

Below-ground biomass and productivity of a grazed site and a neighbouring ungrazed enclosure in a grassland in central Argentina

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Abstract We estimated the below-ground net plant productivity (BNPP) of different biomass components in an intensively and continuously 45-ha grazed site and in a neighbouring enclosure ungrazed for 16 years for a natural mountain grassland in central Argentina. We measured approximately twice as much dead below-ground biomass in the grazed site as in the ungrazed site, with a strong concentration of total below-ground biomass towards the upper 10 cm of the soil layer in both sites. The main contribution to total live biomass was accounted for by very fine (<0.5 mm) and fine roots (0.5–1.0 mm) both at the grazed (79%) and at the ungrazed (81%) sites. We measured more dead biomass for almost all root components, more live biomass of rhizomes, tap roots and bulbs, and less live biomass of thicker roots (>1 mm) in the grazed site. The seasonal variation of total live below-ground biomass mainly reflected climate, with the growing season being limited to the warmer and wetter portion of the year, but such variation was higher in the grazed site. Using different methods of estimation of BNPP, we estimated maximum values of 1241 and 723 g m⁻² year⁻¹ for the grazed and ungrazed sites, respectively. We estimated that very fine root productivity was almost twice as high at the grazed site as at the ungrazed one, despite the fact that both sites had similar total live biomass, and root turnover rate was twofold at the grazed site.

Key words: below-ground net plant productivity, fine roots, livestock grazing, long-term enclosure, mountain grassland, root components, root turnover rate.

INTRODUCTION

Grazing by large herbivores is a major structuring force in ecological systems, although the direction of herbivore effects on plant productivity has been much debated in the literature (McNaughton 1979; Belsky *et al.* 1993). Studies of the effects of grazing on above-ground net plant productivity (ANPP) have shown a variety of responses, including no detectable changes (Milchunas & Lauenroth 1993; Beaulieu *et al.* 1996), stimulation during brief periods (McNaughton 1979) or complete growing seasons (McNaughton 1985), and a reduction of ANPP (Biondini *et al.* 1998; Pucheta *et al.* 1998a).

Despite the importance of total (above- and below-ground) primary productivity as a regulator of energy flow through ecosystems (McNaughton *et al.* 1989), the published work refers mostly to above-ground

studies, and there is very little information on the effects of herbivores on below-ground net plant productivity (BNPP), either below-ground (Bardgett *et al.* 1999; Denton *et al.* 1999) or above-ground (van der Maarel & Titlyanova 1989; McNaughton *et al.* 1998).

Early pot studies of the effects of defoliation on individual plants showed that clipping often reduces short-term root growth (Jameson 1963). More recently, however, several authors have found a variety of responses to this experimental treatment, sometimes stimulatory, sometimes without response and sometimes inhibitory (Georgiadis *et al.* 1989; de Mazancourt *et al.* 1998). Similarly, field studies indicate that grazing can produce no effect (Milchunas & Lauenroth 1989; McNaughton *et al.* 1998), can decrease (Beaulieu *et al.* 1996; Biondini *et al.* 1998) or can increase root biomass or BNPP (van der Maarel & Titlyanova 1989). Clearly, a general pattern of response of ANPP and BNPP to grazing in grassland ecosystems is yet to be identified, although conceptual and quantitative models have been proposed in order

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to predict structural and functional changes in grasslands along gradients of grazing intensity, grazing history and environmental moisture (Milchunas & Lauenroth 1993; McNaughton *et al.* 1998).

In the present study, we compare the biomass and BNPP of different below-ground components in a grazed pasture and a neighbouring long-term ungrazed enclosure in a natural mountain grassland in central Argentina.

Previous results from this site have shown that continuous grazing promotes diversity (Díaz *et al.* 1994; Pucheta *et al.* 1998a), a biomass increase of graminoids and prostrate forbs, and a decrease in total standing crop and ANPP, as compared with long-term excluded grasslands (Pucheta *et al.* 1998a).

METHODS

Study area

The present study was performed in Pampa de Achala, a high plateau at 2150 m a.s.l. in central Argentina (31°24'–31°50'S, 64°45'–64°52'W). The bedrock is granitic with residual deposits accumulated during the Pleistocene (Gordillo & Lencinas 1979). The climate is temperate. The mean temperatures of the coldest and warmest months are 4.0 and 11.4°C, respectively, and the annual rainfall is 850 mm, highly concentrated in the warm season from November to March. Snowfall is likely from April to November and there is no frost-free period (Cabido *et al.* 1987).

