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Floristic composition, biomass, and aboveground net plant production in grazed and protected sites in a mountain grassland of central Argentina

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Abstract – Changes in plant community composition, diversity, aboveground biomass, and aboveground net primary production (ANPP) of different plant growth-forms were assessed in sites protected from livestock grazing for 2, 4, and 15 years, and in a heavily-grazed site.
Species richness was maximum at the grazed site and decreased significantly after 4 years of protection. Diversity decreased significantly only after 15 years of protection. No alien or weedy species were found at grazed or protected sites. Grazing exclusion produced a shift from grazing-tolerant or grazing-avoiding species with a graminoid or prostrate growth-form to taller species with a tall tussock growth-form. Grazing produced a 33 % decrease in standing biomass but little change in ANPP when compared to the site protected from grazing for 2 years, but important changes in both biomass and ANPP respect to the sites protected for 4 and 15 years. Consumption was near 35 % of ANPP. © Elsevier, Paris

biomass, consumption, diversity, floristic composition, growth form, livestock grazing, moveable cages

1. INTRODUCTION

Conceptual and quantitative models have been proposed in order to predict changes in plant species composition, diversity, growth-forms and primary production in grasslands along gradients of evolutionary histories of grazing and environmental moisture [33, 34]. After a comprehensive review, Milchunas and Lauenroth [33] concluded that changes in plant species composition and growth-forms in response to grazing are primarily related to environmental moisture, – or its correlate aboveground net primary production (ANPP) – the evolutionary history of grazing, and the recent level of consumption by the herbivores. Differences in ANPP between ungrazed and grazed sites may also be related to the number of years of protection from grazing. They also pointed out that changes in ANPP are not necessarily coupled with changes in species and growth-form composition. Moreover, changes in ANPP in response to grazing may be both positive or negative, regardless of the magnitude of changes in species composition.

Concerning the evolutionary history of grazing, there is evidence for ancient occupation of the montane grassland belt of Cordoba by large herbivores, *Glyptodon* (Glyptodontidae), *Scelidotherium* (Mylodontidae), *Lama* and *Paleolama* (Camelidae), *Macrauchenia* (Macrauchenidae), *Equus* (Equidae) and *Toxodon* (Toxodontidae), being the most important species before the massive Pleistocene extintions [9, 24; A. Tauber, pers. comm.]. According to McNaughton [31], the absence of significant densities of large herbivores between the Pleistocene and the colonial period is a distinctive pattern of South American grasslands. While this holds true in many cases, the generalization seems too broad and does not hold for all South American regions. Neotropical savannas have a short evolutionary history of grazing [47] whereas Andean and Andean-related peoples are known to have raised large herds of Camelidae for thousands of years [15, 16, 18, 21]. Closer to our study area, Sala [44] has explained the marked changes in the species composition of Argentine pampean grasslands under present livestock grazing as the response to a disturbance agent for which the local plant populations were not adapted [cf. 39]. In that area, heavy stocking rates were not introduced before the 18th Century, although there are reports of earlier occupation by wild native ungulates and wild horses and cattle [49]. The grazing history of the Central to North-Western area of the country where we performed our study is quite different due to ecological

Nomenclature: Hunziker (1984) for generic level. Nomenclature of species may be requested from the authors.

and socio-historical factors. Unlike the southern parts of the country, the population of Spanish origin had taken over a great proportion of the Córdoba montane areas by the early 17th Century. The Spanish breed livestock, especially mules and later shifting to cattle and sheep. The stocking rates at that time are difficult to quantify, but they seem to have been similar or probably heavier than currently occur [1, 15].

The introduction of domestic ungulates about 350 years ago has apparently not produced major changes in plant species composition, contrary to what has been observed in grasslands that were previously ungrazed or grazed by only a few large herbivores, where alien species tend to dominate in grazed sites [17, 25, 34].

