

REVIEW

Effects of grazing on grassland soil carbon: a global review

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Soils of grasslands represent a large potential reservoir for storing CO₂, but this potential likely depends on how grasslands are managed for large mammal grazing. Previous studies found both strong positive and negative grazing effects on soil organic carbon (SOC) but explanations for this variation are poorly developed. Expanding on previous reviews, we performed a multifactorial meta-analysis of grazer effects on SOC density on 47 independent experimental contrasts from 17 studies. We explicitly tested hypotheses that grazer effects would shift from negative to positive with decreasing precipitation, increasing fineness of soil texture, transition from dominant grass species with C₃ to C₄ photosynthesis, and decreasing grazing intensity, after controlling for study duration and sampling depth. The six variables of soil texture, precipitation, grass type, grazing intensity, study duration, and sampling depth explained 85% of a large variation ($\pm 150 \text{ g m}^{-2} \text{ yr}^{-1}$) in grazing effects, and the best model included significant interactions between precipitation and soil texture ($P = 0.002$), grass type, and grazing intensity ($P = 0.012$), and study duration and soil sampling depth ($P = 0.020$). Specifically, an increase in mean annual precipitation of 600 mm resulted in a 24% decrease in grazer effect size on finer textured soils, while on sandy soils the same increase in precipitation produced a 22% increase in grazer effect on SOC. Increasing grazing intensity increased SOC by 6–7% on C₄-dominated and C₄-C₃ mixed grasslands, but decreased SOC by an average 18% in C₃-dominated grasslands. We discovered these patterns despite a lack of studies in natural, wildlife-dominated ecosystems, and tropical grasslands. Our results, which suggest a future focus on why C₃ vs. C₄-dominated grasslands differ so strongly in their response of SOC to grazing, show that grazer effects on SOC are highly context-specific and imply that grazers in different regions might be managed differently to help mitigate greenhouse gas emissions.

Keywords: carbon sequestration, grasslands, grazing, grazing intensity, precipitation, soil organic carbon, soil texture

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Introduction

With the historically recent rise in atmospheric carbon dioxide, it has become increasingly necessary to understand the global carbon cycle and particularly, the role of various potential carbon sinks. Soil is the largest terrestrial reservoir of carbon (Chapin *et al.*, 2009), storing more than twice the amount of carbon than the atmosphere (Percival *et al.*, 2000) as decomposed plant litter and residue (Cole *et al.*, 1993). As grasslands cover ca. 40% of the earth's land surface (LeCain *et al.*, 2002; Wang & Fang, 2009) and many have suffered recent losses of soil carbon due to intensive livestock or agricultural uses, they may have a high potential to store an appreciable fraction of atmospheric CO₂ as stable C in the soil (Reid *et al.*, 2004). Nearly 100% of uncultivated grasslands are grazed by large mammals, and thus, grazing may be a key factor controlling the storage of soil carbon. However, despite considerable

research over the past 40 years, much uncertainty exists regarding the effects of grazing on soil carbon.

The major factors that influence soil carbon storage are thought to be related to two types of variables: environmental, including mean annual precipitation and soil type, and study design or sampling methods, such as study duration and soil sampling depth. Biotic variables, such as grassland species composition and grazing intensity are also likely to modify grazer impacts on soil carbon. However, despite strong hints in recent reviews (Derner & Schuman, 2007; Pineiro *et al.*, 2010) that grazing has varying effects in different environments, the influence of biotic variables is not well explored.

Previous reviews have found mixed results of grazing effects on soil organic carbon (SOC) (Milchunas & Lauenroth, 1993; Derner *et al.*, 2006), with studies showing positive (Smoliak *et al.*, 1972; Wienhold *et al.*, 2001; Reeder & Schuman, 2002), neutral (Nosetto *et al.*, 2006; Raiesi & Asadi, 2006; Shrestha & Stahl, 2008) or negative effects of grazing (Su *et al.*, 2005; Pei *et al.*, 2008; Zuo *et al.*, 2008; Golluscio *et al.*, 2009). To further

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explore the drivers of grazer effects on soil carbon, we gathered existing studies of grazing effects on SOC density to conduct a standard statistical meta-analysis. Meta-analyses offer an important advantage over traditional narrative reviews in that they provide a *quantitative* approach to comparing results between studies (Arnqvist & Wooster, 1995). Through the use of a common measure of effect size that represents the results of independent treatment comparisons rather than the responses of independent subjects, meta-analyses allow us to determine the combined magnitude of the effect under study and to properly assess its significance (Arnqvist & Wooster, 1995). Meta-analyses have proven to be a powerful statistical tool in ecological reviews, yet our study represents a relatively novel approach to the question of how grazing impacts SOC.

Our focus is on grazer effects on carbon *density* as effects on soil carbon *concentration* may be confounded by grazer effects on soil bulk density. Thus, while much informative research has been done using % C and C concentrations, as we were interested mainly in soil's potential to sequester CO₂ (Smith *et al.*, 2008), we thought it important to consider only carbon density in our review. We tested for the influence of six factors on grazer impacts on SOC density. These not only included some previously tested such as soil type, precipitation, and study duration (Derner & Schuman, 2007) but also new factors, including whether dominant grass species use C₃ vs. C₄ photosynthesis. More importantly, we explicitly tested for interactions between different factors.