The vegetation consists of natural grasslands that have been subjected to grazing by livestock since the seventeenth century, but native herbivores, mainly *Camelidae*, were common during the Pleistocene (Díaz *et al.* 1994). At a local scale, the spatial distribution of vegetation is mainly determined by edaphic patchiness and soil moisture regime (Cabido *et al.* 1987). On relatively deep, well-drained soils, the dominant vegetation consists of a matrix of tall tussock grasslands (dominated by *Deyeuxia hieronymi*, *Festuca tucumanica* and *Poa stuckertii*), which is transformed by moderate to heavy grazing into patches of short grazing lawns (dominated by *Eragrostis lugens*, *Agrostis pyrogea*, *Agrostis montevidensis*, *Alchemilla pinnata*, *Oreomyrrhis andicola*, *Carex fuscula* var. *distenta*, *Galium richardianum*, *Noticastrum marginatum* and *Gentiana parviflora*). The dominance of tall tussock grasses or turf species is related to the intensity of grazing, which promotes plant diversity, a decrease of total above-ground biomass, and an increase in above-ground biomass and productivity of turf species (Pucheta *et al.* 1998a).

Nomenclature of plant species follows Zuloaga *et al.* (1994) and Zuloaga and Morrone (1996, 1999).

Sampling design and data analysis

A 45-ha site grazed by cattle and horses was compared with a neighbouring 25 m × 25 m enclosure with 16 years of protection from large-herbivore grazing. The grazed site had been continuously grazed at a moderate-to-high stocking rate (approximately 0.25 horses and 0.50 cows ha⁻¹) for at least 10 years before and after building the enclosure and had not been burned during the previous 16 years. Sipowicz *et al.* (1978) reported close similarities in habitat conditions and initial vegetation between the grazed and ungrazed sites prior to establishment of the enclosure. Although this does not solve the statistical problem of a lack of true replicates (Hurlbert 1984; but see Oksanen 2001), the similarity between sites increases the likelihood that significant differences are a result of the long-term protection from grazing. This long-term enclosure represents a unique opportunity to study the effect of long-term enclosure on the mountain grasslands of central Argentina, and has been utilized in previous studies (Díaz *et al.* 1994; Pucheta *et al.* 1998a).

Below-ground biomass was harvested at both sites, taking into account seasonal variations in rainfall and temperature, on 22 October 1993 (spring) and on 5 February (summer), 7 April (autumn) and 24 August (winter) 1994. Harvests consisted of 10 compound samples, each including six monoliths extracted at two soil depths, 0–10 and 10–20 cm, by means of a 37-mm-diameter iron corer.

The washing and classification of material involve the most serious practical problems in studies of below-ground biomass, because of their high labour and financial costs (Persson 1990). For the present study, we developed a device similar to that used by Lauenroth and Whitman (1971) to wash and separate roots from the soil more efficiently. It consisted of three vertically connected recipients (50 cm in diameter), each of them separated by 1/16-, 1/64- and 1/196-cm meshes. Before washing, samples were shaken in a bath with 10% chlorine solution for 15 min to allow separation of roots from the soil, and then treated with 1% solution of sodium hexametaphosphate for 1 h to disperse the remaining soil particles and facilitate root separation (Dahlman & Kucera 1965). After soaking, samples were transferred to the device described above for separation.

After mesh separation, below-ground structures were manually classified under a dissecting microscope into seven components according to their average diameter and function: (i) very fine roots, <0.5 mm; (ii) fine roots, 0.5–1.0 mm; (iii) thick roots, >1.0 mm; (iv) crowns; (v) bulbs (e.g. *Nothoscordum* and *Zephyranthes longistyla*); (vi) rhizomes (e.g. *Alchemilla pinnata*); and (vii) tap roots (e.g. *Oreomyrrhis andicola*). Each of these components was further split into live and dead matter, taking into consideration texture,

consistency and colour (Aerts *et al.* 1989). All very fine roots were considered to be alive, since their high decomposition rate makes them unlikely to be detected when dead. The different components were oven-dried at 60°C to a constant weight and subsamples from each sample were combusted in a furnace at 600°C for 6 h in order to determine ash content and apply an ash-free correction factor to each sample.

