). The sharp topographical differences in the area allowed us to study pastures with different primary productivity (low productivity at uplands and high productivity at lowlands) under the same semiarid climatic regime. We used herbivore exclusions to compare grazed and ungrazed treatments in uplands and lowlands, and estimated herbivore biomass consumption and aboveground biomass patterns in order to better explain root distribution under grazing.

2. Material and methods

2.1. Study area

The research was conducted in a 330 ha dehesa located in Central Spain (40°23′N, 4°12′W) during 2002, 2003 and 2004. Mean elevation is 690 m. Climate is semiarid continental-Mediterranean. Mean annual temperature is 12.6 °C and mean annual rainfall is 432.6 mm with a drought period in summer. The substrate is sandy to sandy-loamed, and lays upon a fractured bedrock of granite. Vegetation is typical of a dehesa ecosystem, i.e. a pasture matrix punctuated by holm oak (*Quercus ilex*) forest remnants and isolated individuals. The herbaceous layer is mainly composed by winter annual species. The typical dehesa landscape with a gentle undulating topography causes water and soil fertility to increase from uplands to lowlands, leading to marked differences in productivity between the two zones (see Table 1). Consequently, herbaceous vegetation can be divided into low productivity pastures composed mainly of short plants (on upland habitats), and higher productivity pastures composed mainly of taller plants and some perennial species (on lowland habitats). The approximate cover of perennials in uplands and lowlands is 0.25% and 27%, respectively (Rueda, 2006). The dehesa is mainly grazed by a dense native population of wild European rabbits (about 10 warrens/ha) (Rueda et al., 2008) and a transhumant flock of 600 free-ranging sheep (about 2 sheep/ha). Sheep graze from December until the end of June. In summer, when most aboveground herbaceous biomass is dry, sheep are moved to nearby mountain pastures.

2.2. Experimental design and sampling

In August 2001, five replicate blocks with three grazing treatments were set up at both upland and lowland areas (30 plots in total), which were at least 900 m apart. The three grazing treatments were: sheep + rabbit-grazed (the natural situation or control), rabbit-grazed, and non-grazed. They consisted of 36-m^2 fenced herbivore exclosure plots with a 1 m high chicken mesh (width 2.5 cm). The mesh in rabbit-grazed plots was lifted 20 cm aboveground level to allow rabbit access but excluding sheep. In non-grazed plots, the mesh was buried 30 cm into the soil forming an "L" shape to avoid rabbits burrowing underneath it. Sheep + rabbit-grazed plots had no fences to allow free access to both herbivores.

Root mass was estimated from 7 cm diameter and 12 cm deep soil cores in 2002, 2003 and 2004. Detached roots below 12 cm were negligible. Five soil cores per plot and year were collected in April and May (for uplands and lowlands, respectively), approximately the time of peak aboveground biomass production. Cores were trimmed to remove aboveground plant material. Root

Table 1
Mean ± SE values of plant and soil variables at uplands and lowlands; *t*-test statistic results for upland–lowland mean values comparison, and methods employed to obtain variables. Variables were recorded in 2002. Aboveground plant biomass, plant height and green cover were measured at the productivity peak season (April–May) in seven 20 × 20 cm quadrats randomly laid out in five upland and lowland sampling plots (see methods for details). Soil variables were measured using four random 8-cm deep soil samples collected at each sampling plot in spring. All variables resulted significantly higher at lowlands (*t*-test, $p < 0.05$).

Variables	Uplands	Lowlands	Statistic values	Methods
Plant aboveground biomass	230.4 ± 47.1	837.5 ± 239.6	$t = -2.48$, $p = 0.037$	Aboveground biomass clipped up to ground level, dried (55 °C) and weighed (g m^{-2})
Plant height	3.4 ± 0.2	13.0 ± 1.6	$t = 5.79$, $p < 0.001$	Mean height of herbaceous vegetation (cm)
Plant green cover	53.0 ± 8.4	95.6 ± 3.9	$t = 4.54$, $p = 0.002$	Visual aerial green cover (%)
Soil moisture	6.6 ± 0.3	29.4 ± 2.4	$t = -9.30$, $p < 0.001$	Difference in weight (%) of the samples before (just collected) and after drying (100 °C)
Soil nitrogen	0.07 ± 0.1	0.26 ± 0.02	$t = -6.87$, $p < 0.001$	Total soil N (%) determined using micro-kjeldahl digestion
Soil organic matter	1.72 ± 0.2	5.58 ± 0.59	$t = -6.12$, $p < 0.001$	Organic matter (%) determined using the Walkley and Black (1934) method

samples were washed with tap water and separated from the soil by successive decanting through a 0.5 mm sieve. Roots were dried to constant mass at 55 °C and weighed. After that, roots where combusted in a furnace at 500 °C for 8 h in order to determine ash content and apply an ash-free correction factor for each sample. Drier samples were not separated in live and dead categories. In 2004, vertical root mass distribution was also analyzed. For this, each soil core was sliced into three segments (0–4, 4–8 and 8–12-cm depths) that were treated as explained above.