First, we tested hypotheses related to the environmental variables of mean annual precipitation and soil texture type. SOC is generally expected to increase with precipitation because of its association with higher productivity and a greater volume of plant litter inputs, particularly belowground (Cole *et al.*, 1993; Derner & Schuman, 2007), which increases C inputs to soil. However, two separate reviews (Derner & Schuman, 2007; Pineiro *et al.*, 2010) found that, under grazing, soil carbon sequestration was increased only at sites with a mean annual precipitation of 600 mm or less. This pattern is attributed to the greater, more active microbial biomass C and more labile organic matter pools in wetter environments, which may increase C turnover under grazing (Zak *et al.*, 1994; Derner & Schuman, 2007). The difference in C storage between semiarid and mesic environments may also be the result of semiarid areas having lower initial SOC pools, greater root C to soil C ratios, and a grazing-induced compositional shift of plant community to greater C₄ dominance (Derner *et al.*, 2006), which may trigger a greater transfer of fixed carbon belowground to roots (Derner & Schuman, 2007). In contrast, a different set of studies,

mostly from central Asia, found negative effects of grazing on SOC at sites with less than 600 mm mean annual precipitation. In several of these studies (Su *et al.*, 2005; Pei *et al.*, 2008; Zuo *et al.*, 2008; Golluscio *et al.*, 2009), this effect appears to be related to increased erosion due to a decrease in vegetation cover associated with continuous, heavy grazing (Pei *et al.*, 2008). Erosion can amplify the negative effects of heavy grazing on leaf area and carbon inputs, as was found in several studies included in our analysis (Li *et al.*, 2008; Steffens *et al.*, 2008) that featured sparse vegetation cover and/or coarse, sandy soils which are less resistant to wind and rainfall than are finer textured soils.

Finer soil texture may also potentially strengthen grazer effects on SOC because soils with higher clay content are believed to form tight aggregates that protect SOC from microbes (Feller & Beare, 1997; Percival *et al.*, 2000; Bronick & Lal, 2005) and many studies have found SOC to be correlated with clay content (Hassink, 1994; Arrouays *et al.*, 1995; Alvarez & Lavado, 1998; Percival *et al.*, 2000). Greater precipitation and finer soil texture may thus amplify the magnitude of grazer effects, either positive or negative, rather than shift the direction of effects (Milchunas & Lauenroth, 1993).

We also tested hypotheses related to the influence of two biotic variables: grazing intensity and dominant grass species composition. Higher grazing intensity is generally thought to decrease soil carbon by potentially reducing CO₂ fixation from the loss of photosynthetic tissue and reduction in belowground C inputs through lower root production and higher root litter turnover (Gao *et al.*, 2008; Klumpp *et al.*, 2009). However, grazing-induced changes in allocation of carbon belowground and alteration of root C : N is associated with positive effects of grazing on SOC (Bardgett *et al.*, 1998; Reeder & Schuman, 2002). These different responses may in part be due to the dominant grass species, as grazers often increase carbon storage on C₄-dominated grasslands (Wienhold *et al.*, 2001; Derner *et al.*, 2006; Sanjari *et al.*, 2008), but decrease SOC on C₃-dominated grasslands (Potter *et al.*, 2001; Li *et al.*, 2008; Steffens *et al.*, 2008). We expected that grazing intensity might interact with dominant grass species to yield a pattern of positive effects of higher grazing intensity on SOC in C₄ grasslands and negative effects of increasing grazing intensity in C₃-dominated grasslands.

As a control for differences in the sampling design and longevity of experiments, we tested two hypotheses that grazing impacts on soil C would be greater (positive or negative) in longer studies and/or those that sampled only shallow (<20 cm) depths. We expected that longer studies would have more time for differences in C sequestration to accumulate and would thus show a greater effect. Also, as grazing-induced

changes in organic matter may be more likely to occur in the top soil layers, and would thus be diluted by sampling C deeper in the soil profile, we expected a greater effect of grazing in those studies that sampled only at shallower depths.

We considered the influence of these six factors (precipitation, soil texture, grass species composition, grazing intensity, study duration, and soil sampling depth) on grazing impacts on soil C in an ANCOVA analysis that allowed us to determine for the first time the potential separate and interactive influences of biotic and study design variables on grazing effects on SOC, once differences in environmental variables were statistically controlled. This meta-analysis thus provides a potentially more rigorous view of grazing effects on SOC and possible resolution of the disparate experimental results across studies thus far.

Materials and methods

In an attempt to find virtually every paper that looked at the effect of grazing on soil carbon storage, we conducted a comprehensive search of the ISI Web of Knowledge [v.4.6] – Web of Science® database with the keywords: soil carbon and grazing; soil organic carbon and grazing; soil carbon storage and grazing; carbon sequestration and grazing; grazing intensity and carbon; and livestock grazing and soil carbon. To find additional papers, we checked all references of papers revealed in the database search. We made every attempt to find studies from all continents to examine effects across large precipitation gradients. These searches resulted in over 230 papers that studied soil carbon dynamics under different land uses. We narrowed down our sample to 17 studies by including only those studies that compared a grazed sample plot to an ungrazed plot and reported grazer effects on soil carbon density (mass per unit area), or % C together with bulk density, from which we could calculate carbon density, and by including only the most recent results from any ongoing long-term experiments. Unfortunately, many studies reported only % C or C concentrations in g kg^{-1} . Because effects of grazers on soil bulk density can cancel or even reverse effects on C concentration, effects on C concentration may not accurately predict effects on carbon density. These studies were thus excluded from our analysis.