Biomass values of the grazed site and the enclosure and of the biomass components were compared by means of Kruskal–Wallis tests, as the assumptions required for parametric tests were not met by the data (Norušis 1992).

The average BNPP of both the grazed site and the enclosure were estimated from each of 10 individual subsamples by four different methods: (i) summation of all positive increments in total below-ground biomass throughout the entire year; (ii) summation of all positive increments in total live biomass plus positive increments in total dead biomass throughout the entire year; (iii) summation of all positive increments observed in live biomass throughout the entire year; and (iv) summation of all positive increments in live biomass of each root component.

The methods we used to estimate BNPP are likely to suffer from bias leading to overestimation because all positive increments across sampling dates are summed regardless of their significance, and negative differences are not considered (Biondini *et al.* 1991). However, these methods are commonly used, and thus the estimates allow comparison with other grasslands of the world.

We estimated the root turnover rate (RTR) in a similar way to Dahlman and Kucera (1965): $RTR = BNPP / \text{mean below-ground biomass}$, where both BNPP and mean below-ground biomass are estimated from live biomass.

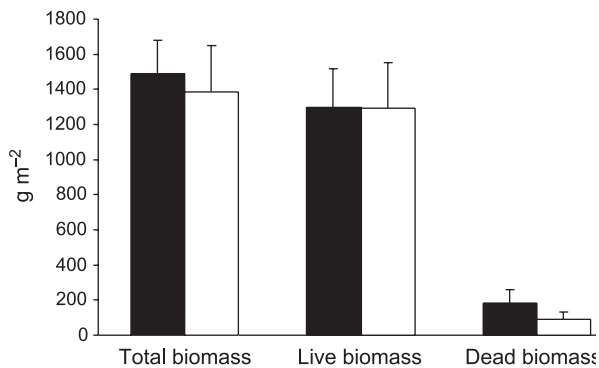


Fig. 1. Measured below-ground total, live and dead biomass ($\text{g m}^{-2} + \text{SD}$) in the soil profile (0–20 cm) in (■) a long-term grazed site and in (□) a long-term ungrazed site in a mountain grassland of central Argentina.

RESULTS

Changes in total below-ground biomass

Our estimate of dead below-ground biomass was twice as high in the grazed site as in the ungrazed site (Fig. 1). Total live biomass made up 87 and 93% of total below-ground biomass on these two sites, respectively. Most of the below-ground biomass was in the upper 10 cm of the soil profile for the grazed site (1264.06 g m^{-2} at 0–10 cm and 221.82 g m^{-2} at 10–20 cm) and for the ungrazed site (1203.33 g m^{-2} at 0–10 cm and 185.92 g m^{-2} at 10–20 cm), making up 85 and 87% of the total estimated biomass, respectively. There were similar values for live biomass at two soil depths for the grazed site and the ungrazed site (Fig. 2); the dead below-ground biomass was greater on the grazed site (approximately twofold greater at the 0–10 cm layer and approximately two orders of magnitude greater at the 10–20 cm layer).

Changes in different below-ground components

The main contribution to total live below-ground biomass was by very fine roots (<0.5 mm, all assumed alive) and fine roots (0.5–1.0 mm) at both the grazed and the ungrazed site (Fig. 3a). Although similar in terms of total live biomass, the grazed site and the ungrazed site had different distributions of live biomass in different root-diameter and functional classes. In the grazed site there was more live biomass of rhizomatous plants (mainly forbs), bulbs and tap roots, and less live biomass of roots thicker than 1 mm (mainly from tall tussock grasses). Live biomass of crowns, mainly graminoids, was very similar in the grazed and the ungrazed sites (Fig. 3a).