In this paper we report differences in species and growth forms composition, and ANPP between one grazed and three ungrazed sites in a mountain grassland from central Argentina. The ungrazed sites differed in the numbers of years they were protected from grazing by large domestic herbivores. Previous reports of ANPP for grasslands in the same region [48], together with available climatic data, suggest that these grasslands may be considered as subhumid and productive according to the ranking by Milchunas et al. [34] and Milchunas and Lauenroth [33]. Based on the analyses of Milchunas and Lauenroth under these circumstances we should expect that grazing promotes species richness, dominance by grazing tolerant/avoiding plant species or growth forms, and no invasion by alien species. As the time of protection from grazing increases, we should find a decrease in species richness, and an increase of tall species or growth forms and an increase in ANPP.

2. MATERIAL AND METHODS

2.1. The study area

The study area is located in Pampa de Achala, a high plateau at 2150 m altitude in Córdoba Province (31°24'-31°50' S and 64°45'-64°52' W) (*figure 1*). The bedrock is crystalline with sedimentary deposits formed during the Pleistocene [20]. The climate is temperate with cold winters (May to September) and cool summers (October to April). Mean temperature of coldest (winter) and warmest (summer) months are 5 and 11.4 °C, respectively, and mean annual precipitation for a 12 year record is 850 mm; rainfall is highly concentrated between October and April. Snows and frosts are likely to occur from April to November [8].

The vegetation is a climatically determined grassland subjected to pastoral use. At a local scale, spatial distribution of vegetation is mainly determined by soil texture influence on soil moisture regime [8]. Vegetation in grazed areas consists of a matrix of medium-to-

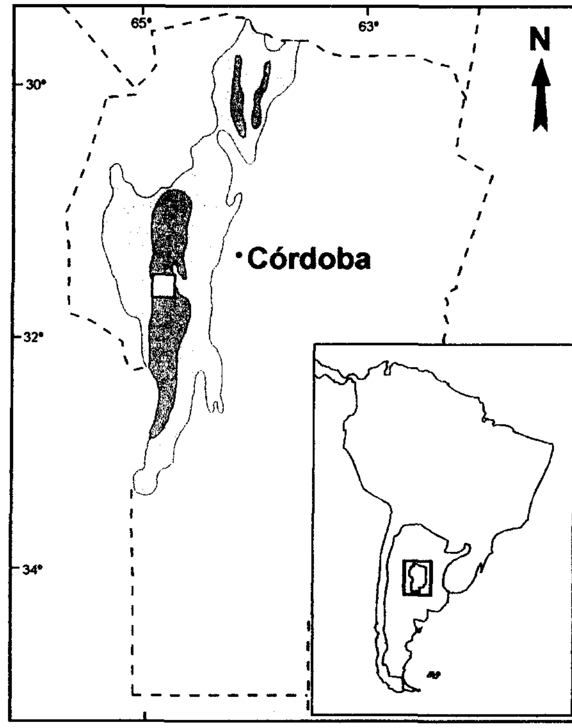

Figure 1. Location of the sudy area in Córdoba mountains, central Argentina. Light grey: xerophytic woodland belt; dark grey: grassland belt; open square: the study area.

tall grass species (*Deyeuxia hieronymi, Festuca tucumanica, Sorghastrum pellitum, Eragrostis lugens, Agrostis pyrogea, Agrostis montevidensis,* and *Poa stuckertii*) interspersed with turf species (*Alchemilla pinnata, Oreomhyrris andicola, Carex fuscula* var. *distenta, Relbunium richardianum, Noticastrum marginatum* and *Gentiana parviflora*). Tall tussock grasses like *Deyeuxia hieronymi* and *Festuca tucumanica* are the dominant species in ungrazed natural grasslands [8].

2.2. Sampling design

Plant species diversity and aboveground biomass were surveyed during the 1993-94 growing season.