From these 17 studies, we then selected all possible independent pairwise contrasts by first accounting for different sites within a study that differed in one or more of our explanatory variables (such as dominant grass type or soil type) and then accounting for different grazing intensities (light, moderate, or heavy) to a paired ungrazed control within each site. Values of explanatory variables were often averages for each site as studies did not typically provide data for each replicate. This resulted in 47 independent contrasts that compared soil carbon among replicate ungrazed plots to paired grazed plots and in which plot pairs differed in soil type, precipitation, or grazing intensity. For example, a study may have had three

different grazing treatments (i.e., low, moderate, and high grazing intensity) being monitored on two sites with different soil texture types (i.e., coarse, sandy soil and fine, clayey soil) (Potter *et al.*, 2001). Provided the study met all other criteria and included ungrazed controls to match each grazing intensity/soil combination, this study would yield six independent contrasts, one for each combination of soil type and grazing intensity. Most of the 17 studies yielded multiple independent contrasts because of within-site variation in grazing intensity and soils, although a few contained sites that also differed in other variables such as mean annual precipitation, dominant grass species type, or study duration.

Our goal is to explain the possible influences of three types of variables, (i) environmental, (ii) biotic, and (iii) study design and sampling methods, on the impact of grazers on soil C. For environmental factors, we considered mean annual precipitation and soil type. Mean annual precipitation values were either reported explicitly within the study or were determined using study location. Soil type was based on soil texture and determined either from authors' reported soil classifications or by using a Soil Textural Class triangle (USDA Natural Resources Conservation Service, 1938) and reported percentages of sand, silt, and clay. Soil types were then assigned into one of six 'soil type' classes that fell along a continuum ranging from coarse, sandy soils (1) to fine-textured, clay soils (6). Classes 1–3 had <35% clay and >30% sand with decreasing sand and/or increasing clay proportions as you move further along the continuum into classes 4, 5, & 6. While other soil characteristics, such as cation exchange capacity, total nitrogen, and pH, may influence soil carbon, these were not reported consistently across studies and therefore could not be evaluated. Next, we included the biotic variables grass type and grazing intensity. Grass type refers to the dominant type of grasses in the community and was determined to be either C_3 , C_4 , or mixed C_3 – C_4 depending on the authors' classification or our classification based on the reported dominant species of the site. Due to a large discrepancy in both the grazing animals used (i.e., cattle, goats, sheep) and the units measured (dry sheep equivalent ha^{-1} , ha steer^{-1} , AUM ha^{-1} , etc.), grazing intensity was based on the authors' qualitative classification as light, moderate, or heavy. In a few cases, when a qualitative grazing level was not given, we classified a contrast between grazed and ungrazed conditions based on the authors' description of a site and quantitative information provided on stocking rates relative to precipitation. Finally, for the effects of study design and sampling, we examined both the duration of the treatment and depth of the sampled profile. Rather than treat sampling depth as a continuous variable, we used three depth classes of 0–15, 16–40 cm, and >40 cm to avoid biases from a greater preponderance of studies with shallow (<15 cm) sampling depths. We did not include 'study' as a treatment as other variables such as precipitation, soil type, grass type, and study duration together explained much of the variation among studies.

Next, we calculated the effect size of grazing. To do this, we used the standard log response ratio, which entailed taking the natural log of the total C in the grazed site divided by the

total C in the ungrazed site (Effect size = $\ln(C_{\text{grazed}}/C_{\text{ungrazed}})$) (Gurevitch & Hedges, 2001). Effect size was used as the dependent variable in our univariate ANCOVA analysis.

With IBM SPSS Statistical Software (IBM Corp., 2010), we tested univariate relationships between effect size and each of the six variables using linear regression. We tested for but did not find a correlation between our two quantitative variables (mean annual precipitation and study duration, $r = -0.15$). We also tested for heteroscedasticity in the relationship between precipitation and effect size, which could be used to infer whether precipitation amplified grazer effect size, by using the Goldfeld–Quandt test (Goldfeld & Quandt, 1965), a version of variance comparison F-tests adapted for linear regression. As we were primarily interested in relationships within each level of the model (environmental, biotic, and design/sampling), we limited interactions to only those between variables at each level. In addition, we were unable to test some interactions across levels due to the lack of representation of grazing effects across the range of values or levels in both independent variables. For example, we were unable to test the interaction between grass type and precipitation because mixed grass types only occurred at a narrow range of annual precipitation (400–600 mm yr⁻¹). Mixed grass sites were similarly poorly represented across the range of soil types. Therefore, interactions tested in our analysis included precipitation × soil type, grass type × grazing intensity, and sampling depth × duration. Significant main effects were reported but not interpreted if interaction terms were significant.

We started our ANCOVA analysis with a full hierarchical model (Table 1) that included all of our six variables (soil type, grass type, grazing intensity, and sampled depth as fixed variables and mean annual precipitation and study duration as covariates) and the three interaction terms (precipitation × soil type, grass type × grazing intensity, depth × duration) simultaneously. We then proceeded to test a set of 17 additional candidate models (Supplemental Information S1) based on relationships between the different groups of factors (environmental, biotic, and study design). Next, we used Akaike's Information Criterion with small-sample bias adjustment (AIC_C) and respective AIC weights (Supplemental Information S2) to narrow these down to a smaller set of best models (Table 2). The family of four best models was chosen based on the lowest AIC_C scores and the highest AIC weights and included models that all had AIC weights bigger by a magnitude of 1×10^2 or more than the remaining 14 models in the candidate set (Table 2). From this family of best models we then identified a single best model with an AIC weight at least 20 times as big as the others (Tables 2 and 3).