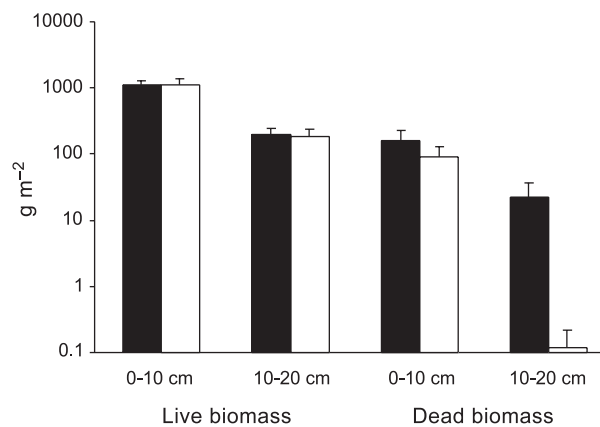


Fig. 2. Measured live and dead below-ground biomass ($\text{g m}^{-2} + \text{SD}$) at two soil depths in (■) a long-term grazed site and in (□) a long-term ungrazed site in a mountain grassland of central Argentina.

Dead below-ground biomass was greater in the grazed compared to the ungrazed site in all the components studied, except bulbs (Fig. 3b).

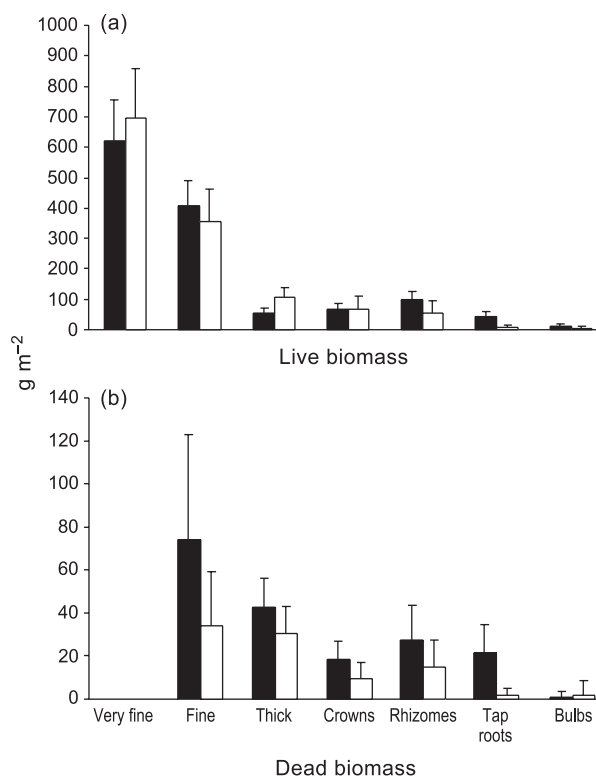


Fig. 3. Measured biomass ($\text{g m}^{-2} \pm \text{SD}$) of (a) live and (b) dead matter of the different below-ground components studied in (■) a long-term grazed site and in (□) a long-term ungrazed site in a mountain grassland of central Argentina.

Seasonal changes in below-ground biomass

The seasonal patterns of total live below-ground biomass mainly reflected seasonal variations in temperature and rainfall, with the growing season being restricted to the warmer and wetter period of the year between spring and autumn (Fig 4a,b). We measured a

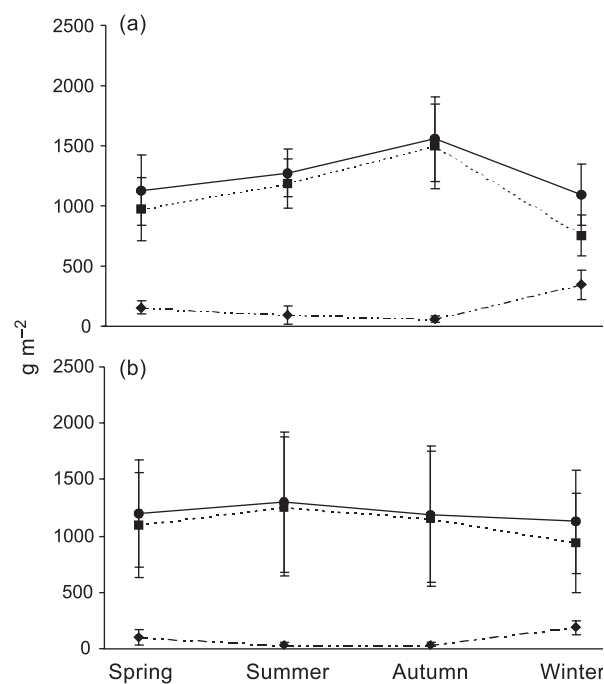


Fig. 4. Seasonal variations in (■) live, (◆) dead and (●) total below-ground biomass ($\text{g m}^{-2} \pm \text{SD}$) in (a) a long-term grazed site and (b) a long-term ungrazed site in a mountain grassland of central Argentina.

