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Grazing intensity levels influence C reservoirs of wet and mesic meadows along a precipitation gradient in Northern Patagonia

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Abstract Wet meadows are important ecosystems for forage production and as carbon reservoirs in semi-arid areas. In Patagonia, Argentina, large areas of wet meadows have been classified as overgrazed by livestock. The objective of this study was to determine whether long-term overgrazing has affected carbon (C) storage in plant and soil pools in wet and mesic meadows. The study occurred in Northern Patagonia, in three study sites located along a precipitation gradient. Our results indicate that long-term overgrazing reduced, on average, 35 % of the total ecosystem C pool. There was significantly lower aboveground and belowground plant production in heavily grazed compared to lightly grazed sites, $419 \pm 262 - 128 \pm 110$ g m^2 year^{-1} and $3796 \pm 2622 - 1702 \pm 1012$ g m^2 year^{-1}, respectively.

Soil C concentrations were also less in heavily grazed sites ($184 \pm 98 - 105 \pm 58$ g kg^{-1} at 1 m depth, respectively). The response of meadows to long-term heavy grazing also appears to be influenced by different levels of precipitation, with sites in drier areas being apparently more susceptible to overgrazing. Our results indicate that new management and restoration practices are needed to stop and reverse meadow deterioration in degraded meadows of Northern Patagonia.

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Introduction

Grazing by livestock in Patagonia (Argentina) initiated during the end of the 19th century (Willis 1914). Historically, livestock grazing in Patagonia was conducted without management, which led to an estimated 30 % of the region (24,000,000 ha) being overgrazed (Failde and Ramilo 2006). Overgrazing, defined here as grazing beyond the natural capacity of the system to sustain stock for extended periods of time, is widespread in both dry steppes (León and Aguiar 1985; Golluscio et al. 1998) and in wet and mesic meadows (seasonal wetlands locally named "mallines") in Patagonia (Del Valle et al. 1998; Chimner et al. 2011).

The vegetation in the semi-arid steppe of North Patagonia is spatially heterogeneous, and the landscape is dominated by grass-shrub and grass steppes, with *Pappostipa speciosa*, *Pappostipa humilis*, *Poa ligularis*, *Festuca pallescens*, *Mulinum spinosum*, *Nassauvia sp.*, and *Senecio filaginoides* being the most frequent species (León et al. 1998). In this matrix, meadows occupy around 3 % of the regional area (Easdale et al. 2014). Patagonian meadows are typically located in valley bottoms where precipitation, surface run-off, and groundwater accumulate creating seasonally saturated gleysol soils (Burgos 1993; Lanciotti et al. 1999). The wetter soils in meadows enhance plant production (mainly wetland grasses and rushes) compared to the surrounding arid steppe vegetation (Buono et al. 2010; Irisarri et al. 2012). For instance, López et al. (2005) found that net primary production of meadows was 10 to 20 times greater compared to the adjacent arid steppes, and supplied livestock with 30–40 % of their forage, despite covering only 2–4 % of Northern Patagonia territory. Unfortunately, this high plant production concentrates grazing, which has led to 30 % of the meadows in Patagonia being overgrazed (Canevari et al. 1998; Bonvissuto et al. 2008).

Overgrazing in Patagonian and other arid and semi-arid rangelands has been found to reduce primary and secondary production, increase soil erosion, alter plant composition, and cause loss of soil structure and soil organic matter (SOM) (León and Aguiar 1985; Paruelo et al. 1993; Milton and Hoffman 1994; Perelman et al. 1997; García Martinez 2005; Bonvissuto et al. 2008). In addition, up to 90 % of plant biomass in rangeland ecosystems is composed of roots (Fernandez and Caldwell 1975); however, the effects of grazing on belowground net primary production (BNPP) have been much less studied compared to aboveground net primary production (ANPP) and to changes in species composition (Gao et al. 2008). Because root decay and exudates constitute an important carbon input into deeper soil layers (Boddy et al. 2007), heavy grazing may also decrease soil carbon sequestration rates.

Changes in land use can strongly affect ecosystem carbon cycling, and wetlands can be especially susceptible to these processes (Chen and Tian 2007). In Northern Patagonia, extensive livestock grazing is the main land use and has led to a matrix of range conditions with some areas much more heavily grazed than other areas (Bonvissuto et al. 2008). However, it

is unknown if the different grazing levels correspond to changes in carbon cycling. Carbon storage is an important indicator of ecosystem health and provides valuable ecosystem services, but C storage has not been quantified in wetlands of Northern Patagonia. In addition, it has also been found that there is an interaction between grazing intensity and precipitation levels on carbon cycling (Chimner and Welker 2011). Therefore, the objective of this research was to quantify whether different levels of grazing intensity have altered ecosystem carbon storage, and whether these patterns replicate in sites located in areas of different precipitation.

