

Pathways of Grazing Effects on Soil Organic Carbon and Nitrogen

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Abstract

Grazing modifies the structure and function of ecosystems, affecting soil organic carbon (SOC) storage. Although grazing effects on some ecosystem attributes have been thoroughly reviewed, current literature on grazing effects on SOC needs to be synthesized. Our objective was to synthesize the effects of grazing on SOC stocks in grasslands, establishing the major mechanistic pathways involved. Additionally, and because of its importance for carbon (C) biogeochemistry, we discuss the controls of soil organic nitrogen (N) stocks. We reviewed articles analyzing grazing effects on soil organic matter (SOM) stocks by comparing grazed vs. ungrazed sites, including 67 paired comparisons. SOC increased, decreased, or remained unchanged under contrasting grazing conditions across temperature and precipitation gradients, which suggests that grazing influences the factors that control SOC accumulation in a complex way. However, our review also revealed some general patterns such as 1) root contents (a primary control of SOC formation) were higher in grazed than in their ungrazed counterparts at the driest and wettest sites, but were lower at sites with intermediate precipitation (~400 mm to 850 mm); 2) SOM C:N ratios frequently increased under grazing conditions, which suggests potential N limitations for SOM formation under grazing; and 3) bulk density either increased or did not change in grazed sites. Nearly all sites located in the intermediate precipitation range showed decreases or no changes in SOC. We grouped previously proposed mechanisms of grazing control over SOC into three major pathways that can operate simultaneously: 1) changes in net primary production (*NPP pathway*), 2) changes in nitrogen stocks (*nitrogen pathway*), and 3) changes in organic matter decomposition (*decomposition pathway*). The relative importance of the three pathways may generate variable responses of SOC to grazing. Our conceptual model suggests that rangeland productivity and soil carbon sequestration can be simultaneously increased by management practices aimed at increasing N retention at the landscape level.

Resumen

El pastoreo modifica la estructura y el funcionamiento de los ecosistemas, alterando las reservas de C orgánico del suelo (COS). A pesar de que existen revisiones de los efectos del pastoreo sobre la productividad primaria o los cambios en la composición de especies, no se dispone de una síntesis detallada de los efectos del pastoreo sobre el COS. A su vez, discutiremos los controles de las reservas de nitrógeno orgánico del suelo, debido a su importancia en la regulación del ciclo del C. El objetivo de este trabajo fue sintetizar los efectos del pastoreo sobre el COS y analizar los mecanismos a través de los cuales opera. Realizamos una revisión de los artículos que evalúan, mediante comparaciones de sitios pastoreados y no pastoreados, los efectos del pastoreo sobre el COS, incluyendo 67 comparaciones pareadas. La revisión bibliográfica mostró que: 1) el C en las raíces y otros órganos subterráneos fue mayor en zonas pastoreadas que en las no pastoreadas en sitios secos y húmedos, pero menor en sitios con precipitaciones intermedias; 2) el pastoreo aumentó la relación C:N del suelo, sugiriendo limitaciones de N para la formación de materia orgánica del suelo; y 3) la densidad aparente del suelo fue mayor o igual en los sitios pastoreados, respecto a los no pastoreados. Los efectos del pastoreo sobre el COS operarían a través de tres vías: 1) por medio de cambios en la productividad primaria neta, 2) a través de alteraciones en los stocks de NOS, o 3) aumentando la descomposición del COS. El pastoreo afectaría el COS a través de los tres mecanismos simultáneamente, y la respuesta del COS al pastoreo dependerá de la importancia relativa de cada uno. Finalmente, el modelo conceptual propuesto sugiere que la productividad de la biomasa y la cantidad de carbono almacenado en el suelo podrían aumentarse simultáneamente mediante manejos que apunten a incrementar la retención de N a escala de paisaje.

Key Words: belowground production, C:N, herbivores, nitrogen, reactive nitrogen, roots, soil organic carbon

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INTRODUCTION

Grazing modifies the structure and function of ecosystems, affecting their stability and productivity (McNaughton 1985; Sala 1988; Milchunas and Lauenroth 1993; Altesor et al. 1998; Schuman et al. 1999). As a consequence, understanding the effects of grazing at the ecosystem level has been a primary goal of range scientists (Milchunas et al. 1988). However, it has been difficult to synthesize and generalize the effects of grazing on grasslands, particularly its effect on the carbon cycle (Milchunas and Lauenroth 1993). Although grazing effects on some ecosystem attributes such as Aboveground Net Primary Production (ANPP) or species composition have been successfully reviewed (Milchunas and Lauenroth 1993; Oesterheld et al. 1999; Cingolani et al. 2005), current literature on grazing effects on soil organic carbon (SOC) needs to be synthesized.

Soil organic matter (SOM) is the main reservoir of SOC and soil organic nitrogen (SON) in rangelands and determines soil fertility, water retention, and soil structure (Tiessen et al. 1994; Lal 2004a). Grassland soils can store more than 100 and 10 tons per hectare of SOC and SON, respectively, in their first meter (Jobbágy and Jackson 2000), and grazing can increase, decrease, or maintain unaltered the size of both pools (Milchunas and Lauenroth 1993; Derner et al. 2006; Piñeiro et al. 2009). Therefore, management practices aimed to increase SOC and SON contents in rangelands are highly relevant as potential strategies for carbon (C) sequestration (Conant and Paustian 2002; Schuman et al. 2002; Lal 2004a, 2004b).

SOC and SON are tightly associated as structural components of organic matter with a relatively constant mass ratio (C:N) in short- to mid-term time scales (Baisden and Amundson 2003). Although SOM C:N ratios may shift after grazing or other disturbances, SON dynamics frequently constrain C fluxes and SOC accumulation in soils (Wedin 1995; Semmartin and Oesterheld 2001; Baer et al. 2003; Baisden and Amundson 2003; Piñeiro et al. 2006, 2009; Harpole et al. 2007). While most C and N fluxes within ecosystems tend to be coupled, the inputs and outputs of these elements can be decoupled (i.e., photosynthesis and decomposition in the case of C vs. biological fixation and volatilization in the case of N). For this reason input or output processes that involve N exclusively can influence SOC dynamics through cascading effects across within-ecosystem fluxes (Wedin and Tilman 1996; Piñeiro et al. 2006, 2009). However, N is not the only constraint for SOC accumulation. Water availability and C uptake (net primary production) can also limit SOC accumulation, especially in arid sites (Burke et al. 1998).