Three contiguous 25 × 25 m exclosures with 2, 4, and 15 years of protection from grazing, were located inside a 45 ha site grazed by cattle and horses. The grazed site has been continuously grazed for at least 10 years before building the exclosures at a moderate-to-high stocking rate (*c.* 0.25 horse and 0.5 cows per ha) and was not burned the last 15 years. Sipowicz et al. [48] reported close similarities in habitat conditions and initial vegetation between the grazed and protected sites prior to establishment of the exclosures.

However, this does not solve the statistical problem of a lack of true replicates for the grazed or protected sites [23], but increases the likelihood that significant differences between plots are due to the time of protection from grazing.

2.3. Floristic composition and plant species diversity

Frequency values were obtained for all plant species in each site by recording their presence within 10 randomly placed 0.50 × 0.50 m sampling units subdivided into 25 smaller quadrats. Sampling was carried out at the end of the growing season (March). Similarity among grazed and ungrazed sites was calculated using the Sørensen index of similarity [26]. Plant species diversity (H') was calculated for each sample plot using the Shannon-Wiener index [26]. Significant differences in the average number of species per plot and diversity among sites were assessed by means of one-way ANOVA and Bonferroni multiple samples test [37].

2.4. Biomass and aboveground net plant production

Aboveground biomass was harvested sequentially in December, January, February, March, April, July and November 1993-94 in all sites. In the protected sites, aboveground biomass was harvested inside 10 randomly placed 30 × 30 cm sampling quadrats. In the grazed site, biomass consumption and aboveground net primary production were assessed by means of the moveable cage method [32]. Harvests were performed at each sampling date inside and outside ten 0.25 m^2 moveable cages using 30 × 30 cm sampling quadrats as in protected sites. Samples were sorted in the laboratory into 5 plant growth forms according to Díaz et al. [14] and Pucheta et al. [43] (annuals, creeping forbs, short graminoids, rosettes and tall tussock grasses), and separated into live and recently dead components. Litter was collected by hand from each sample quadrat in the field. After separation, plant material was water-cleaned and oven-dried at 75 °C and weighed once a constant weight was attained.

Biomass values of the different sites were compared by means of Kruskal-Wallis one-way ANOVA since the assumptions required for parametric tests were not met by the data [37].

Aboveground net primary production (ANPP) was estimated by two methods: (i) summation of all positive increments in live plus recent dead biomass throughout the entire year, and (ii) summation of all positive increments in live biomass only throughout the entire year. In the grazed site, ANPP resulted from the summation of the differences in biomass between caged plots at time t and uncaged plots at time t-1. Consumption was estimated by summation of the differences in standing biomass between caged and uncaged plots at time t.

The methods we used to estimate ANPP in the grazed and protected sites are likely to suffer from bias leading to overestimation because all positive increments are summed regardless of their significance, and negative differences are not considered [7, 44].

3. RESULTS

3.1. Changes in floristic composition and plant species diversity

We found 51 vascular plant species including 2 ferns (*Selaginella peruviana* and *Ophioglossum crotalophoroides*) in the study area; 41 of these species occurred at the grazed site, while 43, 35 and 23 species were present at the sites protected from grazing for 2, 4 and 15 years, respectively. Thirty two per cent of the total number of plant species were present at all sites. A small number of species were exclusive to each of the 4 sites. Only 2 alien species were recorded (the world-wide distributed *Cerastium arvense* and *Rumex acetosella*). Only 3 annual species (*Gentiana parviflora*, a creeping forb; *Muhlenbergia peruviana* and *Vulpia megalura*, short graminoids), only one geophyte (*Nothoscordum inodorum*) and one shrub (*Baccharis myrtilloides*) were sampled. All other plant species were perennial tall tussock grasses, short graminoids, rosettes or creeping forbs (*table I*).