Results

Experiment-long cumulative changes in SOC due to grazing varied considerably from a minimum of -1.6 to a maximum 1.8 kg m^{-2} , corresponding to a range of maximum effect sizes from -0.33 to 0.38 and encompassing studies with an average duration of 31.6 years ($R^2 = 0.76$, $df = 2, 46$, $P < 0.001$). We also calculated

Table 1 Results of full univariate ANCOVA model to explain grazing effect on soil organic carbon density ($R^2 = 0.848$, Adjusted $R^2 = 0.695$, $AIC_C = -239.82^*$)

Source	df	Type III sum of squares	F	P
Corrected model†	23	0.911	5.566	0.000
Intercept	1	0.006	0.865	0.362
Mean ann precip (mm)	1	0.039	5.411	0.029
Soil type	4	0.067	2.355	0.084
Mean ann precip (mm) × soil type	4	0.169	5.929	0.002
Grass type	2	0.062	4.380	0.024
Grazing intensity	2	0.000	0.025	0.976
Grass type × grazing intensity	4	0.149	5.229	0.004
Depth category (cm)	2	0.053	3.730	0.040
Duration of treatment (years)	1	0.012	1.662	0.210
Depth (cm) × Duration (years)	2	0.071	4.986	0.016
Error	23	0.164		
Total	47	1.089		
Corrected total	46	1.075		

*Akaike's Information Criterion (AIC) (Akaike, 1985; Burnham & Anderson, 1992) with the small-sample bias adjustment ($AIC_C = n * [\ln(SSE/n)] + 2K + [(2K * (K + 1)) / (n - K - 1)]$) (Hurvich & Tsai, 1995; Burnham & Anderson, 2002).

†'Corrected Model' is composed of variability sources from all 10 parameters in the model, from 'Intercept' to 'Depth (cm) × Duration (years)'. Bold type indicates variables also present in the best model shown in Table 3.

amounts of carbon stored annually by dividing cumulative changes by study duration and found maximum gain and loss both were ca. 150 g m^{-2} , again reflecting the same range in effect sizes from -0.33 to 0.38 . In this case, effect size accounts for nearly 60% ($R^2 = 0.59$, $df = 2, 46$, $P = 0.003$) of the variation in annual change in C.

Most variables in our review were represented by a wide range of values across the different study sites. Mean annual precipitation ranged from 134 to 932 mm. Soil type ranged from coarse, sandy soils to silt loams to mostly clay soils. Grass type was classified as either a community dominated by C₃ grasses, C₄ grasses, or a mixture of both. Grazing intensity ranged from none in the ungrazed controls to light, moderate, or heavy in the grazed treatments. Duration of treatment ranged from 5 to 130 years. Depth of the soil profile sampled ranged from 4 to 200 cm. Despite a wide range in all variables, we found that all studies came from either temperate or subtropical regions, with none in tropical grasslands. In addition, all studies included in this analysis measured only effects

Table 2 Model selection results of the four best models in the meta-analysis, based on Akaike's Information Criterion with small-sample bias adjustment (AIC_C) and AIC weights (w_i) (see Supplemental Information S2 for explanation)

Model	K*	SSE†	AIC_C ‡	Δ_i §	w_i ¶
P , S**, PxS††, G‡‡, GxGI§§, D¶¶, DxDu	8	0.164	-246.14	0.00	0.897
PxS, GxGI, DxDu	4	0.235	-240.07	6.07	0.043
P, S, PxS, G, GI***, GxGI, D, Du†††, DxDu	10	0.164	-239.82	6.32	0.038
P, S, PxS, GxGI, DxDu	6	0.217	-238.67	7.47	0.021

*Number of parameters in the model, including intercept.

†Sum of squares error in the model.

‡Akaike's Information Criterion (AIC) (Akaike, 1985; Burnham & Anderson, 1992) with the small-sample bias adjustment ($AIC_C = n * [\ln(SSE/n)] + 2K + [(2K*(K+1))/(n-K-1)]$) (Hurvich & Tsai, 1995; Burnham & Anderson, 2002).

§Difference between best model and each model in set, $AIC_i - AIC_{min}$.

¶AIC weight, $w_i = \exp(-0.5 * \Delta_i) / \sum_{r=1}^R \exp(-0.5 * \Delta_r)$ (Burnham & Anderson, 2002).

||Mean annual precipitation (mm).

**Soil texture type (see Methods for category descriptions).

††An interaction term for precipitation and soil type.

‡‡Dominant grass species type (C_3 , C_4 , or mixed).

§§An interaction term for grass type and grazing intensity (light, moderate, or heavy).

¶¶Sampled soil depth (cm).

|||an interaction term for soil depth and study duration (years).

***Grazing intensity.

†††Study duration.

of livestock grazers, rather than native herbivores, on soil carbon storage.

Our full model, with effect size as the dependent variable, started with all nine (six independent and three interaction terms) variables and gave us an adjusted R^2 of 0.695 and an AIC_C of -239.82 (Table 1). Significant variables included mean annual precipitation, grass type, depth, and interactions between precipitation and soil type, grass type and grazing intensity, and depth and duration. Using the 18 candidate models (see Supplemental Information S1 for full description and results), we calculated AIC_C and AIC weights (Supplemental Information S2) to identify a set of four best models that best explained variability in effect size (Table 2). Included in this set were our full model, a model with only interactions from each level, a model with environmental variables plus biotic (grass \times grazing intensity) and design (depth \times duration) interactions, as well as our hypothesized best model which included environmental variables, biotic and design interactions plus grass type and depth main effects.

Table 3 Best model to explain grazing effect on soil organic carbon based on AIC_C and AIC weights from a set of 4 best models ($R^2 = 0.848$, Adjusted $R^2 = 0.695$, $AIC_C = -246.14^*$)

Source	df	Type III sum of squares	F	P
Corrected model†	23	0.911	5.566	0.000
Intercept	1	0.006	0.865	0.362
Mean ann precip (mm)	1	0.039	5.411	0.029
Soil type	4	0.067	2.355	0.084
Mean ann precip (mm) \times Soil type	4	0.169	5.929	0.002
Grass type	2	0.062	4.380	0.024
Grass type \times Grazing intensity	6	0.152	3.565	0.012
Depth category (cm)	2	0.053	3.730	0.040
Depth (cm) \times Duration (years)	3	0.085	3.996	0.020
Error	23	0.164		
Total	47	1.089		
Corrected total	46	1.075		

*Akaike's Information Criterion (AIC) (Akaike, 1985; Burnham & Anderson, 1992) with the small-sample bias adjustment ($AIC_C = n * [\ln(SSE/n)] + 2K + [(2K*(K+1))/(n-K-1)]$) (Hurvich & Tsai, 1995; Burnham & Anderson, 2002).