Materials and methods

Study design and study sites

Meadows are inherently heterogeneous type of rangeland that are structured by environmental variables at both regional scale (e.g., mean precipitation and temperature) and at a site scale (e.g., water table level, which in turn depends on the size and shape of the associated watershed and precipitation). Due to the inherently heterogeneous nature of these ecosystems, we conducted a non-manipulative mensurative study where the main objective is long-term grazing impacts. As precipitation can influence water availability at both regional and site level (and the response to grazing), we picked three study sites situated along a West-East precipitation gradient in North Patagonia, Argentina. Each site was located in a different ecological region, approximately 100 km from each other (Bran et al. 1998; León et al. 1998): Site 1 with two sub-sites (A 41°02′34.06″S, 71°04′19.6″W and B 41°10′16.75″S, 71°05′13.66″W), in the Pre-Andes Range; Site 2 (41°03′33.4″S, 70°31′06.6″W), in the Occidental Hills and Plateaus; and Site 3 (41°35′4″S, 69°22′39″W), in the Oriental Hills and Plateaus. Based on the climatic gradient, from West to East study sites are in areas with High-650 mm (Site 1: A and B), Medium-280 mm (Site 2), and Low-150 mm (Site 3) mean annual precipitation. The mean annual temperature for all the study sites is between 7.5 and 9 °C. Precipitation (rainfall and snow) is concentrated in winter months (from May to August), while the growing season (from December to March) is dry.

Meadows in Patagonia typically show a soil water gradient that create two main plant communities:

Table 1 Brief list of the dominant plant species at each study site (Bonvissuto et al. 2008): wetland types and grazing conditions at each study site

Study sites	Sampling sites			
	Wet meadow		Mesic meadow	
	Lightly grazed	Heavily grazed	Lightly grazed	Heavily grazed
Site 1-high	Dominated by *Juncus balticus.* Additional species include: *Carex spp.*, *Poa pratensis*, *Hordeum halophyllum*, *H. pubiflorum*, *Holcus lanatus*, *Deschampsia caespitosa* and *Trifolium repens.*	The same as lightly grazed condition but with the disappearance of *D. caespitosa.*	Dominated by *Festuca pallescens.* Additional species include: *Poa spp.*, *Carex spp.*, *Taraxacum Officinale* and *T repens.*	The same as lightly grazed condition but with the appearance of *Rumex acetosella.*
Site 2-medium	Dominated by *J. balticus.* Additional species include: *Carex spp.*, *P. pratensis*, *H. halophyllum*, *H. pubiflorum*, *H. lanatus*, *D. caespitosa*, *Alopecurus sp*; *T. Repens* and *T. officinale.*	The same as lightly grazed condition but with the disappearance of *D. caespitosa, Alopecurus sp.* and *T. Officinale.*	Dominated by *F. pallescens.* Additional species include: *Agrostis pyrogea, Hordeum spp, Puccinelia pusilla, Carex spp, J. balticus, Boopis gracilis, Nitrophila Australis, Pratia repens, T. officinale, T. repens,* and *Azorella trifurcata.*	The same as lightly grazed condition but with the appearance of *Distichlis spp.*
Site 3-low	Dominated by *J. balticus and Distichlis spp.* Additional species include; *Agrostis sp., Hordeum sp., Poa lanuginosa, Puccinelia pusilla, Carex sp.*; apparition of perennial herbs and shrubs.	The same as lightly grazed conditions but with the disappearance of *Agrostis sp., Hordeum sp., Carex sp.* and *Stipa sp.* Major abundance and vigor of *Distichlis spp.*	Absent	Absent

(a) wet meadows dominated by *Juncus balticus* in the wetter topographically central and lower areas, and (b) mesic meadows dominated by *Festuca pallescens* in relatively higher and peripheral drier areas (Iriondo et al. 1974; Burgos 1993). However, not every meadow has both plant communities and sometimes one can be absent. Thus, sampling was performed in both wet and mesic meadow types in Site 1 and Site 2, but only in wet meadows in Site 3 as mesic meadows were not present (Table 1).

For each study site and meadow type, two areas with different long-term grazing intensities (light and heavy) were selected. Due to the long-term widespread grazing in the area, no ungrazed areas could be found. Light grazing is defined in this paper as long-term grazing below the natural carrying capacity, while heavy grazing is defined as long-term grazing over the natural carrying capacity (Table 2). Carrying capacity, defined as maximum stocking rate possible which is consistent with maintaining or improving vegetation or related resources, was calculated for

each site by using local INTA Extension Services Recommendations, which uses average aboveground peak biomass in exclosures (Bonvissuto et al. 2008). Historical grazing intensities were reconstructed based upon interviews with land owners. For all study sites, grazing by livestock (mostly sheep) at both grazing levels occurred continuously and season-long (early October to mid-April) for at least the last 20 years. Except for grazing, there was no evidence of other disturbances such as fire or widespread erosion at selected sites. Besides the difference in grazing intensity, care was taken to select sampling sites that had similar landscape position and similar soil types. Soils of wet meadows of Site 1 and Site 2 were previously classified by López et al. (2005) as Histosols, and soils of mesic meadows as aquic Mollisols, while soils of Site 3 were classified as aquic Mollisols by Bran et al. (1998). Sampling sites of Site 2 and Site 3 were located in the same wetland, but light and heavy long-term grazing intensities were located in different paddocks (Fig. 1). For Site 1,

Table 2 Natural carrying capacity calculated by Bonvissuto et al. ([2008](#)) for the three study locations, and each meadow type (wet meadow and mesic meadow)

Study site	Meadow type	Carrying capacity (SLU ha^{-1})[a]
Site 1-high	Wet meadow	23–30
	Mesic meadow	3.8–7.6
Site 2-medium	Wet meadow	30
	Mesic meadow	5–9.5
Site 3-low	Wet meadow	5.9–7.9

[a] Sheep livestock unit per hectare

sampling sites were located in different nearby wetlands, being Subsite A (with wet and mesic meadow) lightly grazed, and Subsite B (with wet and mesic meadow) heavily grazed (Fig. [1](#)). All study sites were meadows without associated streams. Within each sampling site, a grazing exclosure (100 m^2) was installed to prevent short-term grazing and provides an area to quantify total ANPP. Soil and root sampling were conducted outside the exclosures. The final study design is the combination of meadow type (wet and mesic meadow) and grazing intensity (light and heavy) at three study sites for a total of ten sampling sites ($n = 10$) (Table [1](#)).