Mean frequency values of perennial creeping forbs (e.g., *Relbunium richardianum, Mitracarpus cuspidatus,* and *Alchemilla pinnata*), and of short graminoids (e.g., *Carex fuscula* var. *distenta, Agrostis pyrogea, Agrostis montevidensis* and *Eragrostis lugens*) tended to decrease with time of protection from grazing (*table I*). Annual species had higher frequency values at both grazed and 2-years protected sites compared to sites protected from grazing for 4 and 15 years. In contrast, long-term protection from livestock grazing allowed the establishment of perennials like the shrub *Baccharis myrtilloides*, the tall tussock grass *Poa stuckertii,* and an increase in the frequency of other tall tussock grasses such as *Deyeuxia hieronymi* and *Festuca tucumanica.*

The number of species per plot decreased significantly ($F_{1, 16}$ = 72.05, P = 0.00001) after 4 years of protection from livestock grazing, while diversity decreased significantly ($F_{1, 16}$ = 55.93, P = 0.00001) only after 15 years of protection (*figure 2*).

Similarity between grazed and ungrazed sites decreased gradually as the time of protection from grazing increased (*table II*). The grazed site and the site protected for 2 years showed the highest similarity value. The site protected for 15 years showed the

Table I. Mean frequency values (± SE; n = 10; range = 0-25) of species present at a grazed site and at sites protected from grazing for 2, 4, and 15 years, in a mountain grassland from central-western Argentina. A, annuals; Cf, creeping forbs; F, ferns; G, short graminoids; R, rosettes; Sh, shrubs; T, tall tussock grasses.