Plant aerial fraction was also recorded in 2002, 2003 and 2004 to help explain belowground patterns. Aboveground plant mass was measured in seven replicate 20 × 20 cm squares per plot and year in spring. Aboveground plant mass was clipped up to ground level and collected. Samples were sorted in the laboratory into live biomass and dead (litter) fractions, dried to constant mass at 55 °C and weighed. Herbivore consumption was calculated as the difference in live biomass between fenced and unfenced plots, which allowed an approximate estimation of the biomass consumed (McNaughton et al., 1998). Consumption was only calculated using data from the first year of treatment (2002) because litter accumulation in non-grazed plots in successive years may alter estimations.

2.3. Data analyses

Within plot averages of all data were used for statistical analyses. Two-way ANOVAs performed separately for each habitat type (i.e. low productive uplands and high productive lowlands) were used to asses between-plot differences in aboveground biomass herbivore consumption. Two-way ANOVA was also employed to compare proportions of consumed aboveground biomass (i.e. percents of consumed biomass relative to the total amount of aboveground biomass produced) across all plots. In both analyses, grazing treatment was used as fixed factor and block as random factor. Repeated measures ANOVAs were applied to study the overall effects of grazing treatment from year 2002 to year 2004 on the total aboveground biomass and total root mass in uplands and lowlands separately; grazing treatment was the between subject factor, whereas year and year × grazing treatment were the within subject factors. Finally, for each plot, we computed the percentage of root biomass that was allocated to each of the three soil layers analyzed (see above), and then, for each layer separately, we conducted a factorial ANOVA to determine if grazing treatment, habitat productivity, or the interaction between both factors significantly affected root biomass allocation. Significant ($p < 0.05$) differences between means were determined by Fisher LSD-test. Data that did not meet the assumption of normal distribution were log- or squared root-transformed. Percentage data were angular transformed prior to analyses. The statistical package STATISTICA 7.1 (StatSoft, Inc., 2005) was used for all analyses.

3. Results

3.1. Biomass consumption

At uplands, there were not significant differences between the amount of aboveground biomass consumed by rabbits and by sheep + rabbits (Grazing treatment: $F = 1.84$, $p = 0.246$; Block: $F = 22.50$, $p = 0.005$) (Fig. 1a). Contrary, the amount of biomass consumed by herbivores at lowlands was significantly higher at the sheep + rabbit-grazed plot (Grazing treatment: $F = 14.66$, $p = 0.019$; block: $F = 90.93$, $p < 0.001$). When comparing the percentages of aboveground biomass that were consumed by herbivores across all plots, we found that the vegetation of rabbit-grazed plots in lowlands was significantly the less consumed (Fig. 1b) (Grazing treatment: $F = 5.63$, $p = 0.03$; block: $F = 7.73$, $p = 0.005$). The tendency for herbivore biomass consumption in terms of percentage of biomass was: sheep + rabbit-grazed at uplands > rabbit-grazed at uplands > sheep + rabbit-grazed at lowlands > rabbit-grazed at lowlands.

3.2. Above and belowground biomass

Total above and belowground biomasses were notably greater in lowlands than in uplands in all grazing treatments (Table 2). There was no evidence that grazing affected root mass at uplands, but at lowlands root mass was significantly lower in the rabbit- and non-grazed treatments (Table 2a). Contrary, grazing had a significant impact on aboveground biomass at uplands but not at lowlands (Table 2b). In uplands, herbivore grazing reduced significantly aboveground biomass with respect to the non-grazed treatment.