Sampling and analyses

Soil

At each sampling site, and across the whole meadow, three composite soil samples ($n = 3$, composed of 5 sub samples each) were randomly collected at four soil

depths (0–20, 20–40, 40–70, and 70–100 cm) during 2008 and 2009. In the lab, soils were air dried for 24 h, sieved through a 2 and a 0.5 mm mesh, and stored until analyzed. The following physical and chemical characteristics were measured on 2 mm sieved soil samples: pH (Thomas [1996](#)) and electrical conductivity (EC) (Rhoades [1996](#)) (soils: water 1: 2.5). On 0.5 mm sieved soil samples, concentration of soil organic carbon (SOC) was determined by the Walkley and Black method (Walkley and Black [1934](#)). For each depth, bulk density (BD) for dry soils was directly calculated by the core method (Blake [1982](#)), and for wet soils (mostly deeper than 40 cm were the gravimetric technique cannot be applied due to soil saturation), SOC data from soil samples taken at 40–70, and/or 70–100 cm were used to estimate indirectly BD trough Adams's equation (Adams [1973](#)). Soil carbon storage (Soil-CS), expressed as tons of C per hectare, was calculated separately for each soil depth within the soil profile as

$$\text{Soil} - \text{CS} = \left[d \times \text{BD} \times (1000 \times 1000) \times \left(\frac{\text{SOC}}{1000} \right) \right] / 1000, \tag{1}$$

where BD is the soil bulk density (g cm^{-3}), SOC is the soil organic carbon (%), and d is the soil depth in cm.

In order to compare on a mass equivalent basis, soils depths in heavily grazed sites were corrected for compaction using Eq. [2](#).

$$dH = dL/(BDH/BDL), \tag{2}$$

where dH and dL are the pair of soil depths compared between heavily grazed and lightly grazed sites, respectively; and BDH and BDL are the bulk densities
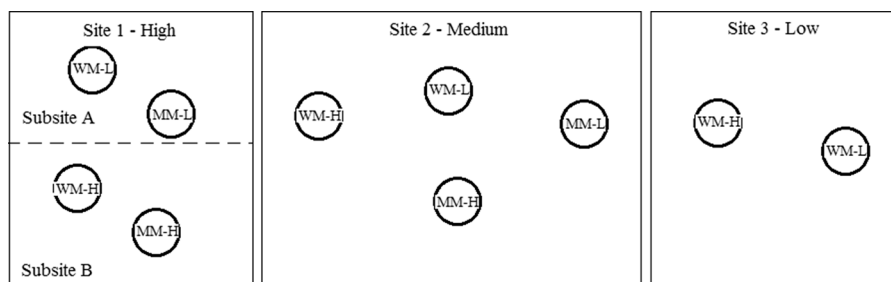
Fig. 1 Scheme of sampling sites for each study site, showing the presence of meadow type (WM: wet meadow, and MM: mesic meadow) and grazing intensity (*L* light, and *H* heavy). *Site 1*, placed in the area with higher precipitation (*High*), is represented by two Subsites: **a** lightly grazed, and **b** heavily grazed; both with WM and MM. *Site 2*, placed in the intermediate area of the precipitation gradient (*Medium*), with all sampling sites. *Site 3*, placed in the driest area of the precipitation area (*Low*), with only WM but with both grazing intensities represented

for heavily grazed sites and lightly grazed sites, respectively (e.g., if at 0–20 cm, $BDL = 0.5$ g cm^{-3}, and $BDH = 1$ g cm^{-3}, then comparisons of soil-CS in tons of C per hectare between grazing intensities must be done at 0–20 cm for light grazing and at 0-10 cm for heavy grazing). Reference depths were 0–20, 20–40, 40–70, and 70–100 cm.

Plant biomass

Annual ANPP was measured within exclosures at all sampling sites at the end of the growing season (April 2009, and 2010) by harvesting five 0.2 m^2 quadrants per site ($n = 5$). Dead material was discarded, and the live material was separated into grasses, sedges, and forbs. Plant material was oven dried at 60 °C until constant weight was achieved. Total carbon content of plant communities, henceforth called aboveground biomass carbon content (AGB-C), was quantified on five composite samples, made with a mixture of leaves that matched the average weight percentages measured in the field communities. Samples were ground with a 0.5 ball mill and analyzed for organic matter concentration by loss on ignition at 400 °C (Topp et al. 1993). Carbon content was assumed to be one-half of the ash-free mass (Shlesinger and Hasey 1981; cf. Reichle et al. 1973, Schlesinger 1977). Carbon storage in AGB (AGB-CS) was calculated using AGB-C and ANPP data.