Site		grazed	2-yr protected	4-yr protected	15-yr protected
number of species		25.20 ± 0.97	23.6 ± 0.68	17.30 ± 0.93	4.40 ± 1.63
diversity		2.84 ± 0.03	2.83 ± 0.03	2.53 ± 0.07	0.68 ± 0.26
Alternanthera pumila	Cf	0.60 ± 0.40			
Gnaphalium gaudichaudianum	R	0.30 ± 0.21			
Oenothera indecora	Cf	0.60 ± 0.60			
Sorghastrum pellitum	G	0.90 ± 0.90			
Stenandrium dulce	R	0.20 ± 0.13			
Relbunium richardianum	Cf	24.80 ± 0.13	21.30 ± 1.66	4.50 ± 0.97	0.20 ± 0.20
Mitracarpus cuspidatus	Cf	16.60 ± 1.91	7.80 ± 1.75	3.80 ± 0.96	
Mosses (mainly *Polytrichum juniperinum*)		19.30 ± 2.19	14.10 ± 2.17		
Carex fuscula var. *distenta*	G	10.10 ± 1.55	10.10 ± 1.58	8.40 ± 1.94	1.70 ± 0.91
Alchemilla pinnata	Cf	12.40 ± 3.16	8.90 ± 3.15	4.70 ± 2.43	
Muhlenbergia peruviana	A	12.20 ± 1.90	3.70 ± 1.63	0.20 ± 0.13	
Agrostis montevidensis	G	6.80 ± 1.73	6.70 ± 2.17	5.30 ± 1.24	
Eragrostis lugens	G	7.70 ± 2.17	7.40 ± 1.48	4.60 ± 1.09	
Agrostis pyrogea	G	7.30 ± 2.16	5.10 ± 1.79	0.90 ± 0.90	1.10 ± 1.10
Gamochaeta filaginea	R	6.80 ± 1.17	5.60 ± 1.28	1.90 ± 0.66	0.80 ± 0.55
Plantago myosurus var. *myosurus*	R	7.00 ± 2.13	6.90 ± 1.91	0.90 ± 0.41	
Selaginella peruviana	F	6.80 ± 1.63	4.10 ± 0.97	3.10 ± 1.41	0.50 ± 0.40
Poa resinulosa	G	4.60 ± 0.82	2.50 ± 1.09	3.80 ± 1.44	0.10 ± 0.10
Bromus auleticus	G	3.60 ± 1.75		1.90 ± 1.32	
Nothoscordum inodorum	G	2.60 ± 0.65	0.60 ± 0.31	0.10 ± 0.10	
Ophioglossum crotalophoroides	F	0.60 ± 0.22	0.20 ± 0.13		
Gentiana parviflora	A	7.50 ± 2.11	18.70 ± 1.87	8.00 ± 2.08	1.00 ± 0.89
Oreomyrrhis andicola	R	12.30 ± 2.66	19.30 ± 1.64	17.60 ± 2.11	2.00 ± 1.89
Lichenes (mainly *Xanthoparmelia* sp.)		6.50 ± 1.29	11.30 ± 2.11		
Plantago brasiliensis	G	3.10 ± 1.33	11.60 ± 2.88	14.40 ± 2.37	1.30 ± 1.30
Noticastrum aff. *marginatum*	R	2.90 ± 1.19	4.10 ± 2.15	4.00 ± 2.02	1.90 ± 1.90
Alchemilla sp.	Cf	5.20 ± 3.16	6.70 ± 3.10	4.00 ± 2.07	
Briza subaristata	G	0.20 ± 0.20	5.90 ± 1.52	2.90 ± 1.46	0.60 ± 0.43
Gamochaeta spicata	R	1.70 ± 0.68	1.30 ± 0.33		
Sisyrinchium unguiculatum	G	0.90 ± 0.23	4.00 ± 1.61	3.10 ± 1.47	
Juncus uruguensis	G		0.60 ± 0.43	0.10 ± 0.10	
Carex boliviensis	G		0.50 ± 0.40		
Deyeuxia hieronymi	G-T	4.90 ± 1.41	11.30 ± 2.39	9.80 ± 3.58	13.30 ± 3.82
Festuca tucumanica	G-T		1.00 ± 0.54	7.70 ± 2.18	10.00 ± 4.08
Eryngium nudicaule	R	0.50 ± 0.40	0.50 ± 0.40	1.50 ± 0.64	1.40 ± 0.98
Stipa juncoides	G		2.60 ± 1.74	2.60 ± 1.40	
Grindelia globulariaefolia	R		0.40 ± 0.40	0.80 ± 0.80	
Taraxacum officinale	R	0.60 ± 0.27	0.30 ± 0.21	1.00 ± 0.39	
Astragalus parodii	Cf	0.60 ± 0.60	0.20 ± 0.20		0.10 ± 0.10
Cardionema ramosissimum	Cf	1.40 ± 0.67	0.50 ± 0.40	0.30 ± 0.21	
Cerastium arvense	Cf	1.80 ± 0.68	0.90 ± 0.71	1.10 ± 0.90	0.30 ± 0.21
Chaptalia integerrima	R	0.70 ± 0.42	0.60 ± 0.34	0.60 ± 0.40	

Table I. *Continued.*

Site		grazed	2-yr protected	4-yr protected	15-yr protected
number of species		25.20 ± 0.97	23.6 ± 0.68	17.30 ± 0.93	4.40 ± 1.63
diversity		2.84 ± 0.03	2.83 ± 0.03	2.53 ± 0.07	0.68 ± 0.26
Facelis retusa	Cf	0.10 ± 0.10	0.30 ± 0.15		
Hieracium giganteum var. *setulosum*	R	0.70 ± 0.30	0.60 ± 0.34	1.30 ± 0.72	0.30 ± 0.30
Luzula hieronymi	G	0.30 ± 0.30	0.30 ± 0.30		
Pratia hederacea	Cf		0.10 ± 0.10	0.10 ± 0.10	
Rumex acetosella	R		0.30 ± 0.30		0.30 ± 0.30
Stipa nidulans	G	2.00 ± 0.71	0.80 ± 0.33	1.20 ± 0.53	0.20 ± 0.20
Vulpia megalura	A		0.70 ± 0.70	0.10 ± 0.10	
Aa achalensis	R				0.30 ± 0.30
Eryngium agavifolium	R				0.90 ± 0.64
Baccharis myrtilloides	Sh				0.50 ± 0.50
Poa stuckertii	T				2.50 ± 2.50

lowest similarity values with respect to all the other sites considered.