†'Corrected Model' is composed of variability sources from all 8 parameters in the model, from 'Intercept' to 'Depth (cm) \times Duration (years)'.

The last model, comprised of mean annual precipitation, soil type, grass type, depth, and precipitation \times soil type, grass type \times grazing intensity, and depth \times duration interactions did indeed turn out to be our best model with the lowest AIC_C (-246.14) and the highest AIC weight (0.897). This best model suggests that all six of the factors we examined had significant influences on grazer impacts on SOC, but their manner of influence was largely different from what we hypothesized.

We found no significant univariate relationship between grazer effect on SOC and either precipitation or soil texture. We also found no significant heteroscedasticity between grazer effect and precipitation (Goldfeld-Quandt test: $F = 0.424$, $df = 1, 31$, $P > 0.5$) that would imply that increased precipitation would amplify either positive or negative effects. Rather, soil type and precipitation exhibited a strong interaction in their influence on grazer effects (Table 3; Fig. 1).

We also found a significant interaction between grazing intensity and grass type (Table 3). Specifically, higher grazing intensity was associated with increased SOC in grasslands dominated by C_4 grasses, but with lower SOC in grasslands dominated by C_3 grasses (Fig. 2). For mixed grass (C_3 and C_4 grasses

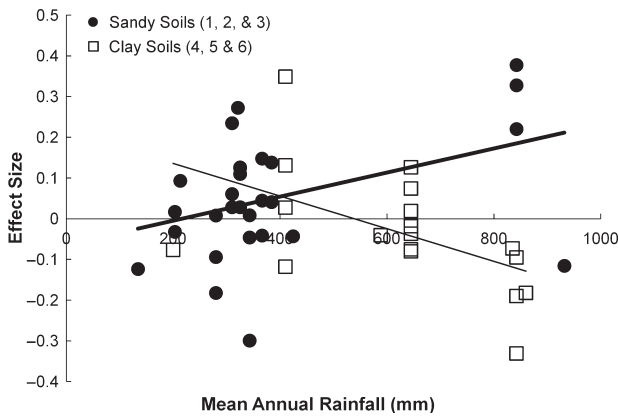


Fig. 1 Significant regressions of effect size of grazing on soil organic carbon associated with mean annual precipitation when presented separately for sandy soil types (indices 1, 2 & 3, solid circles; $df = 1, 26, P = 0.033, R^2 = 0.162$) and finer textured soils (indices 4, 5 & 6, open squares; $df = 1, 17, P = 0.024, R^2 = 0.264$).

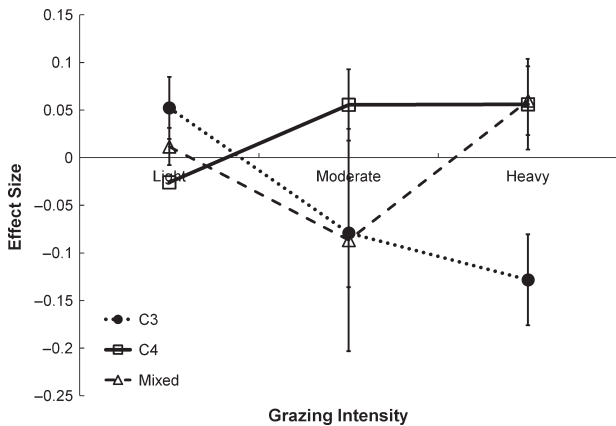


Fig. 2 Mean (\pm SE) residual effect size of grazing on soil organic carbon (SOC) after accounting for associations with soil type, precipitation and a soil \times precipitation interaction for three different categories of grazing intensity (see Methods for definition) and three different types of grass species composition. Contrasts for each grazing intensity level indicate a significant overall interaction between grass species composition and grazing intensity in explaining grazer effects on SOC.

codominant) sites, which had a more limited sample size, the trend was somewhat less clear, with grazing having a positive effect at both light and heavy grazing intensities and a negative effect at moderate intensities (Fig. 2).

Finally, we discovered a significant interaction between study duration and sampling depth. This interaction showed that in short-term studies, sampling to deeper depths (>40 cm) tended to result in positive effects of grazing, while sampling to intermediate (15–40 cm) depths produced more negative effects

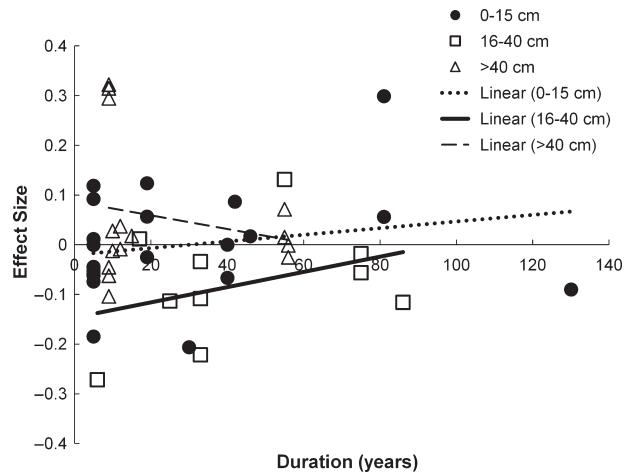


Fig. 3 Relationship between residual grazer effect size on soil organic carbon after incorporating environmental and biotic variables vs. study duration for three different sampling depth classes (see Methods for definition).