3.3. Vertical distribution of root biomass

There were significant main effects of grazing treatment and habitat productivity on the proportion of root mass at the 0–4 cm and 4–8 cm soil layers, with the latter layer having also a significant interaction of both factors (Table 3). In both habitats, root mass decreased with depth, with the first 4 cm accounting for >70% of this biomass at uplands, and for >60% at lowlands in all treatments (Fig. 2). The vertical distribution of root mass was identical in the three grazing treatments at uplands. At lowlands, root mass significantly decreased around 10% in the 0–4 cm soil layer of the rabbit-grazed and non-grazed treatments with respect to the sheep + rabbit treatment ($F = 6.55$, $p = 0.012$). Complementary, root mass significantly increased 7–8% in the 4–8 cm soil layer in the rabbit- and non-grazed treatments ($F = 9.73$, $p = 0.003$).

4. Discussion and conclusion

We have investigated how grazing and habitat productivity affect the distribution of root mass in semiarid Mediterranean pastures dominated by annuals in Central Spain. When we focused on uplands (i.e. low productivity habitats), we found no evidence that grazing, either performed by rabbits or by these and sheep, was affecting the amount and vertical distribution of root mass. Likewise, in lowlands (i.e. more productive habitats with more above and belowground plant masses), the sites not exposed to grazing and those grazed only by rabbits were similar in terms of root biomass production and allocation to different soil layers. However, we did find different patterns for lowlands grazed by rabbits plus sheep, which exhibited more root mass and a higher concentration of it towards the soil surface than the other lowland sites. Interestingly, these root profiles resembled the ones found by McNaughton et al. (1998) in the rainfall-fertility-gradient of the Serengeti, and by Rodríguez et al. (1995) in intensively grazed mesic pastures, which supports claims that ungulate grazed grasslands tend to concentrate root biomass in the uppermost soil layers (Rodríguez et al., 1996).

This said, it should be noted that in our study area the grazed and ungrazed root profiles found at uplands presented virtually the same pattern than the sheep + rabbit root profile at lowlands (see Fig. 2). This lead us to think that root processes in semiarid Mediterranean ecosystems can be locally affected by herbivores in more productive sites, while at the landscape level they are largely modulated by abiotic factors such as water and nutrient stress (cf. Rodríguez et al., 1996; Ferraro and Oesterheld, 2002). In this context, shallower root herbaceous plants with larger lateral root spreads were found in water-limited environments by Schenk and Jackson (2002b), which may enable plants to maximize uptake of

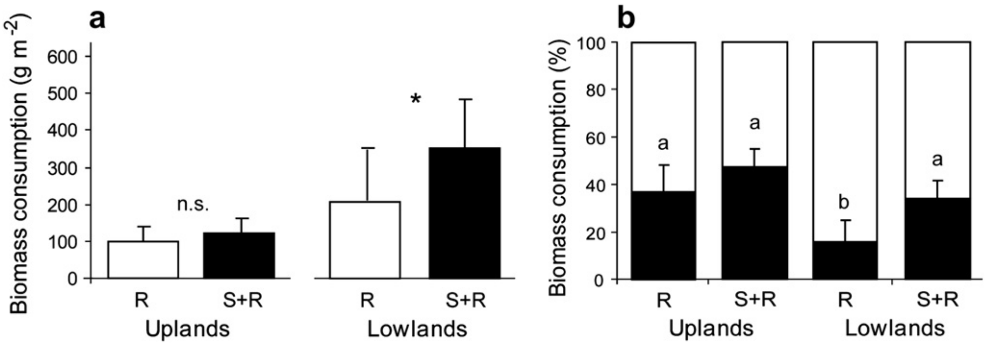

Fig. 1. Absolute (a) and relative (b) values (±1 SE) of aboveground biomass consumed by rabbits (R) and sheep + rabbits (S + R) in uplands and lowlands from August 2001 to April–May 2002. Absolute biomass consumption values (g m^{-2}) were compared by means of two-way ANOVAs performed separately for each topographical location, with grazing treatments being significantly different at lowlands (*; $p = 0.019$) but not at uplands (n.s.; $p = 0.246$). Two-way ANOVA was also used to compare relative biomass consumption values (percentages of consumed biomass relative to the total aboveground biomass produced) across locations and grazing treatments; significant differences found by this analysis ($p = 0.03$) were further explored with Fisher LSD-tests and indicated with different letters in the figure.

shallow soil water from small rainfall events and cope with water stress conditions. For the first case (i.e. lowlands grazed by sheep and rabbits), observed root mass profiles may be an indirect plant response to herbivore defoliation. We suggest that loss of photosynthetic tissue as a result of grazing resulted in an adjustment for water and nitrogen acquisition by increasing biomass allocation to root production. As long as nutrient concentration is higher in the upper soil layers (Jobbágy and Jackson, 2001), adjusts in root profile to upper root concentration would augment and enhance root capacity for nitrogen and water uptake which allow fast new photosynthetical tissue production, crucial to recover part of the tissues lost by grazing. This effect is supported by our data, as contrary to observed at uplands, we did not find significant effects of herbivores in aboveground biomass between treatments in any year, indicating that herbaceous vegetation was able to compensate for the lost shoot tissue.