3.2. Changes in live biomass, standing dead and litter

We detected significant increases in total standing biomass (live plus recent dead) with increasing time of protection from domestic herbivores; total standing biomass was five times higher after 15 years of protection (*table III*). However, the live biomass contribution increased by only 2-fold, whereas, the increase in standing dead and litter were quantitatively more important. Live biomass increased significantly only after 15 years of protection, while standing dead and litter increased significantly after 2 years of protection.

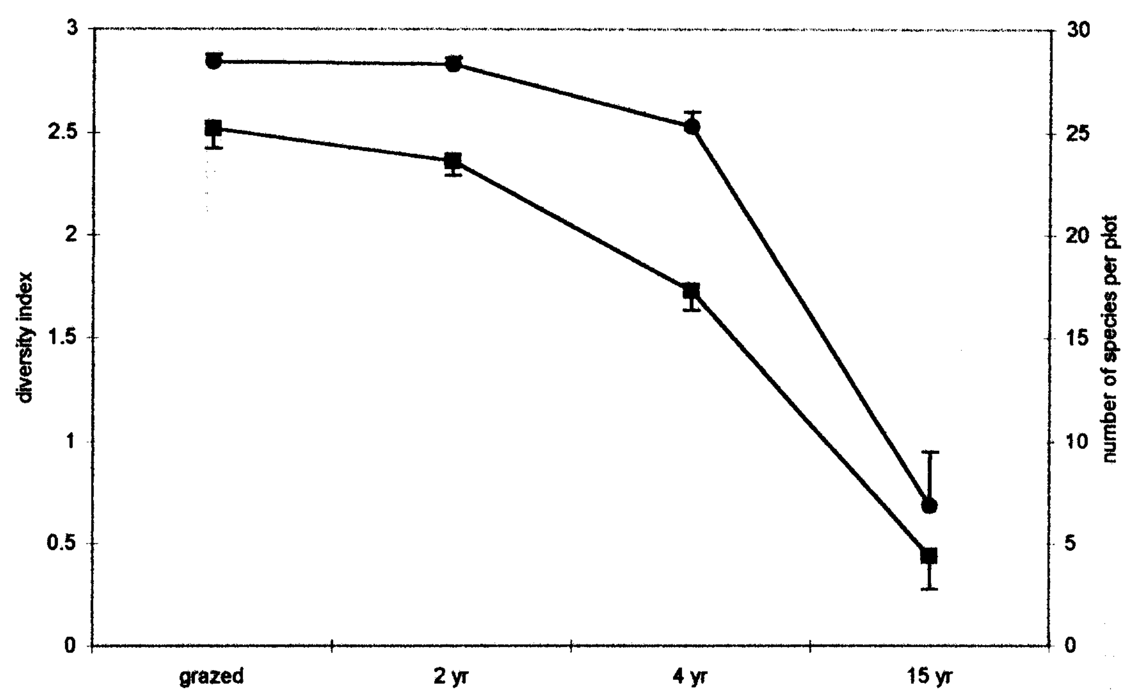

Figure 2. Number of species per plot (squares) and Shannon diversity index (circles) in a site grazed by livestock and in sites with 2, 4, and 15 years of exclusion from grazing, in a mountain grassland from central-western Argentina. Vertical bars, SE values.

Table II. Similarity (Sørensen index) between a grazed site and sites protected from grazing for 2, 4, and 15 years, in a mountain grassland in central-western Argentina.