(Fig. 3). Over the longer term, there was little to no effect of sampling depth, as mean effect sizes approached zero for all depth classes (Fig. 3).

Discussion

Compared to other meta-analyses, our meta-analysis features a relatively small number of studies ($N = 17$) and independent contrasts ($N = 47$), and we were limited to considering only interactions among factors with a wide range of values across sites. Our review also reflects the absence of studies from tropical grasslands and savannas. In addition, we were unable to evaluate several other potentially important factors, such as fire frequency, soil pH, temperature, type of grazing management (rotational vs. continuous), and wild vs. domestic grazers, etc., because they were not measured in most of the studies we surveyed. Therefore, considerable knowledge gaps about the effects of grazing on SOC still exist and suggest major areas of further research. However, despite these limitations, our analysis did reveal several interesting and informative patterns that reflect the importance of considering the environmental and biotic context of grazing in management decisions designed to help mitigate greenhouse gases and store soil carbon. We discuss these patterns in detail below.

Environmental influences

We expected that environmental variables would explain the majority of variation in grazer effects on SOC and in fact, precipitation and soil type and especially their interaction together explained a large

proportion of the variation (partial Eta-squared = 0.989) of grazer effect size in our best model (Table 3). The significant interaction reflected that on soils with higher clay content (soil types 4, 5 & 6), grazing has less positive or more strongly negative effects on SOC at higher precipitation (Fig. 1). The opposite trend was found for coarser soils with a high percentage of sand and lower clay content (soil types 1, 2, & 3). For these soils, there is a positive relationship between precipitation and effect size, with grazers having a more positive effect at higher precipitation (Fig. 1). This surprising outcome indicates that the influence of precipitation may depend on soil texture, highlighting likely an important interplay between soil texture, moisture, and the magnitude and fate of belowground C inputs that is considerably more complex than previously suggested (Derner & Schuman, 2007; Pineiro *et al.*, 2010).

A few possible mechanisms of how soils and precipitation might interact to affect grazing effects on SOC sequestration have been suggested, but otherwise, such interactions remain poorly explored (Ruess & Seagle, 1994; Pineiro *et al.*, 2010). Soils of different texture may harbor different microbial C and N (Paustian *et al.*, 1992; Zak *et al.*, 1994; Knops & Tilman, 2000) and thus impose different demands for C inputs modified by grazing. For example, the positive influence of greater clay content on SOC accumulation may only occur at sites with low precipitation, as decreased microbial activity associated with drier soils may reduce demand for C and amplify the stimulation of belowground production and formation of soil aggregates associated with grazing (Franzliebbers *et al.*, 2000; Dominy & Haynes, 2002). Possibly, at higher precipitation, finer textured soils may become waterlogged more frequently and thereby inhibit root growth and thus allocation of C belowground. Compaction of soils by herbivores may further compound this effect (Proffitt *et al.*, 1993; Sigua & Coleman, 2010). If so, then grazer effects on SOC might become more negative on finer textured soils. On sandy soils with low precipitation, grazing may result in SOC loss as it more markedly reduces vegetation cover and increases bare ground, thereby accelerating soil drying and erosion (Su *et al.*, 2005; Li *et al.*, 2008; Pei *et al.*, 2008; Steffens *et al.*, 2008) and potentially even further coarsening the soil and reducing its capacity to hold SOC (Golluscio *et al.*, 2009). These amplifying effects of erosion were in fact posited as a potential mechanism for negative effects of grazing on C in several studies (Li *et al.*, 2008; Steffens *et al.*, 2008) and may have accounted for some of our most extreme negative effects. Influence of soil texture may also vary with differing soil mineralogy as different minerals have contrasting binding affinities with carbon. However, as most studies did not report

mineralogy, we could not analyze it. The interactive effects of precipitation and soils on grazer effects on SOC may also be driven by grassland species composition associated with different precipitation levels. For example, in the North American Great Plains, decreasing precipitation is associated generally with an increase in the relative abundance of C₄ vs. C₃ grasses and an overall increase in grazing intensity (Naeth *et al.*, 1991; Derner *et al.*, 2006). As we show below, grassland species composition may strongly affect grazer impacts of SOC.

Biotic influences

Virtually no studies have explicitly suggested that grassland species composition should strongly influence grazer effects on SOC or that it should modulate the influence of grazing intensity. However, with the second highest proportion of variance (partial Eta-squared = 0.758) after environmental variables (partial Eta-squared = 0.989) (Table 3), both grass type and grazing intensity appear to be important, and perhaps more so, than previously realized. Our analysis suggests that these two factors may interact as key biotic drivers of grazer effects on SOC independently of effects from precipitation and soil texture. This interaction shows that, at sites dominated by C₃ grasses, grazing had a positive effect on SOC only at light grazing intensities and this effect became negative at moderate to heavy intensities. In contrast, for grasslands dominated by C₄ grasses, grazer effects shifted from slightly negative at light grazing intensities to positive for moderate and heavy intensities.