The fact that regrowth of defoliated plants rely on nutrient uptake from the soil (Ruess et al., 1983; McNaughton and Chapin, 1985; Ferraro and Oesterheld, 2002), might be particularly important in semiarid grasslands (such as those we studied) in which stored root reserves are expected to be low. In this way, the greater amounts of soil nitrogen, organic matter and water availability recorded in lowlands in our study area (see Table 1), may have facilitated water and nutrient acquisition and the recovery of photosynthetic area after grazing, specially in sites that were grazed by both sheep and rabbits, due to the likely positive influence of the depositions of these herbivores on soil fertility (but see Mikola et al., 2005).

On the other hand, provided that plant growth is likely more constrained at more stressful upland environments (with less water and nutrient supply) (Oesterheld and McNaughton, 1991) than at lowlands, and, hence, that root mass might be particularly important for the competitive ability of plants in water-limited environments (Chapin et al., 1993; Schenk and Jackson, 2002a), it was expectable that grazing would have had a greater impact on roots at upland pastures. However, even though aboveground

Table 2
(a) Root mass (g m^{-2}) and (b) aboveground biomass (g m^{-2}) values in uplands and lowlands as affected by the three grazing treatments. Values are means ± SE. Repeated-measured ANOVAs results for root mass at uplands (Grazing treatment: $F = 0.06$, $p = 0.93$; Year: $F = 5.2$, $p = 0.01$; Grazing × year: $F = 1.87$, $p = 0.14$), and at lowlands (Grazing treatment: $F = 3.519$, $p = 0.039$; Year: $F = 0.68$, $p = 0.512$; Grazing × year: $F = 0.84$, $p = 0.51$). Results for aboveground biomass at uplands (Grazing treatment: $F = 6.11$, $p = 0.015$; Year: $F = 6.99$, $p = 0.004$; Grazing × year: $F = 3.22$, $p = 0.030$), and at lowlands (Grazing treatment: $F = 1.01$, $p = 0.39$; Year: $F = 1.13$, $p = 0.33$; Grazing × year: $F = 1.50$, $p = 0.232$). Within each topographical location and year (or average across years), different letters indicate significant differences between grazing treatments as detected by the Fisher LSD-test ($p < 0.05$).

Grazing treatments	Years			Average
	2002	2003	2004	
a) Root mass				
Uplands				
Sheep + rabbit	333.9 ± 35.8 a	323.1 ± 52.7 a	323.8 ± 42.8 a	326.9 ± 23.7 a
Rabbit	334.4 ± 41.7 a	321.7 ± 42.4 a	376.8 ± 62.5 a	344.3 ± 27.3 a
Non-grazed	359.8 ± 37.1 a	289.1 ± 42.7 a	393.3 ± 55.6 a	347.4 ± 27.1 a
Lowlands				
Sheep + rabbit	1259.8 ± 159.9 a	1190.7 ± 181.1 a	1415.2 ± 167.4 a	1307.9 ± 92.0 a
Rabbit	1049.4 ± 169.3 b	1099.5 ± 201.8 a	1075.4 ± 153.5 b	1037.2 ± 95.0 b
Non-grazed	1009.8 ± 172.7 b	893.7 ± 114.7 a	964.9 ± 128.6 b	1000.7 ± 80.5 b
b) Aboveground biomass				
Uplands				
Sheep + rabbit	108.7 ± 13.6 b	110.9 ± 8.9 b	132.1 ± 7.4 b	117.0 ± 6.2 b
Rabbit	134.1 ± 29.4 ab	130.5 ± 9.9 ab	167.9 ± 25.9 ab	144.1 ± 13.2 b
Non-grazed	230.4 ± 47.2 a	252.3 ± 58.8 a	451.9 ± 124.8 a	311.6 ± 52.3 a
Lowlands				
Sheep + rabbit	489.8 ± 73.3 a	569.2 ± 73.8 a	529.6 ± 42.6 a	529.5 ± 35.7 a
Rabbit	686.3 ± 110.8 a	712.0 ± 102.1 a	670.4 ± 54.6 a	689.6 ± 49.6 a
Non-grazed	837.5 ± 239.6 a	607.4 ± 101.7 a	476.3 ± 67.6 a	640.4 ± 92.1 a

Table 3
Results of the two-way ANOVAs for the proportion of root mass at 0–4, 4–8 and 4–8 cm soil layers.