Our objectives were to review and synthesize the effects of grazing on SOC stocks in grasslands and to identify different pathways by which grazing might alter this soil pool. Additionally, and because of its importance for C biogeochemistry, we discuss the controls of SON stocks in grasslands. We present a series of conceptual models aimed to organize the current knowledge on grazing impacts on SOC and SON pools. We also examine the potential effects of grazers on N emissions into the atmosphere, and finally, we discuss how the conceptual models may help to design management strategies oriented to increase productivity and reduce greenhouse gases emissions.

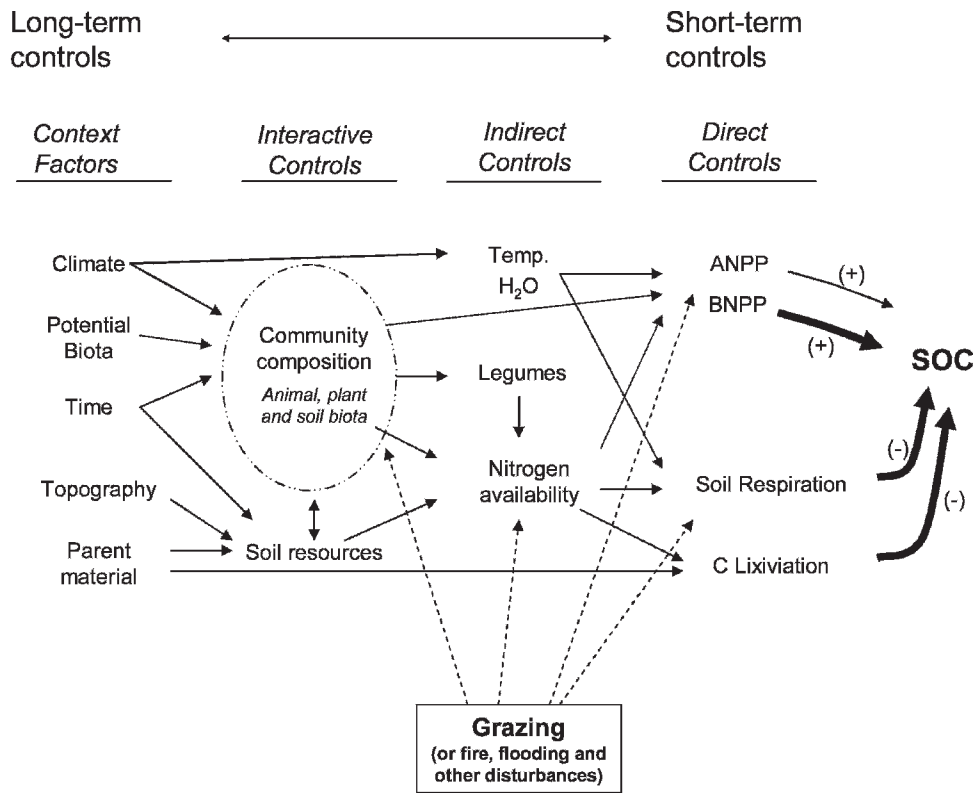
CONTROLS ON SOC AND SON ACCUMULATION

In this section we present conceptual models showing the major controls of C and N accumulation in soils, following the conceptual model for decomposition proposed by Chapin et al. (2002, chapter 6; Fig. 1). Our scheme includes context factors and interactive, indirect, and direct controls as well as the disturbance regime. We constructed the diagrams based on reported controls of SOC and SON accumulation from the literature and arranged them following the rationale by Chapin et al. (2002). Based on the model, we explore the main processes through which grazing (but also other disturbances, such as fire or flooding) may affect SOC and SON accumulation at different time scales (Fig. 1).

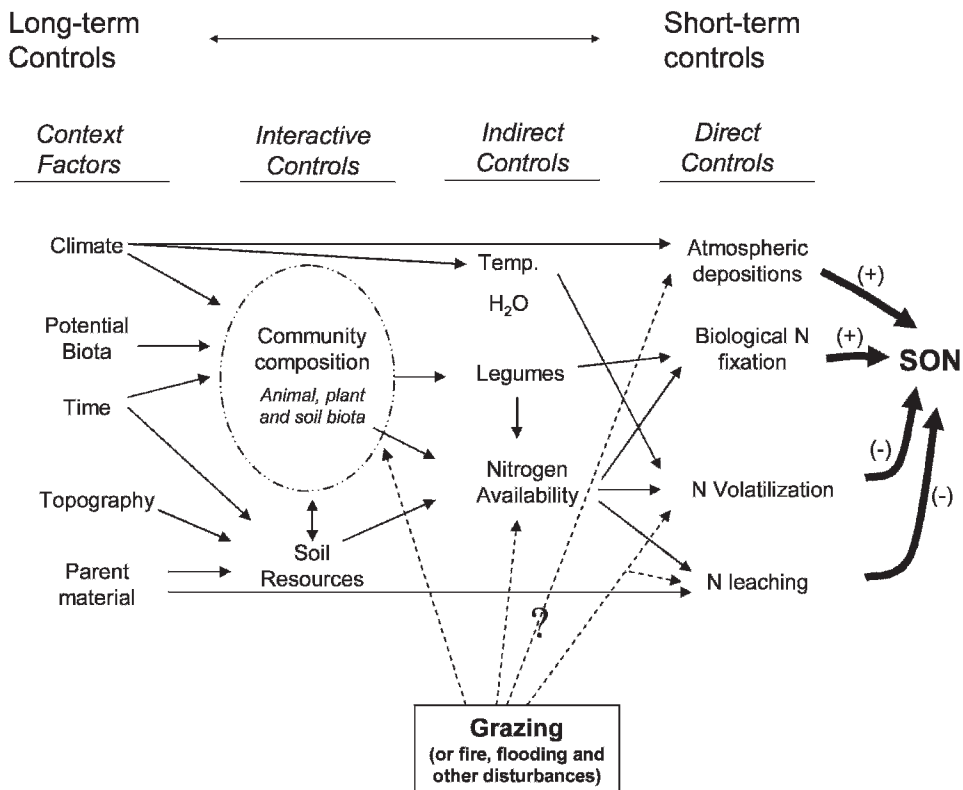
In the short term, SOC and SON contents are a function of direct controls that represent the main inputs to and outputs from these pools (Fig. 1). Changes in SOC and SON stocks are determined by the balance between C and N inputs and outputs in a given period. SOC stocks are directly controlled by Net Primary Production (NPP; C inputs) and respiration and C lexiviation (C outputs), whereas SON stocks are controlled by N atmospheric depositions and biological N fixation (N inputs) and N volatilization and leaching (N outputs; Fig. 1). NPP, but essentially the proportion of NPP that is allocated to belowground organs, controls SOC storage (Jobbágy and Jackson 2000). NPP and SOC are, in turn, mutually dependent, as discussed below. C outputs (leaching and organic matter respiration) are controlled by soil texture, mainly by clay and silt particles that adsorb organic molecules and favor SOM stability (Hassink 1997). Because the direct controls of SOC and SON accumulation differ, a partial decoupling between SOC and SON can be expected in the short term, and thus C and N stocks may change in opposite directions during this time frame (Asner et al. 1997).