Root biomass was measured by collecting 5 cores per sampling site (diameter: 5 cm, length: 40 cm; 785 cm^3), divided into 0–20 cm and 20–40 cm depths ($n = 5$). In the lab, core samples were washed with distilled water and roots were separated from the soil using a 2 and a 0.5 mm sieve, dried (48 h, 60 °C) and weighed. Annual BNPP was measured using the "in-growth core method" (Rydin and Jeglum 2006). Ingrowth cores (diameter: 5 cm, length: 40 cm; 785 cm^3) were filled with native root-free soil and buried at each sampling site at the beginning of the growing season—September 2010—, and collected after one year. All roots were washed from soil, dried (48 h, 60 °C) and weighed. Total carbon content of roots, henceforth called belowground biomass carbon content (BGB-C), was analyzed by first grinding in a ball mill to pass 0.5 mm sieve and then using loss on ignition methods. Carbon content was assumed to be one-half of the ash-free mass (Shlesinger and Hasey

1981; cf. Reichle et al. 1973, Schlesinger 1977). Carbon storage in BGB (BGB-CS) was calculated using BGB-C and BGB data.

Statistical Analyses

The selection of the study sites was based on land owners' permission to work on their land, on the amount of previous information available, and having different grazing intensity levels. For this reason, some of the features of the typical manipulative experimental studies are not present, in particular the presence/absence of meadow types in each study site, or the presence/absence of both grazing intensities in the same site, which in this case are beyond the control of the researchers. This distinction between non-manipulative and experimental studies was debated by several authors (e.g., Hurlbert 1984; Cox and Reid 2000; Schabenberger and Pierce 2002). The implications lie specifically in the scope of the interpretation of the results and conclusions. Due to the study design, long-term grazing and site wetness could not be completely separated for analysis. However, we still hypothesize that response to grazing can be influenced by site wetness, but we do not include it as a factor due to the complexity of the variables to be monitored. Instead, we located the study sites along a regional precipitation gradient where meadows can be found.

For all the variables analyzed, we performed separated ANOVAs at each combination of study sites (Site 1, Site 2, and Site 3) and meadow type (wet and mesic). For all cases, main factor of interest for the statistical analysis was grazing intensity (light and heavy). Depending on the nature of the variable analyzed, different models were used. Variables where sampling included different soil depths (SOC, pH, EC, BD, and Soil-CS; BGB-C, BGB, BNPP, and BGB-CS) the model was a factorial with two factors: grazing intensity and depth, with a variable number of replicates according to the sampled variable (see above). When interaction was significant, it was sliced by depth to compare grazing intensities. Correlation due to soil depth was accomplished using an exponential correlation model (Schabenberger and Pierce 2002). In all other variables, the model considered grazing intensity as main only factor of interest. Statistical analysis was performed with SAS 9.2 (2002–2003).

Table 3 Carbon concentration in soil-SOC (g kg^{-1}), pH, electrical conductivity-EC (dS m^{-1}), and bulk density-BD (g cm^{-3}) at different soil depths (cm) within two grazing intensities (light and heavy)

Soil system			SOC		pH		EC		BD	
Study Site	Meadow type	Soil depth	Light	Heavy	Light	Heavy	Light	Heavy	Light	Heavy
Site 1- high	Wet	0–20	89 (15)	87 (13)	6.5 (0.3)	6.6 (0.2)	0.2 (0.0)	0.2 (0.0)	0.6 (0.2)b	0.9 (0.2)a
		20–40	52 (5)	50 (5)	6.5 (0.1)	6.7 (0.1)	0.1 (0.0)	0.1 (0.0)	0.6 (0.1)b	1.0 (0.2)a
		40–70	25 (2)	33 (3)	6.7 (0.1)	6.8 (0.0)	0.1 (0.0)	0.1 (0.0)	1.3 (0.0)	1.2 (0.0)
		70–100	19 (6)	33 (13)	6.7 (0.0)	6.9 (0.1)	0.1 (0.1)	0.1 (0.0)	1.4 (0.1)	1.2 (0.1)
	Mesic	0–20	96 (7)a	49 (1)b	6.2 (0.0)b	6.6 (0.2)a	0.2 (0.0)a	0.1 (0.0)b	0.7 (0.1)b	1.3 (0.1)a
		20–40	65 (6)a	22 (1)b	6,6 (0.2)b	6.8 (0.1)a	0.1 (0.0)	0.1 (0.1)	0.8 (0.1)b	1.2 (0.2)a
		40–70	27 (3)a	12 (1)b	6.6 (0.0)b	6.9 (0.0)a	0.1 (0.0)	0.1 (0.0)	1.3 (0.0)b	1.5 (0.0)a
		70–100	26 (8)a	8 (1)b	6.7 (0.2)b	7.0 (0.0)a	0.1 (0.0)	0.1 (0.0)	1.3 (0.1)b	1.5 (0.0)a
Site 2- medium	Wet	0–20	160 (13)a	37 (14)b	7.6 (0.4)b	9.2 (0.2)a	0.6 (0.1)b	1.1 (0.2)a	0.6 (0.2)b	1.1 (0.2)a
		20–40	87 (19)a	22 (3)b	7.4 (0.2)b	8.8 (0.1)a	0.3 (0.1)	0.3 (0.0)	0.8 (0.1)b	1.3 (0.1)a
		40–70	42 (27)a	9 (0)b	7.3 (0.1)b	8.7 (0.1)a	0.2 (0.0)	0.2 (0.0)	1.2 (0.2)b	1.5 (0.0)a
		70–100	38 (14)a	8 (3)b	7.2 (0.2)b	8.6 (0.0)a	0.2 (0.0)	0.2 (0.0)	1,2 (0.1)b	1.5 (0.0)a
	Mesic	0–20	56 (7)a	43 (3)b	8.4 (0.2)b	9.4 (0.1)a	0.5 (0.0)b	1.3 (0.3)a	1.0 (0.2)	1.1 (0.2)
		20–40	32 (4)	27 (6)	8.3 (0.1)b	8.7 (0.1)a	0.3 (0.0)	0.3 (0.2)	1.2 (0.1)	1.0 (0.2)
		40–70	20 (3)	19 (5)	8.3 (0.2)b	8.6 (0.1)a	0.2 (0.0)	0.2 (0.0)	1.4 (0.0)	1.4 (0.1)
		70–100	15 (2)	16 (5)	8.4 (0.1)	8.5 (0.1)	0.2 (0.0)	0.2 (0.0)	1.4 (0.0)	1.4 (0.2)
Site 3- low	Wet	0–20	30 (5)a	20 (5)b	9.5 (0.1)a	9.0 (0.2)b	2.7 (0.4)	1.8 (0.1)	0.9 (0.1)b	1.1 (0.2)a
		20–40	19 (5)a	14 (2)b	9.1 (0.3)a	8.7 (0.2)b	0.9 (0.3)	0.8 (0.2)	1.2 (0.0)	1.1 (0.1)
		40–70	11 (1)a	9 (1)b	8.9 (0.1)a	8.6 (0.2)b	1.0 (0.1)	0.9 (0.1)	1.5 (0.0)	1.5 (0.0)
		70–100	9 (1)a	7 (0)b	8.7 (0.1)a	8.6 (0.1)b	1.0 (0.2)	1.0 (0.2)	1.5 (0.0)	1.5 (0.0)