	Protected sites		
	2 yr	4 yr	15 yr
grazed	0.73	0.58	0.16
2 yr protected	1	0.60	0.18
4 yr protected		1	0.20

3.3. Changes in the biomass of different plant growth forms

At the grazed site, 90 % of total biomass was accounted for by perennial plants, mainly short graminoids (48 %) and creeping forbs (32 %). Release from grazing produced a significant decrease in the biomass of annuals (*table IV*). Rosettes increased slightly but significantly as the time of protection increased. This increase was coupled with the replacement of numerous small rosette species present at the grazed site (*Gamochaeta spicata, G. filaginea, Plantago myosurus, Noticastrum marginatum*) by a single large rosette species (*Eryngium agavifolium*) at the site protected from grazing by 15 years (see *table I*). Tall tussock grasses became evident after 4 years of protection. Their component species (*Festuca tucumanica* and *Deyeuxia hieronymi*) were present at all sites, they showed a short graminoid growth-form at the grazed site and at the site protected for 2 years.

3.4. Changes in aboveground net plant production (ANPP)

The method of ANPP estimation that accounted for total standing biomass (live plus standing dead) increments showed a non significant increment of ANPP as time of exclusion increases, but we found significant differences in ANPP when only live biomass increments were considered (*table IV*). Aboveground net plant production estimated by live biomass increments was significantly higher at the sites excluded from grazing for 4 and 15 years, as compared to sites grazed and excluded from grazing for 2 years (*table IV*). Consumption by livestock was 170.1 ± 85.7 $g \cdot m^{-2} \cdot y^{-1}$, near 35 % of ANPP at the grazed site.

4. DISCUSSION

4.1. Changes in species composition and diversity

Differences in species composition between grazed and ungrazed sites increased with time of exclusion, with native grazing-tolerant and grazing-avoiding plant species being dominant in grazed sites, and tall tussock grasses species being dominant at the long term protected site. No alien species were recorded in the grazed site. However, the invasion of alien plant species has been recorded in a ploughed grassland in the same vegetation belt [13, 15], and European ruderals are common in the area along roadsides [pers. obs.] and in the seed bank [G. Funes, unpublished].

Floristic differences between ungrazed and grazed grassland communities have generally been related to: (i) a shift from large-statured species in ungrazed situations to grazing-tolerant or grazing-avoiding species in grazed situations; and (ii) a relatively high invasion by exotic species under grazing in grasslands with a short history of grazing [34, 35]. Our findings are similar to those reported for other subhumid grasslands in North-America [12] and Africa [4, 29, 30], and for semi-arid North-American [35] and Mediterranean [36, 38], all of them considered as having a long history of grazing. Invasion by alien species with grazing has been observed in Pampean [10, 11, 44, 45] and Australian grasslands [27, 42, 51], both considered to have a short history of grazing.

4.1.1. Changes in growth-forms

Sharp differences were observed in the distribution of growth-forms between ungrazed and grazed sites.

Table III. Live biomass, standing dead biomass, and litter ($g \cdot m^{-2} \pm SE$) at a grazed site (caged) and at sites protected from grazing for 2, 4, and 15 yr, in a mountain grassland in central-western Argentina. Different letters denote significant differences between sites at $P < 0.05$ (Mann-Whitney-Wilcoxon U test). The last two columns at the right are results of Kruskall-Wallis One-way test.

	Grazed	Protected			Kruskal-Wallis	
		2 yr	4 yr	15 yr	χ^2	*P*
live	162.8 ± 8.3^{ab}	144.5 ± 12.8^{b}	179.3 ± 9.2^{a}	338.7 ± 26.3^{c}	44.9	0.0001
standing dead	106.9 ± 5.0^{a}	261.8 ± 15.1^{b}	263.9 ± 19.8^{b}	1123.2 ± 71.6^{c}	163.7	0.0001
litter	15.5 ± 2.0^{a}	64.0 ± 7.1^{b}	137.3 ± 8.7^{c}	882.4 ± 85.5^{d}	176.5	0.0001
live + standing dead	269.7 ± 8.4^{a}	406.3 ± 21.7^{b}	443.2 ± 24.9^{b}	1461.9 ± 83.3^{c}	148.2	0.0001

Table IV. Standing biomass (live + recent dead; g · m^{-2} ± SE) of different growth forms at a grazed site and at sites protected from grazing for 2, 4, and 15 yr, in a mountain grassland in central-western Argentina. Different letters denote significant differences between sites at $P < 0.05$ (Mann-Whitney-Wilcoxon U test). The last two columns at the right are results of Kruskall-Wallis One-way test.