Intermediate and long-term changes in SOC and SON would result from cumulative inputs and outputs, but are constrained by factors that operate on these direct controls (indirect controls and interactive factors; Fig. 1). N availability is a critical indirect control of both SOC and SON accumulation (Fig. 1) because it constrains both inputs and outputs of C and N (i.e., N availability can increase NPP, increasing C inputs to the soil, and may also decrease soil respiration, decreasing C outputs from the soil). The same interactive controls that control SOC also affect SON accumulation, supporting the tight association between the two ecosystem pools. Community composition affects and is affected by SOC and SON contents at intermediate to long-term time scales (Jobbágy and Jackson 2000; Altesor et al. 2006). Soil resources, especially N but also phosphorus or other elements (e.g., calcium, iron), may constrain organic matter accumulation in soils (Hedin et al. 2003). Thus, the depletion or accretion of C or N usually promotes losses or gains of the other element or changes in C:N ratios at intermediate to long-term time scales (Asner et al. 1997; Piñeiro et al. 2006). If interactive controls change in time or are suddenly modified by a disturbance (fire, grazing, etc.), they may modify SOC and SON via cascade effects, affecting indirect and direct controls.

Context factors constrain SOC and SON accumulation, establishing their potential ranges (Chapin et al. 2002; Fig. 1).



a



b

Figure 1. Soil organic carbon (SOC; **a**) and soil organic nitrogen (SON; **b**) controls at different temporal scales. Dashed lines show which controls are affected by grazing. ANPP is aboveground net primary production, and BNPP is belowground net primary production. See text for details.

Profuse evidence shows that climate (Jobbágy and Jackson 2000), biota (Jobbágy and Jackson 2000), time (Vitousek and Reiners 1975), topography, and parent material (specifically soil texture; Burke et al. 1989; Torn et al. 1997) control SOC and SON accumulation. Context factors do not affect input and outputs of C and N directly, but operate via cascade effects through other shorter-term controls, thus ultimately controlling SOC and SON stocks. Different contexts result in different responses to grazing. For example, Piñeiro et al. (2009) found that grazing increases SOC in deep soils but reduces it in shallow soils. Recently Derner et al. (2006) showed that in grasslands of North America grazing increased SOC stocks in dry shortgrass steppe ecosystems and decreased them in more humid mid- and tallgrass prairie ecosystems. In our model, similar context factors, interactive controls, and indirect controls affect SOC and SON accumulation, while direct controls differ between SOC and SON (Fig. 1). Thus, SOC and SON responses to grazing may differ in the short term, but will probably converge in the long term.

In addition to context factors the disturbance regime may significantly affect SOC and SON accumulation. SOC and SON response to grazing can be substantially different when interacting with other disturbances such as fire (Briggs et al. 2005; Piñeiro et al. 2006) or flooding (Chaneton et al. 1988). Grazing may modify (increase or decrease) fire frequency and intensity (Oesterheld et al. 1999; Bond and Keeley 2005). Fire–grazing interactions can change SOC accumulation, depending on the relative magnitude of nutrient losses promoted by each disturbance (Briggs et al. 2005; Piñeiro et al. 2006). Fire and grazing are not the only factors that may interact and alter SOC contents. In the Flooding Pampas of Argentina, Piñeiro et al. (2009) found that grazing increased SOC contents at lowland sites (frequently flooded) but decreased it in uplands sites (not flooded).

GRAZING EFFECTS ON SOC AND SON

In this section we present results from a literature review of grazing effects on SOC stocks, performed by compiling papers that report comparisons of grazed vs. ungrazed paired sites. We searched the ISI web of knowledge (www.isiwebofknowledge.com) to identify articles that measured SOC contents under grazed and ungrazed conditions using the keywords “soil and carbon and grazing.” We included only papers performed in grasslands and did not consider some located in savannas (e.g., Savadogo et al. 2007). Unfortunately, several papers were excluded from the review because they did not report SOC stocks corrected by soil bulk density or did not provide data to perform the correction (e.g., Zeidler et al. 2002; Beukes and Cowling 2003; Feral et al. 2003). We did not find any papers from Africa or Australia, although we did find three papers reporting the effects of different grazing intensities or rotational vs. continuous grazing in Australia. We finally included 20 articles reporting 67 comparisons that evaluated grazing effects on SOC stocks (Table 1), and we additionally compiled from these papers SOM C:N ratios, root biomass contents, soil bulk density changes, mean annual precipitation, and mean annual temperature when reported.