Table 1. Seasonal variations of below-ground biomass in the soil profile (0–20 cm) of the different components studied in a grazed site in a mountain grassland of central Argentina

	Spring ($\text{g m}^{-2} \pm \text{SD}$)	Summer ($\text{g m}^{-2} \pm \text{SD}$)	Autumn ($\text{g m}^{-2} \pm \text{SD}$)	Winter ($\text{g m}^{-2} \pm \text{SD}$)	χ^2*	P^*
Live biomass						
Very fine roots	480.54 ± 74.62	653.61 ± 90.76	985.54 ± 234.73	365.21 ± 64.38	32.1395	0.00010
Fine roots	383.43 ± 173.58	451.56 ± 105.84	543.00 ± 141.10	242.64 ± 108.88	18.9816	0.00030
Thick roots	63.66 ± 45.57	50.10 ± 13.19	65.99 ± 35.64	38.92 ± 16.44	3.8927	0.27330
Crowns	57.90 ± 38.86	58.81 ± 33.27	53.98 ± 35.76	95.13 ± 53.60	4.2495	0.23580
Rhizomes	110.43 ± 34.53	118.32 ± 88.89	77.16 ± 45.76	87.23 ± 39.91	2.4283	0.48840
Bulbs	8.51 ± 11.76	15.55 ± 21.47	17.52 ± 22.61	8.84 ± 13.94	1.0284	0.79440
Tap roots	29.47 ± 17.96	33.40 ± 27.04	52.73 ± 51.54	53.58 ± 32.32	3.5557	0.31360
Total live	974.53 ± 265.38	1183.08 ± 203.81	1495.77 ± 348.86	751.90 ± 167.88	21.3465	0.00010
Dead biomass						
Fine roots	50.54 ± 31.02	16.21 ± 16.82	9.01 ± 6.32	220.47 ± 84.08	28.9816	0.00010
Thick roots	49.41 ± 20.36	23.72 ± 8.82	26.86 ± 16.16	70.55 ± 26.88	22.2159	0.00010
Crowns	24.89 ± 6.77	25.61 ± 11.95	33.89 ± 25.80	79.86 ± 55.97	5.2436	0.15480
Rhizomes	35.42 ± 30.17	14.77 ± 21.03	10.04 ± 11.89	49.21 ± 43.51	12.6731	0.00540
Bulbs	4.26 ± 10.72	0.00	0.00	0.00	NA	NA
Tap roots	20.53 ± 16.13	29.47 ± 41.36	10.32 ± 10.09	26.22 ± 22.32	4.0850	0.25240
Total dead	156.76 ± 52.68	89.81 ± 76.18	57.89 ± 23.65	344.13 ± 124.05	27.9287	0.00001

*Results of Kruskal–Wallis test. NA, not applicable.

minimum total live biomass of 752 and 937 g m⁻² at the grazed and ungrazed sites, respectively, and this measure coincided with the end of the driest and coldest period (August). The maximum live biomass, observed in the favourable season, was 1259 and 1496 g m⁻² for the grazed and the ungrazed sites, respectively. Live biomass increased sharply from spring to autumn in the grazed site (Fig. 4a), whereas it did not appear to change throughout the entire growing season in the ungrazed site (Fig. 4b). Dead biomass showed an opposite pattern to that of live biomass: an increase in the unfavourable season, in winter, at both sites.

Live and dead biomass of the different below-ground components showed a similar seasonal pattern to that of total biomass – maximum live biomass in summer (February) and autumn (April), and maximum dead biomass in spring (October) and winter (August) – at both sites (Tables 1,2). Moreover, variations detected in total live biomass during the growing season in the grazed site (Fig. 4a) were mainly explained by changes in the live biomass of very fine and fine roots (Table 1).