Mean ± (SD)

Different letters show significant differences between grazing intensities ($p < 0.05$), for each studied variable, and being $a > b$

Results

Soil

In lightly grazed situations, soil reaction (pH) was slightly acidic in both wet and mesic meadows of Site 1, neutral in wet and moderately alkaline in mesic meadows of Site 2, and strongly alkaline in wet meadows of Site 3, showing a tendency to a higher pH level as water availability decreased. Electrical conductivity also followed this pattern in lightly grazed sites, ranging from 0.1 to 2.7 dS m^{-1} in wet meadows, and from 0.1 to 0.5 dS m^{-1} in mesic meadows (Table 3). Although significant differences were found, there were no consistent differences in pH or conductivity between meadow types or grazing conditions.

Soil bulk density increased with depth at all sampling sites (Table 3). In many cases, sites that were heavily grazed had significantly great BD compared to lightly grazed sites, especially at the 0–20 cm layer (Table 3). Because soils in different grazed areas may have had different initial BD before grazing, another way to assess compaction is to look at the differences between BD in surface compared to deep soils. The average difference in BD between 0 and 20 cm and 70–100 cm is 0.60 g cm^{-3} in lightly grazed soils, but only 0.32 g cm^{-3} in the heavily grazed soils (Table 3).

The greatest concentrations of SOC occurred in the upper 40 cm; however, concentrations of SOC were still high down to 100 cm (Table 3). Significant differences in SOC were found between grazing intensities at most soil depths for most study sites,
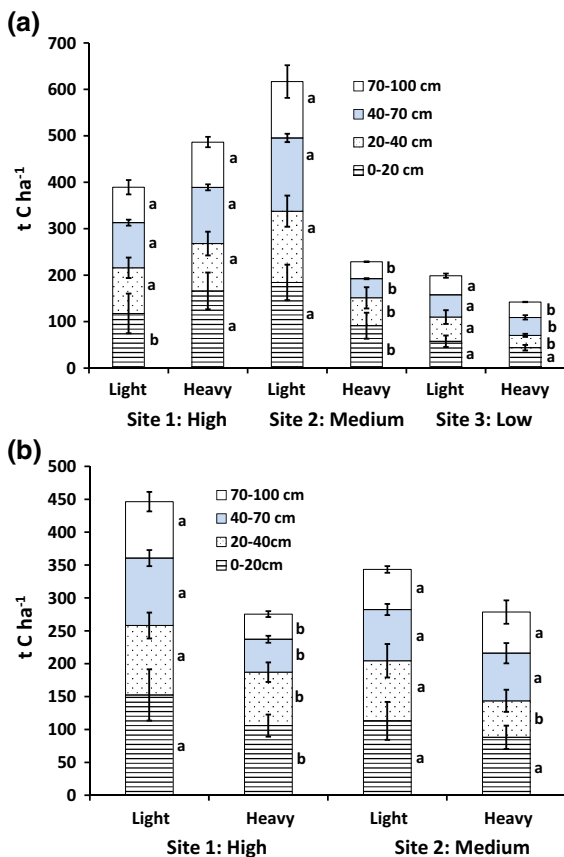
Fig. 2 Total soil carbon storage (Soil-CS), expressed in tons of C per hectare, at reference depths of 0–20, 20–40, 40–70, and 70–100 cm depth, comparing grazing intensities (*Light* and *Heavy*) of **a** wet meadows, and **b** mesic meadows. Different *letters* show significant differences between grazing intensities ($p < 0.05$), for each study site, and being $a > b$

except for wet meadow of Site 1 and deep soil layers of mesic meadow Site 2 (Table 3). Total soil carbon storage (Soil-CS) was significantly greater at each depth at lightly grazed sites compared to heavily grazed sites, with the exception of Site 1 (wet meadow) and Site 2 (mesic meadow) (Fig. 2).