SOC increased, decreased, or remained unchanged under contrasting grazing conditions across temperature and precip-

itation gradients, suggesting that grazing influences the factors that control SOC in a complex way (Table 1). However, our review also revealed some general patterns, such as 1) root contents (a primary control of SOC formation) were higher in grazed than in their ungrazed counterparts at the driest and wettest sites, but were lower at sites with intermediate precipitation (~ 400 mm to 850 mm); 2) SOM C:N ratios consistently increased under grazing conditions; and 3) bulk density either increased or did not change in grazed sites.

Our review showed how grazing affected differentially belowground biomass across one context factor: mean annual precipitation. Following Burke et al.'s (1998) conceptual model for plant–soil interactions, we suggest that grazing results in the stimulation of root production by changing both allocation (Gao et al. 2008) or species abundances (Derner et al. 2006) in dry sites for the capture of water and in humid sites for the capture of soil nutrients. The mechanism operating at intermediate precipitation sites remains unclear but could be probably related to light limitation of NPP. Higher root biomass has been suggested to increase SOC contents because of greater C inputs to the soil (Derner et al. 2006). However, SOC changes in grazed sites were not associated with variations in belowground biomass as expected initially (Table 1). Our review suggests that grazing effects on SOC will depend not only on belowground allocation but also on other site characteristics (probably soil properties) and on grazing-induced modifications of other C and N stocks and fluxes.

Grazing increased or maintained unchanged SOM C:N ratio at nearly all sites, despite increases or decreases in SOC contents (Table 1; grazing increased organic matter C:N ratios at 25 sites, maintained unchanged at 22 sites, and decreased it at two sites, whereas no data were available for 17 sites). This consistent trend in C:N ratios suggests a potential N limitation under grazing. Increases in SOM C:N ratios often occur in the more labile fractions, because recalcitrant fractions have low and constant C:N ratios near 10. Piñeiro et al. (2009) reported increases in the C:N ratios of the particulate (less decomposed) organic matter fraction after grazing removal. Conversely, organic matter fractions associated with mineral particles (a more recalcitrant pool) maintained similar and low C:N ratios at grazed and ungrazed sites, despite the higher C:N ratios of litter and root inputs in grazed sites. These results suggest that the higher C:N ratios of plant debris are only increasing the C:N ratio of the labile SOM fractions. Then, to accumulate C in the recalcitrant SOM fractions, more C will be respired to achieve the low C:N ratios of these fractions, or in other words, N would be limiting SOM accumulation in stable pools. Because grasslands accumulate the majority of SOC in recalcitrant fractions, grazing may reduce SOM formation via N limitation. However, N limitation is not the only factor constraining SOC accumulation under grazing, because either increases or decreases of SOC occurred when grazing significantly increased SOM C:N ratios (Table 1).

As expected, soil bulk density increased or remained invariant at grazed compared to ungrazed sites. Soil compaction under grazing is attributed to trampling by herbivores (Taboada and Lavado 1993). Soil compaction reduces water infiltration and increases runoff under grazing conditions, decreasing water available for plant growth (Abdel-Magid et al. 1987; Savadogo et al. 2007). Additionally, less pore space can

Table 1. Grazing effects on different soil properties and belowground biomass in grasslands.

Author	Mean annual precipitation	Mean annual temperature	Δ SOC ¹	Δ C:N SOM ¹	Δ bulk density ¹	Δ roots ¹	<i>n</i> (total 67)	Sampling depth	Experiment type, age (yr)	Observations
Frank et al. (1995)	n/d	n/d	Decreases	Increases	n/d	=	1	0–100	Exclosures, 75	Moderate grazing
Frank et al. (1995)	n/d	n/d	=	=	n/d	Increases	1	0–100	Exclosures, 75	Heavy grazing
Neff et al. (2005)	207	11.6	Decreases	Increases, =	=	n/d	1	0–30	Never grazed	Wind erosion
Shrestha and Stahla (2008)	213	n/d	=	=	=	n/d	1	0–15	Exclosures, 43	High elevation
Shrestha and Stahla (2008)	200	n/d	=	=	=	n/d	1	0–15	Exclosures, 47	High elevation
Shrestha and Stahla (2008)	203	n/d	=	=	=	n/d	1	0–15	Exclosures, 41	High elevation
Shrestha and Stahla (2008)	203	n/d	=	Decreases	=	n/d	1	0–15	Exclosures, 41	High elevation
Smoliak et al. (1972)	310	n/d	Increases	Increases	=	Increases	1	0–10	Exclosures, 42	Three grazing intensities
Derner et al. (2006)	321	8.6	Increases	n/d	=	=	1	0–30	Exclosures, 65	Shortgrass
Reeder et al. (2004)	325	n/d	Increases	Increases	Increases	Increases	1	0–90	Exclosures, 56	Heavy grazing
Manley et al. (1995)	338	n/d	Increases	n/d	Increases	n/d	2	0–90	Grazing, 11	Significant only at 0–7.6
Wu et al. (2008)	345	1.1	Decreases	Decreases, =	n/d	n/d	5	0–40	Exclosures, 2 to 27	Chronosequence
Cui et al. (2005)	350	0.2	=	n/d	n/d	Increases	2	0–80	Exclosures, 20	Natural vegetation
Cui et al. (2005)	350	0.2	Decreases	n/d	n/d	n/d	1	0–80	Exclosures, 10	Degraded
Schuman et al. (1999)	384	n/d	Increases	Increases, =	Increases	Decreases	2	0–60	Grazing, 12 (40 exclosures)	Heavy grazing
Henderson et al. (2004)	350–480	6.25	=	n/d	Increases	n/d	8	0–100	Exclosures, 20 to 71	Correction to equivalent soil mass
Xie and Wittig (2004)	411	5.9	Decreases	n/d	Increases	Decreases	1	0–40	Exclosures, 18	Four levels of grazing
Mikhailova et al. (2000)	587	5.4	=	Increases	Increases	=	1	0–10	Exclosures, 72	Correction to equivalent soil mass
Derner et al. (2006)	588	11.9	=	n/d	=	Decreases	1	0–30	Exclosures, 96	Midgrass
Fuhlendorf et al. (2002)	766	18.3	Decreases	Increases	n/d	Decreases	1	0–10	Exclosures, 50	Restoration
Derner et al. (2006)	835	12.8	Decreases	n/d	=	Decreases	1	0–30	Exclosures, 35	Tallgrass
Potter et al. (2001)	842	17	Increases	=	Increases	n/d	1	0–60	Exclosures, 11	Clay soils
Potter et al. (2001)	842	17	Decreases	Increases	=	n/d	1	0–60	Exclosures, 11	Sandy soils
Piñeiro et al. (2009)	861	15	Increases	Increases	=	Increases	2	0–100	Exclosures, max 30	Lowlands
Chaneton and Lavado (1996)	~ 900	14.5	Increases	Increases	n/d	n/d	1	0–10	Exclosures, 12	Lowlands
Chaneton and Lavado (1996)	~ 900	14.5	=	Increases	n/d	n/d	1	0–10	Exclosures, 16	Uplands
Lavado et al. (1995)	~ 900	14.5	=	=	n/d	n/d	1	0–15	Exclosures, 13	Lowlands
Gill (2007)	932	1.3	=	=	=	n/d	11	0–15	Exclosures, ~ 90	Subalpine
Piñeiro et al. (2009)	1 099	15	Increases	Increases	=	Increases	1	0–100	Exclosures, 5	Lowlands
Piñeiro et al. (2009)	1 099	15	Decreases	Increases	Increases	Increases	3	0–100	Exclosures, max 11	Deep soils
Piñeiro et al. (2009)	1 099	15	Increases	Increases	Increases	Increases	2	0–100	Exclosures, max 7	Shallow soils
Piñeiro et al. (2009)	1 161	15	Decreases	Increases	Increases	Increases	1	0–100	Exclosures, 13	Deep soils
Welker et al. (2004)	1 200	n/d	Increases	Increases	=	n/d	1	0–10	Exclosures, 73	No significant difference from 0–60
Piñeiro et al. (2009)	1 300	15	Decreases	Increases	Increases	Increases	3	0–100	Exclosures, 30	Deep soils
Piñeiro et al. (2009)	1 406	15	Decreases	Increases	Increases	Increases	1	0–100	Exclosures, 8	Deep soils
Piñeiro et al. (2009)	1 406	15	Increases	Increases	Increases	Increases	2	0–100	Exclosures, 18	Shallow soils