Changes in below-ground net plant productivity

The estimation of BNPP with four different methods, taking into account increments in different biomass compartments, ranged from 708 to 1241 g m⁻² year⁻¹ for the grazed site and from 116 to 723 g m⁻² year⁻¹ for the ungrazed site (Table 3). Although there were no significant differences in BNPP between the grazed and ungrazed sites, there were significant differences in annual productivity of very fine and fine roots and crowns (Table 4). At the grazed site, very-fine-root productivity almost doubled that of the ungrazed site, and fine-root productivity was detectable only at the grazed site. We measured crown productivity to be threefold greater in the ungrazed site. In contrast, we measured a greater biomass of rhizomes and bulbs and lower productivity in the grazed site, and conversely, lower biomass and higher productivity in the ungrazed site (Table 4).

Root turnover rate showed that 95% of the biomass was renewed each year in the grazed site, compared with the site that had been ungrazed for 16 years, in

Table 2. Seasonal variations of below-ground biomass in the soil profile (0–20 cm) of the different components studied in a long-ungrazed enclosure in a mountain grassland of central Argentina

	Spring (g m ⁻² ± SD)	Summer (g m ⁻² ± SD)	Autumn (g m ⁻² ± SD)	Winter (g m ⁻² ± SD)	χ ² *	P*
Live biomass						
Very fine roots	632.59 ± 139.65	640.28 ± 257.22	889.90 ± 444.27	615.14 ± 352.62	4.3741	0.2238
Fine roots	445.96 ± 260.86	435.93 ± 194.83	340.82 ± 181.74	205.62 ± 99.74	10.4751	0.0149
Thick roots	114.03 ± 55.12	122.24 ± 90.69	96.41 ± 54.80	89.28 ± 68.24	1.7693	0.6216
Crowns	37.78 ± 29.00	133.09 ± 119.98	44.60 ± 53.28	50.71 ± 71.75	6.9006	0.0751
Rhizomes	22.09 ± 21.72	82.04 ± 93.06	68.84 ± 111.82	46.32 ± 51.42	2.9829	0.3943
Bulbs	0.49 ± 1.11	3.93 ± 3.86	12.61 ± 25.01	1.47 ± 3.13	4.3601	0.2251
Tap roots	2.46 ± 5.31	9.66 ± 16.98	4.91 ± 6.45	12.12 ± 20.11	2.7283	0.4354
Total live	1094.41 ± 462.17	1258.80 ± 614.33	1153.44 ± 597.26	936.85 ± 443.57	2.3465	0.5018
Dead biomass						
Fine roots	58.66 ± 60.37	3.32 ± 1.55	3.46 ± 2.24	71.15 ± 21.69	24.7883	0.0001
Thick roots	33.28 ± 25.58	17.70 ± 10.24	20.52 ± 14.96	49.81 ± 32.22	10.2097	0.0169
Crowns	2.70 ± 1.96	9.09 ± 9.80	8.86 ± 14.10	16.76 ± 25.55	3.9502	0.2669
Rhizomes	8.60 ± 18.02	6.45 ± 14.51	5.88 ± 11.16	38.98 ± 34.59	14.4307	0.0024
Bulbs	0.00	0.00	0.00	8.02 ± 25.36	NA	NA
Tap roots	0.00	2.13 ± 3.38	0.00	4.91 ± 11.35	7.7962	0.0504
Total dead	103.17 ± 65.46	38.63 ± 17.71	38.59 ± 20.62	189.36 ± 61.06	22.5437	0.0001

*Results of Kruskal–Wallis test. NA, not applicable.

Table 3. BNPP estimated by four different methods, taking into account positive increments of different biomass components, in a long-term grazed pasture and long-term protected enclosure in a mountain grassland of central Argentina

BNPP estimation	Grazed site (g m ⁻² year ⁻¹ ± SD)	Ungrazed enclosure (g m ⁻² year ⁻¹ ± SD)
Total biomass	712.96 ± 401.38	116.40 ± 782.18 (NS)
Live biomass plus dead biomass	708.39 ± 382.42	116.33 ± 767.77 (NS)
Live biomass	848.18 ± 365.67	191.52 ± 764.91 (NS)
Live biomass of seven root components	1241.06 ± 299.44	723.41 ± 564.64 (NS)

BNPP, below-ground net plant productivity; NS, not significant.

which only 56% of the biomass was renewed each year (Table 4). Considering the live biomass of different root classes, two groups of responses to grazing could be detected: those components that increased RTR and those that decreased it. In the grazed site, we measured a higher turnover rate of different components, whereas in the ungrazed site, we measured a higher turnover rate of below-ground components with some type of reserve function, such as crowns, rhizomes, bulbs and tap roots.