C₄ grasses and their response to grazing may be responsible for most cases where positive effects of grazers on SOC have been measured. Several studies implicate the stimulation of fine, shallow roots by grazing in C₄ species, such as *Bouteloua gracilis*, in grazer-induced increases in SOC (Frank *et al.*, 1995; Derner *et al.*, 2006). Such increase in belowground C allocation may provide C₄ grasses with a competitive advantage, and the difference in SOC in a few studies may be a reflection of the relative dominance of C₄ grasses under grazed conditions and C₃ grasses in the absence of grazing. Such species shifts may explain the response in SOC to grazing we observed in the studies of mixed-C₃-C₄ grass assemblages in our database (Reeder & Schuman, 2002; Reeder *et al.*, 2004) (Fig. 2). Ungrazed and moderately grazed plots may have been typically dominated by C₃ grasses such as *Pascopyrum smithii*, which may have responded in the ways mentioned above that led to a significant decline in SOC (Reeder & Schuman, 2002). At higher grazing intensity, C₄ species, such as *B. gracilis*, may have largely replaced C₃ species, and typical C₄ grass responses to grazing

significantly stimulated SOC (Frank *et al.*, 1995; Reeder & Schuman, 2002; Derner *et al.*, 2006). C₄ grasses may also yield more SOC than C₃ grasses because of higher root-to-shoot ratios and greater transfer of photosynthate belowground (Reeder *et al.*, 2004), or because of greater root density and turnover and possibly, higher rates of root exudate (Frank *et al.*, 1995).

Differences in mycorrhizal association with C₃ and C₄ grasses may also help explain the importance of species composition in SOC response to grazing. Mycorrhizae have been shown to infect the roots of C₄ grass much more than C₃ grasses (Wilson & Hartnett, 1998) and grazing can stimulate the production of mycorrhizal hyphae (Eom *et al.*, 2001; Johnson *et al.*, 2006; Medina-Roldan *et al.*, 2008). Mycorrhizae excrete a substance called glomalin which acts like a glue that binds soil into aggregates (Treseder & Turner, 2007). Thus, increased mycorrhizal production and associated glomalin excretion could be significant in allowing soil under C₄ grasses, as opposed to C₃ grasses, to store carbon under heavier grazing (Franzluebbers *et al.*, 2000; Treseder & Turner, 2007; Klumpp *et al.*, 2009; Wilson *et al.*, 2009).

Yet another mechanism that might explain differences in C₃ vs. C₄ grassland SOC response to grazing is an interaction between fire and grazing. C₄ grasses appear to burn more frequently and putatively have evolved high flammability to promote fire (Clark *et al.*, 2001; Keeley & Rundel, 2005). While much of aboveground biomass consumed by herbivores may be respired as CO₂, up to 50% may be deposited on the ground surface as dung. Under some conditions, a considerable fraction of dung can be incorporated into soil organic matter (Bol *et al.*, 2000; Dungait *et al.*, 2009). Grazers may therefore effectively redirect carbon from a source of aboveground loss (combusted biomass) to a source of belowground sequestration (soil organic matter), and this effect would be stronger where fire frequencies are higher. Because of the greater propensity for C₄ grasslands to burn, this possible redirection of carbon by grazing may make it more likely that grazing, particularly heavy grazing, increases SOC in C₄-dominated grasslands. To our knowledge, the consequences of fire-grazer-soil interactions for SOC sequestration in grasslands have not yet been explored.

Higher grazing intensity is generally expected to lead to greater SOC loss because greater removal of photosynthetic tissue and subsequent respiration of assimilated C by grazers reduces potential C inputs to soil organic matter (Derner & Schuman, 2007; Gao *et al.*, 2008; Klumpp *et al.*, 2009). A recent mesocosm experiment done in France (Klumpp *et al.*, 2009) showed that by shifting disturbance (i.e., grazing and/or clipping) frequency of C₃-dominated grass turfs from a previous

long-term (14-year) low disturbance regime to high frequency disturbance led to a cascading set of effects that included a reduction in root biomass, a decline in soil fungi, and an increase in gram (+) bacteria that ultimately hastened decomposition of old (>6 months) particulate organic C. Greater decomposition released plant available nitrogen and further stimulated microbial decomposition and lowered SOC (Klumpp *et al.*, 2009). Our review supports these findings for the C₃-dominated grasslands of Inner Mongolia and Patagonia (e.g., Steffens *et al.*, 2008; Golluscio *et al.*, 2009), but clearly shows an opposite trend in both mixed C₃-C₄ and C₄-dominated grasslands where increasing grazing intensity was associated with more positive effects of grazing on SOC.

Influences of study design

In our analysis, we expected that longer studies with shallow sampling would detect a larger grazer effect. SOC accumulation typically takes years to detect, particularly in sparsely replicated field experiments, because soil annual changes are small relative to standing stocks of SOC and SOC can vary considerably over distances of a few meters (Paustian *et al.*, 1992; Conant *et al.*, 2001). Consequently, a large percentage change in soil carbon is often required to measure significant differences in SOC density. Shorter studies (<20 years' duration) might be less likely to detect differences in SOC between treatments. Shallower sampling might more readily detect changes in SOC as changes in C inputs more likely affect shallow soil layers where the majority of root production occurs (Medina-Roldan *et al.*, 2008). However, we failed to detect a univariate association between effect size and either duration or sampling depth and together design variables accounted for the lowest proportion of variance (partial Eta-squared = 0.588) in our model (Table 3). In the studies we reviewed, most exclosures had been in place 10–25 years, and measured differences in SOC between treatments may not have been as sensitive to differences in duration as other environmental and biotic factors that differed between sites. Instead an interaction between study duration and sampling depth showed positive effects of grazing in short-term studies that sampled to deeper depths (>40 cm), but negative effects in those that sampled to intermediate (15–40 cm) depths (Fig. 3). Perhaps sampling to intermediate depths is more sensitive to declines in root biomass at depth with grazing, which even for C₄ grasses declines at deeper depths (Nippert *et al.*, 2012), whereas sampling to deeper depths may pick up carbon sequestered in the finer textured soil that occurs at greater depth (Jobbagy & Jackson, 2000; Pineiro *et al.*, 2009). These hypotheses are

speculative as data are generally lacking on the simultaneous effects of grazing on rooting depth and soil carbon.