¹“Increases” means that SOC, roots, SOM C:N, or bulk density are higher under grazed conditions. SOC indicates soil organic carbon; SOM, soil organic matter; C:N, carbon to nitrogen ratio; and n/d, no data.

limit gas exchange and reduce root growth. Both mechanisms suggest that soil compaction reduces plant production and thus SOC storage. However, soil compaction is not the only way by which herbivores alter SOC stocks, because both increases and decreases of SOC have been reported with increases in soil bulk density (Table 1). Thus, as for N limitation, other mechanisms should be co-occurring with compaction to generate the observed patterns in SOC changes.

Based on the influence of the three factors outlined before, and considering that all operate simultaneously, we would expect decreases in SOC contents under grazing in the sites located in the middle of the typical grasslands' mean annual precipitation range (~400–850 mm). In this range all the factors would decrease SOC stocks: root biomass decreases, soil compaction increases, and N limitation increases. Articles reporting data for 15 sites included in this precipitation range showed either a decrease or no changes in SOC contents under grazing compared to the herbivore exclosures, except one site located near the 850 precipitation edge (Table 1).

The studies we reviewed that evaluate SOC changes using the grazing-exclosure approach present at least four shortcomings. The first two are related to the experimental setting, and the last two relate to the type of observation made. The grazing vs. exclosure approach relies on the assumption that differences in space (ungrazed vs. grazed plots) are equal to changes through time (pregrazing vs. postgrazing). Soil heterogeneity can add noise to these comparisons, curtailing their statistical power, and independent variables that are changing during the exclosure treatment period can interact with grazing effects in a complex way (e.g., the increasing atmospheric concentration of CO₂ could have differential effects on grazed vs. ungrazed plots). An additional assumption made in the exclosure approach has to do with the symmetry and reversibility of grazing-exclosure treatments. Strictly, exclosures test the effects of removal of grazing, not the effects of addition of grazing (Burke et al. 1997). Are exclosures representing pregrazing conditions? Or can they just tell us how grazing interruption works, with no clues about the reverse treatment? Observational limitations often arise when SOC data are not accompanied by bulk density measurements, allowing us to estimate C stocks in an equivalent soil mass (Davidson and Ackerman 1993). This often leads to an overestimation of SOC in grazed treatments because of soil compaction (Henderson et al. 2004). Finally, a substantial number of studies evaluated only grazing effects on surface soil (first 5 cm or 15 cm), although some more recent studies have explored the whole soil profile (Henderson et al. 2004; Reeder et al. 2004). Surface changes in SOC can differ from whole profile analysis (Baker et al. 2007). All the limitations mentioned above may also contribute to the contradictory effects of grazing on SOM and should be further investigated.

PATHWAYS OF GRAZING EFFECTS: SOC AND SON

To synthesize grazing effects on SOC contents, we grouped the mechanisms proposed by each author to explain their observed SOC changes at grazed vs. ungrazed sites according to different pathways. Most of the papers reviewed explained their results based on one or more mechanisms that could be clumped in

three main pathways: grazing altered SOC contents by changing the magnitude or the proportion of NPP that reaches the soil (*NPP pathway*), by changing SON stocks (*nitrogen pathway*), and/or by altering SOM decomposition (*decomposition pathway*; Fig. 2). We propose that grazing may alter SOC contents simultaneously via these three pathways and thus generate variable responses.