	Grazed	Protected			Kruskal-Wallis	
		2 yr	4 yr	15 yr	χ^2	*P*
annuals	28.2 ± 2.4^a	not measured	5.3 ± 0.6^b	0.3 ± 0.1^c	153.5	0.0001
creeping forbs	85.6 ± 7.8^a	125.1 ± 11.3^b	21.2 ± 2.3^c	3.6 ± 1.2^d	171.9	0.0001
short graminoids	129.3 ± 6.3^a	253.9 ± 16.6^b	166.2 ± 10.5^a	18.2 ± 3.2^c	157.4	0.0001
rosettes	26.6 ± 2.1^a	27.3 ± 3.6^a	26.4 ± 2.2^a	34.2 ± 7.6^b	14.3	0.002
tall tussock grasses	0	0	224.1 ± 27.3^a	1405.5 ± 85.2^b	86.0	0.0001

Table V. Aboveground net plant production (ANPP, g · m^{-2} · yr^{-1}) estimated by two methods in a grazed site and in sites protected from grazing for 2, 4, and 15 years, in a mountain grassland from central-western Argentina. Different letters denote significant differences between sites at $P < 0.05$ (Mann-Whitney-Wilcoxon U test). The last two columns at the right are results of Kruskall-Wallis One-way test.

ANNP estimation	Grazed	Protected			Kruskal-Wallis	
		2 yr	4 yr	15 yr	χ^2	*P*
Live plus standing dead	455 ± 55	453 ± 57	679 ± 162	758 ± 100	2.07	0.557
Live	522 ± 45^a	404 ± 40^b	757 ± 53^b	830 ± 201^b	15.13	0.002

This was due to a shift from grazing-tolerant or grazing-avoiding species with a graminoid or prostrate growth-form in the former, to canopy-competitor species with a tall tussock grass growth-form in the latter. Short graminoids and creeping forbs dominated the grazed site, while tall tussock grasses and rosettes were the most abundant growth-forms after 15 years of protection. In Mediterranean grasslands grazed by domestic livestock for > 5000 years, Noy-Meir et al. [38] observed that tall perennial and tall annual grasses dominated in ungrazed sites, whereas small prostrate annuals were abundant in heavily grazed sites. They found that grazing response was strongly associated with plant growth-form, even though individual species were not always consistent across sites in their response to grazing. Maintenance of grazing lawns by herbivores with a dominance of prostrate forms and short graminoids has also been reported for African [29, 30] and North-American grasslands [12, 35, 50], both having a long evolutionary history of grazing.

4.1.2. Changes in biomass and ANPP

Standing biomass was 33 % lower at the grazed site than at the site protected from grazing for 2 years, but ANPP did not differ significantly between these sites, and consumption represented almost 35 % of ANPP. There was a trend of increasing biomass and ANPP with increasing time of protection.

There has been much controversy concerning the hypothesis that herbivory may in some situations increase productivity [2, 3, 5, 6, 29, 40, 41]. Milchunas and Lauenroth [33], on the basis of their world-wide dataset, predicted negative effects of grazing for sites with long evolutionary history of grazing, high ANPP and many years of protection from herbivores. The sites excluded for 4 and 15 years were in line with these predictions. The ANPP response of the recently excluded site (2-year), in contrast, was positive. With respect to changes in floristic composition and growth forms between ungrazed and grazed sites, our findings resemble those reported by these authors for subhumid grassland communities with a long evolutionary history of grazing.

This is consistent with information from historical sources that strongly suggests a long history of grazing by wild and domesticated herbivores in the mountains of central-western Argentina.

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