Plants

Aboveground carbon

On average, ANPP was much greater (2–4 times) in wet than in mesic meadows (Table 4). ANPP was significantly ($p > 0.05$) lower at heavily grazed sites compared to lightly grazed sites, averaging 128 ± 110 and 419 ± 262 g m^{-2} year^{-1}, respectively, and across both meadow types (Table 4). AGB-C did not vary consistently by site or meadow type and only showed significant differences ($p > 0.05$) between grazing intensities at Site 1, being greater in the lightly grazing conditions (Table 4). AGB-CS was significantly higher at all lightly grazed compared to heavily grazed sites, for both meadow types (Fig. 3).
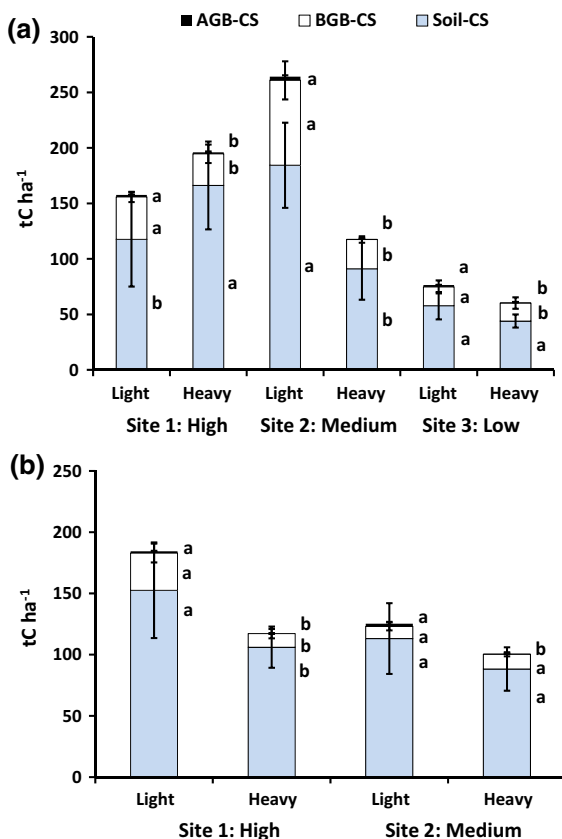
Belowground carbon

Root biomass varied greatly with soil depth (Table 5). In general, the top 0–20 cm of soil had about 10 times more root biomass than did soil from 20 to 40 cm depth. Total below ground biomass (BGB = roots + rhizomes, combined for all depths) was notably greater

Table 4 Carbon concentration in aboveground biomass-AGB-C (g kg^{-1}), and aerial net primary production-ANPP (g m^2 year^{-1}) at different grazing intensities (light and heavy)

Aboveground biomass (m^2)		AGB-C		ANPP	
Study site	Meadow type	Light	Heavy	Light	Heavy
Site 1-high	Wet	462 (4)a	434 (7)b	722 (155)a	294 (141)b
	Mesic	460 (2)a	442 (7)b	184 (60)	36 (24)
Site 2-medium	Wet	431 (4)	463 (6)	674 (204)a	97 (66)b
	Mesic	432 (9)	462 (9)	295 (67)a	74 (31)b
Site 3-low	Wet	468 (8)	472 (3)	220 (86)a	137 (17)b
Average		457 (14)	448 (19)	419 (262)a	128 (110)b

Mean ± (SD)

Numbers with different letters show significant differences between grazing intensities ($p < 0.05$), for each studied variable, and being $a > b$

Fig. 3 Carbon storage expressed in tons of C per hectare in soil (Soil-CS), belowground (BGB-CS), and aboveground (AGB-CS) biomass, in different grazing intensities (*light* and *heavy*) at surface reference depth (0–20 cm) of the **a** wet meadows, and **b** mesic meadows. Different *letters* show significant differences between grazing intensities of the same wetland type ($p < 0.05$), for each study site, and being $a > b$

than total above ground biomass (AGB) within each meadow type, comprising ~85 % of the total plant biomass for wet meadows and ~88 % for mesic meadows (Table 6).

Similarly to ANPP, BNPP was significantly different between grazing intensities for all study sites, generally being greater in lightly grazed meadows with the exception of Site 3 (Tables 5 and 6). BNPP was also greater in wet meadows than in mesic meadows (Table 5). Almost no significant differences were found in BGB between grazing intensities, with the exception of wet and mesic meadows of Site 1 at 0–20 cm, and wet meadow Site 2 at 20–40 cm, which showed higher BGB values in lightly grazed than in heavily grazed meadows (Table 5). As was the case for AGB-CS, we found significant differences in

BGB-CS between grazing intensities for both meadow types of all sites, with the only exception in mesic meadow Site 2 (Fig. 3).