Several authors discussed how grazing affected SOC contents by changing NPP or by affecting the amount of NPP that actually reaches the soil (see the NPP pathway in Fig. 2). Normally an important portion of ANPP is consumed and respired by herbivores, increasing C outputs from the ecosystems and decreasing C available for SOC formation (Fig. 2). Grazing may additionally decrease NPP by removing large portions of aboveground biomass and decreasing leaf area and light interception. In contrast, herbivores also remove or break down standing dead biomass that shades green leaves, and they consume relatively old plant tissues that have low radiation use efficiency (McNaughton 1983; Knapp and Seastedt 1986). The net direct effect of defoliation on NPP will result from the balance of these two opposite mechanisms.

Grazing can also change C allocation patterns affecting the amount of C entering the soil. Belowground biomass directly enters the soil and contributes more to SOM formation than aboveground tissues (Johnson and Matchett 2001). Thus, grazing may affect the amount of C available for SOC formation by changing the proportion of NPP that is allocated to below or aboveground organs. Grazing effects on ANPP are variable, but mostly negative, and do not seem to vary across a precipitation gradient (Oesterheld et al. 1999). In contrast, belowground net primary production seems to increase with grazing (McNaughton et al. 1998; Pucheta et al. 2004; Derner et al. 2006), but again, some studies reported lower BNPP (or root biomass) under grazing (Johnson and Matchett 2001; Kauffman et al. 2004). Our review showed that grazing effects on root biomass varied across a precipitation gradient (Table 1), and that grazing frequently increases the proportion of C allocated to belowground organs, potentially increasing SOM formation.

On the other hand, grazers may change NPP indirectly by altering species composition or soil resources or by decreasing water availability (Fig. 2). Grazing affects community composition in several ways depending on the history of grazing and moisture gradients (Milchunas and Lauenroth 1993; Cingolani et al. 2005). Several mechanisms by which herbivores alter plant community composition have been proposed: selective grazing, changes in resource availability, physical breakdown of fragile species, etc. (Semmartin and Oesterheld 2001; Bakker et al. 2003). Leoni et al. (2008) found that grazing-tolerant species have lower relative growth rates than species present in the ungrazed sites, determining the lower ANPP of grazed sites. The long or short history of grazing also constrains NPP responses to grazing, because sites with a long history of grazing usually have a similar species composition in grazed and ungrazed plots, whereas sites with a short history of grazing usually have contrasting species composition in grazed and ungrazed plots (Milchunas and Lauenroth 1993; Adler et al. 2004; Cingolani et al. 2005). Based on differing grazing-resistance plant traits, Adler et al. (2004) suggested that productivity of the upland plant communities in the Patagonian steppe (with a long history of grazing) will be less affected by grazing than the productivity of

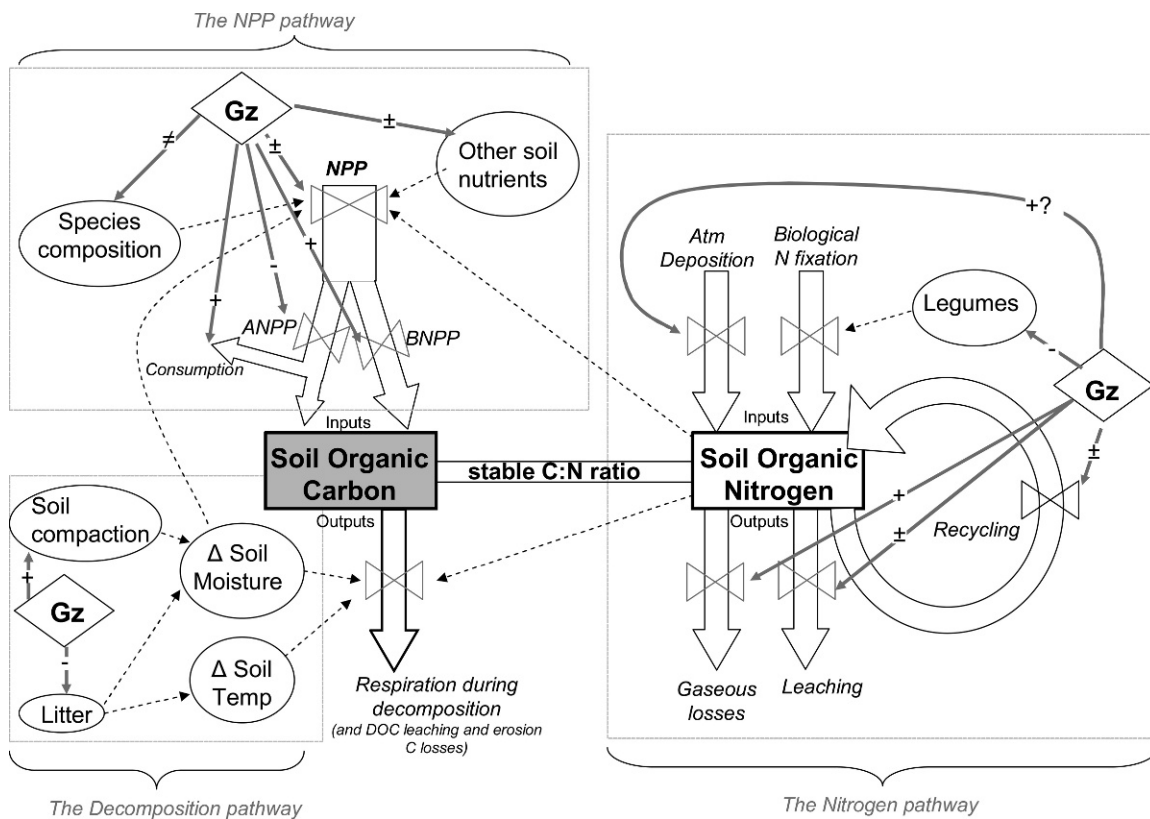


Figure 2. Grazing effects on soil organic carbon stocks through different pathways. We separated three main pathways by which grazing modifies soil organic carbon stocks in rangelands: via affecting net primary production, by changing nitrogen stocks and cycling, or by altering soil organic carbon decomposition. Gz indicates grazing; NPP, net primary production; ANPP, aboveground NPP; BNPP, belowground NPP; C:N, carbon to nitrogen ratio; and DOC, dissolved organic carbon.

the sagebrush steppe in the United States (with a short history of grazing). In addition, soil compaction may decrease soil moisture and reduce NPP (Savadojo et al. 2007; Fig. 2). Finally, grazing may also constrain NPP by altering soil nutrients, especially N, as discussed below (Fig. 2).