On the other hand, for longer term studies, sampling depth had little to no effect. Longer term studies may not show any effect of depth possibly because the grazed and ungrazed conditions are at or near their respective equilibria throughout the soil column after 25–40 years (Conant *et al.*, 2001). Given that these design influences account for the residuals after incorporating all the other major factors, these results are unlikely to result from hidden correlations between study duration, sampling depth and soil type, such as if fine-textured soils tended to be sampled to shallower depths because of the difficulty in coring tight soils.

Implications for global change

In our analysis of a global range of studies, we found that grazing has significantly large, but highly variable, effects on SOC density that depend on the context of climate, soils, grass type, and grazing intensity. First, grazer effects on SOC, whether positive or negative, are potentially large, with cumulative changes of up to 1.6 kg m^{-2} (16 tons ha^{-1}) over 10–30 years and annual changes as large as $\pm 150 \text{ g m}^{-2}$ ($1.5 \text{ tons ha}^{-1} \text{ yr}^{-1}$). The roughly equal distribution of positive and negative effects suggests that, as noted in previous studies, the sign of the effect of grazers on SOC is highly context-dependent. Secondly, interactions between the different levels of factors (soil type and precipitation, dominant grass type and grazing intensity, and study duration and sampling depth) were much stronger than relationships between grazer effects and any single factor.

Our results have some key implications for management of grazing to sustain soil organic matter and to generate C offsets for carbon markets that seek to help reduce greenhouse gases (Henry *et al.*, 2005; Lal *et al.*, 2007; Smith *et al.*, 2008). For example, reducing grazing might be counterproductive on C_4 grasslands but may, in fact, be necessary to avoid chronic SOC loss in C_3 grasslands. Currently, there may be major regions of the globe where grazing is already sequestering carbon, such as in tropical or temperate grasslands dominated by C_4 grasses (Holdo *et al.*, 2009). There may also be large areas degraded by past overgrazing, such as in many of the world's C_3 -dominated grasslands, where decreasing grazing intensity could lead to C sequestration (Conant *et al.*, 2001). Such actions could allow grazing to significantly contribute to mitigating greenhouse gases and help increase the impact of soils as global carbon sinks (Lal *et al.*, 2007). However, climate may also influence appropriate prescriptions for management, as intense grazing may not be appropriate at

some coarse soil sites, regardless of dominant grass type. Furthermore, it is important to consider how grazing effects on soil C may be impacted by expected changes in climate such as an increased frequency of drought and heat wave events that might turn grasslands into C sources (Ciais *et al.*, 2005). Other impacts, such as the combination of long-term drought with high atmospheric CO_2 concentration could decrease soil microbial biomass and promote shifts in functional microbial types, in turn leading to further changes in biogeochemical cycles and C sequestration (Barnard *et al.*, 2006; Bloor & Bardgett, 2012; Pinay *et al.*, 2007). Finally, it is also necessary to consider impacts of grazing management on other biogenic greenhouse gases like N_2O and CH_4 , as increased emissions of these gases could potentially offset substantial C sequestration (Conant *et al.*, 2005) and thereby limit the utility of management actions.

Our results also provide insight on how grazing might influence grasslands' vulnerability to climate change. For example, moderate grazing in tropical grasslands that generates positive soil carbon storage could additionally result in increases in productivity and soil water-holding capacity (Belknap *et al.*, 2005; Teague *et al.*, 2011) that might make grasslands better able to withstand climatic changes. On the other hand, intense grazing in grasslands on dry, sandy soils such as those found in Central Asia, may cause them to become more vulnerable to drought through the cyclical forces of reduced vegetation cover, increased wind erosion, and coarsening of the soil— all factors which might cause grasslands to become a carbon source rather than a sink. In contrast, grazing on finer textured soils may become more sustainable with a drying climate as our results show positive effects of grazing at arid sites with clay soils (Fig. 2). Finally, a shift to a drier, warmer climate may produce a shift in dominant species composition from C_3 to C_4 grasses in many parts of the world, which may make moderately intense grazing a more suitable land use practice than under current conditions in C_3 grasslands.

Ecologists and land managers should consider this complete context before they can fully understand the potential influence of grazing on soil carbon. Nevertheless, our review provides a statistical model that explains considerable (partial Eta-squared = 0.848) variation in grazing effects among and even within sites, despite the relatively small number of available studies and independent contrasts of grazing effects on carbon density. Our results suggest that ecologists still have much to learn about how grazing affects soil carbon because all factors in our analysis, including soil texture, precipitation, grass species composition, grazing intensity, sampling depth, and study duration,

interacted in complex ways to determine effects of grazing on SOC density. The patterns we detected contradict many of the current favorite hypotheses about grazing effects on SOC, such as the expected general dependence of positive grazing effects on low rainfall and finer textured soils.

Another key discovery is that grazing effects on SOC density in tropical grasslands remain virtually unstudied. By virtue of the dominance of C₄ grasses in the tropics, moderate grazing might increase SOC, making tropical grasslands an important global carbon sink (Holdo *et al.*, 2009). Because of the potential importance of grasslands in building soil fertility for sustainable development and in reducing greenhouse gases, the role of grazing in affecting SOC in tropical regions would seem to be an important, and fruitful, area of future research.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Model descriptions and model selection results of full set of 18 models in the meta-analysis, based on Akaike Information Criterion with small-sample bias adjustment (AIC_c) and AIC weights (w_i).

Data S2. Detailed explanation of the use of AIC weights (w_i) in model selection.