Ecosystem carbon pools

Soil carbon contained >90 % of the total ecosystem C pool (soil + plant C pools) for both meadow types (Fig. 3). Soil was the largest C pool, followed by belowground and aboveground biomass (~100:10:1, respectively). In general, total ecosystem C pools were significantly lower (on average 35 %) in the heavily grazed meadows compared to the lightly grazed meadows (Fig. 4). The lower total ecosystem C in heavily grazed meadows resulted predominantly from lower soil C ($p = 0.023$ for wet meadows, and $p = 0.041$, for mesic meadows) (Fig. 4), but also from lower above and below plant biomass (Fig. 3).

Discussion

Results of this study indicate that long-term overgrazing has altered C cycling in Patagonian wet and mesic meadows. One of the first degradation symptoms due to overgrazing that can be observed is the reduction of above ground plant biomass, which is followed by an important decrease in root biomass. These processes can lead to the reduction in above and below ground C inputs into the soil. This negative feedback can be difficult to measure in short-term C stock studies, but it was detected in our study using long-term grazing patterns.

Long-term overgrazing sites had, on average, 35 % less total ecosystem C compared to lightly grazed sites. There have only been a few studies done on grazing impacts on wetlands of arid and semi-arid areas, but our results are in concordance with Wu et al. (2010) and Li et al. (2006) who found that fencing in wet meadows in China increased soil C sequestration and storage.

The largest differences in ecosystem carbon pools between grazing levels occurred in the shallow soil layers. However, deeper soil layers also showed less SOC in heavily grazed meadows. To our knowledge, there have been few to no studies that have looked at overgrazing impacts on deep soil carbon in wet meadows. Carbon incorporation into soil due to root decomposition, litter decay, and compaction are factors

Table 5 Carbon concentration in belowground biomass-BGB-C (g kg^{-1}), belowground biomass-BGB (g m^2), and estimated belowground net primary production-BNPP (g m^2 year^{-1}) at different grazing intensities (light and heavy)

Belowground biomass (m^2)			BGB-C		BGB		BNPP	
Study site	Meadow type	Ref soil depth(cm)	Light	Heavy	Light	Heavy	Light	Heavy
Site 1-high	Wet	0–20	317 (20)	318 (13)	12,041 (1462)a	8,976 (2616)b	2,107 (663)a	523 (62)b
		20–40	332 (26)a	298 (22)b	956 (710)	905 (338)	602 (45)a	246 (8)b
	Mesic	0–20	316 (16)	280 (31)	9,440 (2373)a	3,990 (1046)b	1,752 (221)a	762 (54)b
		20–40	293 (31)	297 (11)	1,009 (647)	181 (50)	770 (128)a	329 (33)b
Site 2-medium	Wet	0–20	364 (9)a	333 (21)b	22,066 (4940)	19,847 (4431)	5,915 (471)a	2,389 (635)b
		20-40	358 (17)	349 (12)	9,610 (4505)a	2,569 (736)b	1.803 (274)a	650 (79)b
	Mesic	0–20	350 (13)	347 (18)	2,853 (914)	3,578 (500)	1,574 (176)	1,329 (215)
		20–40	330 (36)	348 (12)	272 (117)	419 (286)	659 (272)	581 (178)
Site 3-low	Wet	0–20	338 (9)	333 (34)	4,929 (1700)	4,860 (1546)	2,709 (579)b	4,l225 (36)a
		20–40	377 (8)	342 (26)	1,351 (486)	1,214 (604)	2,314 (261)a	1,193 (210)b
Average			342 (26)	325 (30)	6,453 (6996)	4,098 (5400)	1,893 (1609)	1,223 (1201)

Mean ± (SD)

Numbers with different letters show significant differences between grazing intensities ($p < 0.05$), for each studied variable, and being $a > b$

Table 6 Net primary production (NPP) (g m^2), and ANPP/BNPP ratio at different rangelands conditions

Data from ANPP/BNPP and BNPP/NPP ratio belong to 0–20 cm depth

| ANPP/BNPP relationships		NPP		ANPP/BNPP		BNPP/NPP	
Study site	Meadow type	Light	Heavy	Light	Heavy	Light	Heavy
1-High	Wet	2,829	817	0.34	0.56	0.74	0.64
	Mesic	1,936	779	0.11	0.02	0.90	0.98
2-Medium	Wet	5,093	2,486	0.15	0.04	0.87	0.96
	Mesic	1,802	1,249	0.14	0.06	0.87	0.94
3-Low	Wet	2,929	4,350	0.08	0.03	0.92	0.97

that favor higher C concentration in the upper soil layers (upper 30–40 cm). Thus, most studies of SOM associated with grazing dynamics are usually focused on the superficial soil layers (Jobággy and Jackson 2000; Povirk et al. 2001), and deep SOC patterns are not analyzed. Despite the reduction of SOC, we still found soil profile development in wet and mesic meadows up to more than 1 m in depth. The SOC of the deep wet meadow soils is as high as the surface soils in the surrounding steppe soils (Gaitán 2002).

In addition to having less carbon, surface soils of heavily grazed sites also had greater soil bulk densities. Bulk density was most likely increased by trampling that decreases number and size of soil pores that prevent normal water and air flow (Villamil et al. 2001) and the reduction of root inputs, which limits

new additions of organic matter to the soil (Brevik et al. 2002).