Herbivory can reduce SOC stocks by increasing decomposition through micrometeorological changes (soil temperature and moisture; see the decomposition pathway in Fig. 2). A grazing-induced reduction of litter pools (Savadojo et al. 2007) would indirectly increase soil temperature and evaporation, which in turn may increase SOM decomposition (Bremer et al. 1998; Burke et al. 1998). Soil temperature in summer can be 10°C higher at grazed sites compared to ungrazed sites (G. Piñeiro, unpublished data, 2006). Increases in soil bulk density (see Table 1) reduce infiltration rates and increase soil moisture variations under grazing, potentially increasing SOM decomposition (Abdel-Magid et al. 1987; Savadojo et al. 2007; Fig. 2).

Changes in SOC contents at grazed sites should be related to changes in SON that, in turn, affect both NPP and SOC decomposition rates (see the N pathway in Fig. 2). Grazers can alter SON stocks by both increasing or decreasing N inputs and N outputs. Regarding outputs, grazers promote higher N losses from urine and dung patches (Whitehead and Raistrick 1993) but can also stimulate N retention by decreasing N losses through greater root allocation. Grazing promotes an increase in root biomass at both extremes of the precipitation gradient (Table 1), and such an increase in belowground allocation may

result in greater N uptake, lower N losses, and higher N retention (Heckathorn and Delucia 1996; Derner et al. 2006; Piñeiro et al. 2009). Regarding inputs, grazing can decrease N inputs by decreasing legume biomass or cover. Higher N volatilization would increase N redeposition from the atmosphere, partially compensating for N losses, as discussed further (Figs. 1 and 2).

Additionally, grazing may either increase or decrease N recycling (Fig. 2). Herbivores accelerate N returns in urine and dung patches. As most grasslands experience some level of N limitation, faster N returns have been suggested as a possible

Table 2. Nitrogen (N) emissions from herbivore excretions in the Río de la Plata Grasslands.

Productivity, $\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ (Paruelo et al., this issue)	5 800
Percentage of aboveground net primary production consumed (Oesterheld et al. 1992)	58
Consumption of forage, $\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$	3 364
Carbon (C) consumed, $\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$	1 682
C:N ratio of consumed forage (estimated based on a green:standing dead ratio of 4)	20
N consumed, $\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$	84
Percentage of N consumed that returns to the soil (Whitehead and Raistrick 1993)	70–80
N emissions, $\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$	17–25

Nitrogen Cycle in Grazed Ecosystems

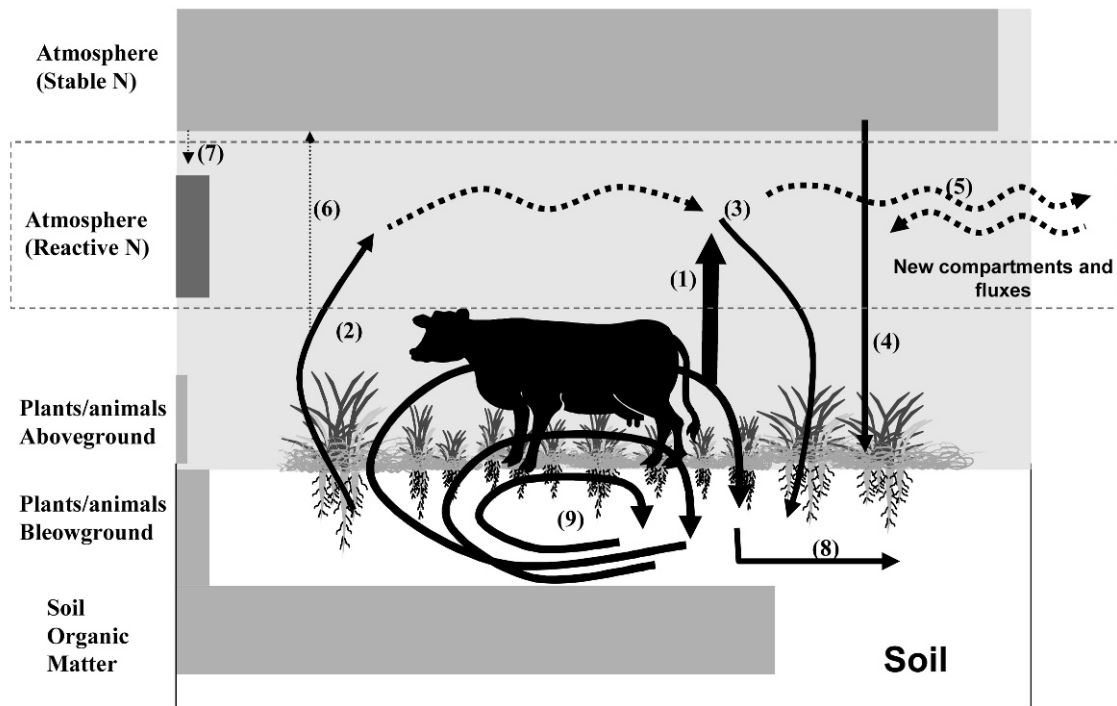


Figure 3. Diagram of the nitrogen (N) cycle in grazed ecosystems, showing traditional fluxes (solid arrows) and pools (light gray boxes) and new fluxes (dashed arrows) and pools (dark gray box) proposed to better understand N cycling at regional scales. The numbers in the figure are (1) N volatilization from urine and dung patches, (2) N reactive emissions from the soil, (3) redeposition, (4) biological N fixation, (5) N exports to adjacent ecosystems, (6) N_2 emissions, (7) conversion of N_2 to N reactive by lightning, (8) leaching, and (9) N recycling through soil biota, vegetation, and herbivores.