DISCUSSION

For the two sites in the present study, we measured a total below-ground biomass that was threefold greater than that found in other mountain regions with more rainfall (Sundriyal 1992), and greater than that described in a precipitation gradient from 350 to 1200 mm in the Serengeti plains (McNaughton *et al.* 1998). Notwithstanding this, our values are within the range described for several other temperate and subtropical grasslands (San José *et al.* 1982; Milchunas & Lauenroth 1989).

We measured the total below-ground biomass values in the grazed site to be similar to those for the site excluded from grazing for 16 years. These results are similar to those reported by several authors who found few positive or no changes in root biomass with grazing in grasslands with a long evolutionary history of grazing (Milchunas & Lauenroth 1989; van der Maarel & Titlyanova 1989; McNaughton *et al.* 1998). In a previous study in the same area, Pucheta *et al.* (1998a) found that long-term protection from grazing (16 years) increased the total above-ground biomass and decreased the live : dead biomass ratio by 500%, compared with moderately to heavily grazed samples.

We measured a strong vertical concentration of below-ground biomass towards the upper 10 cm of the soil profile, both in the grazed and in the ungrazed sites.

Although we only have data from the first 20 cm of the soil, we believe that more than 80% of the total biomass was located in this upper layer, as described in most other studies (Dahlman & Kucera 1965; Milchunas & Lauenroth 1989; McNaughton *et al.* 1998). The vertical distribution of the total below-ground biomass was similar between the grazed site and the ungrazed site, although the finest roots were found deeper in the soil profile in the grazed site. Therefore, we did not find an extension of the 'grazing lawn concept' below-ground, as suggested by Milchunas and Lauenroth (1989).

The seasonal variations of below-ground biomass mainly reflected climatic constraints, with the growing season being limited to the warmer and wetter period of the year, from early spring in October to early autumn in April. A similar pattern in seasonal root variation has been found in a wide variety of grasslands (Dahlman & Kucera 1965; Sundriyal 1992; McNaughton *et al.* 1998). Minimum biomass was reached at the beginning of the rainy season, whereas maximum biomass appeared at the favourable-unfavourable season transition. In the grazed site, we measured a higher difference in below-ground biomass between the maximum, at the end, and the minimum, at the beginning of the growing season, suggesting a grazing effect on root growth and mortality.

The main contribution to total live below-ground biomass was accounted for by the finest roots (<1 mm), both in the grazed site and in the ungrazed site. In the grazed site, we measured more biomass of below-ground organs with spreading (rhizomes) or reserving function (bulbs, tap roots), and less biomass of thick roots, mainly from tall tussock grasses. The dead below-ground biomass of all different components was greater in the grazed site, with the exception of bulbs.

Most published reports on below-ground biomass in grasslands distinguish only gross biomass components, such as total standing (Dahlman & Kucera 1965; Sundriyal 1992), live and dead (McNaughton *et al.*

Table 4. BNPP, mean annual live biomass and RTR of the different below-ground components studied at a long-term grazed site and a long-term enclosure in a mountain grassland of central Argentina

	BNPP estimation (g m ⁻² year ⁻¹ ± SD)		Mean live biomass (g m ⁻² ± SD)		RTR (year ⁻¹)	
	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed
Very fine	844.08 ± 610.82 ^a	492.09 ± 1442.47 ^b	621.23 ± 135.12	694.48 ± 163.68	1.36	0.71
Fine	256.35 ± 611.01	–	405.16 ± 85.41	357.08 ± 104.83	0.63	NA
Thick	30.75 ± 139.14	9.56 ± 310.88	54.67 ± 15.78	105.49 ± 33.71	0.56	0.09
Crowns	37.10 ± 185.94 ^a	116.39 ± 344.40 ^b	66.45 ± 21.47	66.55 ± 43.45	0.56	1.75
Rhizomes	18.01 ± 255.48	69.84 ± 352.15	98.29 ± 28.43	54.82 ± 39.18	0.18	1.27
Bulbs	12.01 ± 81.65	20.81 ± 57.68	12.61 ± 8.92	4.63 ± 6.58	1.01	2.01
Tap roots	42.74 ± 133.70	14.70 ± 62.42	42.30 ± 17.45	7.29 ± 6.89	0.95	4.49
Total live	1241.06 ± 1156.35	723.41 ± 15099.32	1300.71 ± 217.12	1290.34 ± 263.13	0.95	0.56