Aboveground plant biomass values for our study sites were similar to those reported locally in other North Patagonian wet and mesic meadows (Bonvissuto et al. 2008), and in meadows of other regions (Manning et al. 1989; Bernard 1990; Jakrlová 1993; Kathleen et al. 2004). Belowground biomass was the largest plant fraction of the meadows, and this is the first report on this compartment for North Patagonian wet and mesic meadows. Belowground biomass in most of the sampling sites (between 74 and 92 % for lightly, and between 64 and 98 % for heavily grazed) exceeded the fraction of total biomass found by other studies, which is between 60 and 81 % (Van der Maarel and Titlyanova 1989; Henry et al. 1990; Aerts
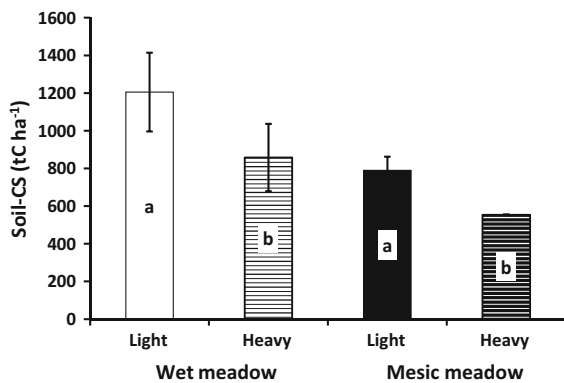
Fig. 4 Ecosystem Carbon Pool (soil + aboveground + belowground) of the three study sites at 1 m depth, expressed in tons of C per hectare, differentiating meadow types (wet and mesic), for each grazing intensity (*light* and *heavy*). Different *letters* show significant differences between grazing intensities for each meadow type, and being a > b ($p < 0.05$)

et al. 1992; Jackson et al. 1996; Fisk et al. 1998; Kathleen et al. 2004). Furthermore, values of BNPP found in this work exceeded the range of 150–900 g m^{-2} given by Bernard et al. (1988) for other riparian meadows dominated by similar graminoid species (Manning et al. 1989; Fiala 1993; Otting 1998; Toledo and Kauffman 2001; Kathleen et al. 2004). We suggest that this high belowground production and biomass could be due to the high variation in water table depth during the year, which allows not only short periods of soil flooding in winter but also long periods of aerated soils in spring-summer, stimulating root exploration and development.

Significant differences in plant production were found between grazing intensities, with lower above and below production in heavily grazed sites. Findings from other studies where different grazing intensities were tested in a variety of experimental conditions showed a decline in root production (Pandey and Singh 1992; Biondini et al. 1998), but other studies reported that grazing stimulated (Sims and Singh 1978; Frank et al. 2002; Pucheta et al. 2004), or had no effect on BNPP (McNaughton et al. 1998; Milchunas and Lauenroth 1993). Gao et al. (2008) speculated that the reduction in BNPP could be attributed to C reallocation to shoot growth when the system is degraded, but in our case, the reduction of BNPP is probably related to long-term processes, as the reduction of ANPP, the loss of plant cover, and in some cases a change in floristic composition. There was an exception to this at Site 3, where the large increase in

total net primary production (NPP) is due to a large increase in BNPP (42 % = 9900 t C ha^{-1}). We hypothesize that heavy grazing did not cause a massive root stimulation, but a change in plant species composition occurred with a large increase in *Distichlis* (a species adapted to salty soil conditions), which develops numerous surficial rhizomes (Bonvissuto et al. 2008).

Precipitation levels in Patagonian region have been found to strongly affect water table levels and groundwater chemistry (Chimner et al. 2011). Lower precipitation levels were found to reduce maximum water table levels and the length of time that the soil was saturated (Castelli et al. 2000; Martin and Chambers 2002). Meadows in areas with low precipitation are more salty probably due to less groundwater flushing and greater evapotranspiration. The site in the wettest area (Site 1) showed the least change in soil organic carbon from heavy grazing, but losses were greater in the more arid study sites (Site 2 and Site 3). We hypothesize that the greater water table fluctuations and salinity have made these ecosystems more susceptible to grazing (Chimner and Welker 2011). This is similar to finding from Norton et al. (2014) who found that more constantly wet meadows were more resilient to current light to moderate levels of grazing but seasonally wet meadows were more vulnerable to grazing. These results suggest that the wet meadows with greater average precipitation could be more resilient to overgrazing than the wet meadows in drier areas. These findings have important implications for current range management, especially with predicted changes in precipitation patterns that are expected for the region (Nuñez et al. 2005).

Conclusion

Results of this work suggest that historical grazing in Patagonia wet meadows was not adequate to maintain long-term ecosystem carbon cycling, and consequently has reduced their grazing potential. Ecologically, land degradation is accepted as one of the main causes of CO_2 increase, and overgrazing will probably lead meadows to switch from CO_2 sinks to CO_2 sources. We hypothesize that long-term overgrazing has affected Patagonian wet and mesic meadows C reservoirs through (a) reduction of superficial C inputs caused by a reduction in ANPP and the consequent

reduction of litterfall, vegetation consumption by cattle, and a reduction of plant cover, (b) reduction of belowground C inputs from root decay related to the decline of BNPP, (c) increase in soil temperature in areas with plant cover reduction that favor microbial activity and SOM decomposition, and (d) higher frequency of wet-dry periods and salinity in degraded areas, where strong compaction and high surface temperatures can cause soil aggregates to breakdown and, consequently, SOM degradation. New management and restoration practices are needed to stop and reverse meadow deterioration in degraded meadows of Northern Patagonia.

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