mechanism to explain grazing-induced increases in productivity (Frank and Evans 1997; McNaughton et al. 1997; Holdo et al. 2007; Semmartin et al. 2007). However, grazing may accelerate N recycling in nutrient-rich systems but decelerate N recycling in nutrient-poor systems (Frank and McNaughton 1993; McNaughton et al. 1997; Augustine and McNaughton 2006). Lower SON contents or accelerated recycling under grazing could explain observed increases in SOM C:N ratios. If grazing determines a net loss of N, then we would expect an increase in SOM C:N ratios and a decrease in total SON contents. C:N ratios should decrease if C limits SOM formation. Our review shows that grazing mostly increased or did not alter SOM C:N ratios (Table 1), despite increases or decreases in SOC contents. Our result supports the hypothesis that grazing increases N limitation in grasslands.

GRAZING EFFECTS ON ATMOSPHERIC REACTIVE N

Our conceptual models suggest that in grazed systems the atmospheric reactive N should be included as an important N pool. Reactive N pools refer to those N forms that are not stable in atmosphere and biosphere and consequently have significant effects on N dynamics (Schlesinger 1991); they include NH_3 , NH_4 , NO_x , N_2O (and other inorganic oxidized forms), and other organic compounds (Galloway et al. 2004). As suggested before, grazing may accelerate N recycling but

increase N losses. N losses by grazing are mainly gaseous NH_3 , a reactive N form. Very simple calculations for the Río de la Plata Grasslands in South America suggest that 17 kg to 25 kg $N \cdot ha^{-1}$ are lost each year from these grasslands (Table 2). Some of this N may be lost by leaching, but probably half or more is lost as NH_3 volatilization. NH_3 has a short residence time in the atmosphere (~ 5 d), and thus it is redeposited near emission sources. In agreement, similar but lower values (~ 7 kg $N \cdot NH_4 \cdot ha^{-1} \cdot yr^{-1}$) were measured as wet deposition in rain events in Río de la Plata Grasslands, suggesting that some N is being redeposited within the region, but some has been exported out of the region (Piñeiro et al. 2007). Similar results were obtained in North America, indicating a positive trend in regional N deposition associated with increased N emissions generated by larger pig stocks (Aneja et al. 2003).

We suggest that this new compartment (atmospheric reactive N) and four new fluxes should be included explicitly when analyzing N cycling in rangelands. The new fluxes are N emissions in reactive forms, N emissions in nonreactive forms (N_2), local redeposition, and reactive N export to adjacent ecosystems (Fig. 3). Higher reactive emissions (Flux 1 in Fig. 3) can be locally redeposited (Flux 3). Thus, higher N emissions can be partially attenuated by redeposition, but can also be lost by atmospheric transport to other regions (Flux 5), increasing N loadings on them. As a result, grazing “opens” the N cycle, reducing internal recycling (Flux 9), and increases ecosystem dependence on atmospheric loadings. Finally, because N volatilization in grazed ecosystems occurs mainly as NH_3

(Ruess and McNaughton 1988; Whitehead and Raistrick 1993; Frank and Zhang 1997), while N volatilization in ecosystems without herbivores occurs mainly as N₂O and NO_x (Zheng et al. 2002), herbivores may shift N volatilization from N₂O and NO_x forms to NH₃, potentially reducing the unwanted N₂O and NO_x emissions (Piñeiro et al. 2006). While NO_x has a short residence time in the atmosphere (~ 1 d), N₂O has a relatively long life (~ 150 yr), being more stable in the atmosphere and therefore being a strong greenhouse gas that also depletes O₃ in the stratosphere (Schlesinger 1991). Additionally, NO_x emission generates O₃ in the troposphere, which is also unwanted. Therefore, grazing may alter N fluxes and emission to the atmosphere, altering regional biogeochemistry with implications for climate change and ozone formation (Bouwman et al. 2002; Neff et al. 2002). Soil N storage in grasslands can be a potential solution for decreasing atmospheric reactive N, enhancing both NPP and SOC accumulation.

MANAGEMENT IMPLICATIONS

Identifying the pathway by which grazing may alter SOM stocks in different regions is a key step for designing locally adapted management practices to increase SOC storage. For example, the change in species composition that results as a consequence of grazing may be a key factor for determining the net effect of grazing on SOC changes in a region, since both the *NPP pathway* and the *nitrogen pathway* are affected by changes in species composition. It has been shown that intensive grazing can increase forbs with low NPP and thus decrease C inputs to the soil. On the other hand, in other regions shrub encroachment or increased abundance of highly productive species can enhance NPP and thus increase C inputs to the soil under grazing. Ranchers and decision makers should use regional evidence of grazing effects to evaluate which of the three pathways suggested by our model is the most important for determining SOC storage, and then apply management practices to decrease grazing impacts on that/those pathway/s. For example, grazing systems able to manage community composition through seasonal and annual resting periods may counteract the negative impact of grazing on community composition that leads to decreases in SOC, additionally increasing forage quality and accessibility.

Our model can be used to help organize and analyze the complex effects of grazing on rangeland functioning and suggests that one of the key aspects to maximize SOC storage is N dynamics. NPP, and particularly BNPP, is an important pathway to increase SOC contents, but the positive effects of grazing on C inputs and belowground allocation would be sustainable only if N losses are reduced or N inputs augmented. Several alternatives aimed to manage N losses and inputs can be implemented; however, caution should be put in avoiding unwanted N emissions such as N₂O and NO_x, which can derive from excessive N loadings. A better understanding of source, residence time, and transferences of reactive N within a region would provide a critical piece of information allowing for the design of local management practices aimed at conserving and redistributing N at the landscape level. Higher N conservation will allow greater C sequestration in soils and increased soil fertility, which opens the possibility of a win-win situation in

terms of ranchers' economy and global greenhouse gases reduction initiatives.

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