	F	d.f.	*P*-value
Soil depth: 0–4 cm			
Grazing treatment	8.94	2	0.001
Habitat productivity	26.09	1	< 0.001
Grazing × productivity	2.00	2	0.157
Soil depth: 4–8 cm			
Grazing treatment	14.52	2	< 0.001
Habitat productivity	86.53	1	< 0.001
Grazing × productivity	3.82	2	0.036
Soil depth: 8–12 cm			
Grazing treatment	1.32	2	0.28
Habitat productivity	0.20	1	0.65
Grazing × productivity	0.32	2	0.72

biomass decreased with grazing at uplands, herbivores did not have a significant effect neither on root mass nor on its vertical distribution in these areas. A possible explanation is that their soil resources are so scarce that plants have no capacity to modify their growth patterns in response to grazing (e.g. in a way similar to that we proposed above to explain grazing effects on roots in lowlands), thus resulting in that the distribution of roots is not affected by herbivores. In fact, at low levels of nitrogen, the ability of plants to tolerate defoliation would be affected by the removal of stored nutrients and the reduction in the capacity to take up nutrients when they are in low supply (McNaughton and Chapin, 1985). Moreover, the observed upper root amalgamation at uplands in grazed and ungrazed grasslands might be another reflection of the low productivity of these areas, which would result in smaller sized plants both above and belowground.

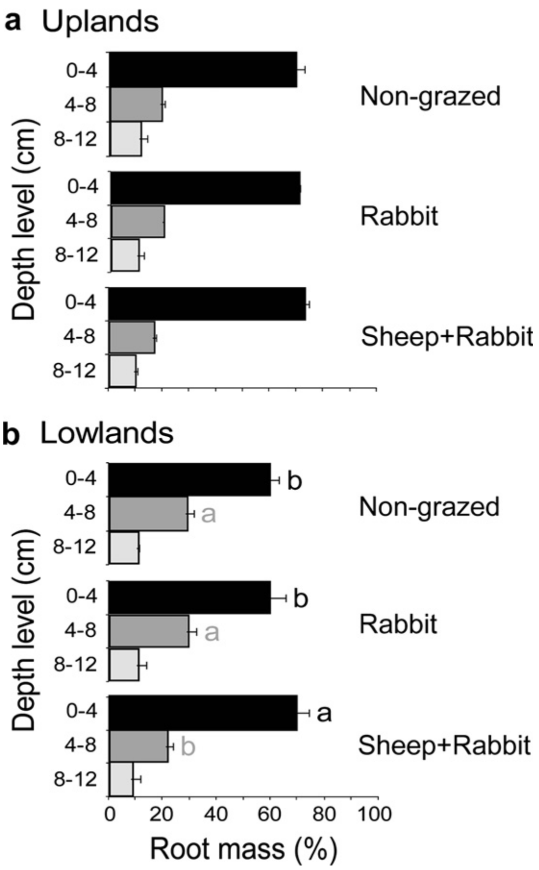

Fig. 2. Vertical profiles of root mass percentages in each grazing treatment at uplands and lowlands. Root mass was measured in 4-cm soil intervals; i.e. at 0–4, 4–8 and 8–12 cm soil depths. For each topographical location and soil layer, different letters indicate significant statistical differences of percent root mass between grazing treatments (Fisher LSD-test, $p < 0.05$).

Summarizing, our results highlight the importance of habitat productivity in predicting herbivore impact on belowground processes in semiarid environments dominated by annuals. Thus, while at less productive sites (uplands) we observed no herbivory effects on root mass patterns, at more productive sites (lowlands) grazing increased root mass in the upper soil layers. Herbivore effect was only observable when both sheep and rabbits were included in the assemblage, which may suggest that different-sized herbivores can affect differently root attributes such as have been demonstrated for plant community structure and plant diversity (Olofsson et al., 2004; Bakker et al., 2006). However, more research would be necessary to confirm this extreme. Finally, we would like to note that grazing effect on root vertical distribution is not negligible considering that 70% of total root mass was concentrated in the first 4 cm of soil. This might have important consequences for plant–plant interactions and grazed plant community dynamics, particularly because a higher concentration of belowground biomass towards the upper soil layers may result in both increased competition for water and nutrients, and reduced opportunities for the establishment of new plants.

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