^{a,b}Significantly different ($P < 0.05$, Kruskal–Wallis test). –, none detected; BNPP, below-ground net plant productivity; NA, not applicable; RTR, root turnover rate = BNPP/mean annual live biomass.

1998), different plant species (Shaver & Billings 1975), roots and crowns (Milchunas & Lauenroth 1989), and fine roots alone (Jackson *et al.* 1997). Studies considering more detailed components, such as the present study, are very rare, and we found no published studies taking into account finer details such as different diameters and functional classes. Our measurements allowed us to compare changes in below-ground compartments with those of above-ground compartments reported in a previous study (Pucheta *et al.* 1998a).

Changes in the below-ground biomass of the different components as a result of grazing mirrored those previously observed above-ground on different plant functional groups (Pucheta *et al.* 1998a). For example, we measured more below-ground biomass of rhizomes and finest roots paired with an increase in above-ground biomass of prostrate-stoloniferous plants and graminoids in the grazed site, and an increase in both thicker roots and tall tussock grasses in the enclosure.

Our estimates of BNPP are within the range of most grasslands, but are closer to results reported for more mesic sites (Bulla *et al.* 1980). We found our estimate of BNPP depended on the method we used – with higher values being obtained using the method that took into account increments in live biomass of the seven below-ground components, and lower values being obtained using the method that considered increments in total below-ground biomass. We believe that the real value might fall between these estimates. Notwithstanding, all methods estimated a higher BNPP in the grazed site, which was an average of 459% higher than that of the ungrazed site. Although there are few studies of the effects of grazing on grassland BNPP, a generalized view until recently was that clipping or grazing reduces root growth (Sundriyal 1992). However, there is an increasing bulk of evidence favouring the view that herbivores produce undetectable (Cargill & Jefferies 1984; McNaughton *et al.* 1998) or positive effects on BNPP (van der Maarel & Titlyanova 1989).

We measured a very fine root productivity that was almost twice as great at the grazed site relative to the ungrazed site, despite the fact that their total live biomass differed only slightly. Many authors have stressed the importance of fine-root growth on ecosystem processes (Bardgett *et al.* 1999; Gordon & Jackson 2000). Fine roots are the primary pathway for water and nutrient uptake by plants – playing the same role as leaves for carbon and energy uptake – and they are also an important sink for carbon acquired in terrestrial net primary productivity (Hendricks *et al.* 1993; Jackson *et al.* 1997). Taking into account RTR, 95% of the below-ground biomass was renewed each year in the grazed site, compared with 56% in the ungrazed site. Root turnover is a critical component of ecosystem nutrient dynamics and carbon sequestration

and is also an important sink for plant primary productivity. Although at a global scale differences in RTR mainly correlate to environmental variables and ecosystem type (Gill & Jackson 2000), the role that plant functional types and herbivory play within ecosystems is little understood.

Taking into account data on above-ground plant biomass and productivity in the same sites (Pucheta *et al.* 1998a), we can estimate the total (above-ground plus below-ground) biomass at approximately 1750 g m⁻² for the grazed site (root : shoot ratio 5.5) and 2845 g m⁻² for the ungrazed site (root : shoot ratio 0.94). In this subhumid mountain grassland, grazing enhances floristic diversity, decreases total biomass and ANPP, increases biomass and above-ground productivity of graminoid and prostrate species (Pucheta *et al.* 1998a), and increases foliar nitrogen content of grazed plants (Pucheta *et al.* 1998b). The measurements in the present study suggest that grazing could enhance root turnover, fine-root productivity and total BNPP, despite the fact that no changes in total below-ground biomass have been observed.

We think that the results reported in the present study and in our previous studies suggest an impact of grazing that deserves more detailed study.

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