PREDICTING SOIL ORGANIC CARBON IN AGROECOSYSTEMS UNDER CLIMATE CHANGE

A Global Meta-Analysis of Grazing Impacts on Soil Health Indicators

Ryan C. Byrnes, Danny J. Eastburn, Kenneth W. Tate, and Leslie M. Roche*

Abstract

Grazing lands support the livelihoods of millions of people across nearly one-half of the globe. Soils are the backbone of stability and resilience in these systems. To determine livestock grazing impacts on soil health, we conducted a global meta-analysis of soil organic carbon (SOC), total N, C/N ratio, and bulk density responses to grazing strategies (continuous, rotational, and no grazing) and intensities (heavy, moderate, and light grazing) from 64 studies around the world. Across all studies and grazing intensities, continuous grazing significantly reduced SOC, C/N, and total N compared with no grazing. Soil compaction (i.e., increased bulk density) was greater under both continuous and rotational grazing compared with no grazing; however, rotational grazing had lower bulk density than continuous grazing. Rotational grazing had greater SOC than continuous grazing and was not different from no grazing. The positive responses of SOC to rotational grazing could create climate change mitigation opportunities. Grazing strategy comparisons were minimally conditioned by aridity class (i.e., arid, subhumid, and humid); however, complete observations were notably limited or missing for many rotational grazing comparisons. For continuous and no grazing strategy comparisons, we found that grazing management can significantly influence soil function and health outcomes; however, site-specific environmental factors play important moderating roles. Greater coordination across regional, national, and global efforts, as well as consistent guidelines for soil health evaluation, would help overcome these knowledge gaps and vastly improve our collective understanding of grazing impacts on soil health, providing greater management and policy impacts.

Core Ideas

- Grazing increases soil compaction relative to no grazing.
- Rotation improves soil bulk density and organic carbon over continuous grazing.
- Reduced grazing intensity improves soil bulk density and organic carbon.
- Site-specific environmental factors play important moderating roles.
- Rotational grazing strategies could create climate change mitigation opportunities.

Copyright © American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America. 5585 Guilford Rd., Madison, WI 53711 USA. All rights reserved.

J. Environ. Qual. doi:10.2134/jeq2017.08.0313 This is an open access article distributed under the terms of the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/). Supplemental material is available online for this article. Received 7 Aug. 2017. Accepted 12 Mar. 2018. *Corresponding author (Imroche@ucdavis.edu).

LOBAL grazing lands occupy up to one-half of the earth's , terrestrial surface, ${\sim}3.4$ billion ha (FAO, IFAD, and WFP, 2015), supporting the livelihood benefits and subsistence of millions of people (Glenn et al., 1993; LeCain et al., 2002; Sayre, 2007; Derner et al., 2017). These lands are often marginally productive compared with more intensive agricultural landscapes, occupying land otherwise not historically suitable for agronomic cultivation. However, the pressures of a growing global population are increasingly exposing grazing lands to risks of conversion to other land uses such as higher value, intensively managed crops or urban development (Cameron et al., 2014). This is of concern, because grazing lands support high levels of biodiversity (Fuhlendorf and Engle, 2001; Fabricius et al., 2003; Havstad et al., 2007). Grazing lands also supply a multitude of ecosystem services including regulation and storage of water flows (Schlesinger et al., 2000; Havstad et al., 2007), nutrient cycling, and C sequestration (Schuman et al., 1999; Conant and Paustian, 2002; Morgan et al., 2016). Globally, grazing lands play a major role in climate change due to massive stores and fluxes of C, storing >10% of total biomass C, up to 30% of the total soil organic C (SOC), and 0.5 Pg C yr⁻¹ (Scurlock and Hall, 1998). Recent estimates suggest that improved grassland management could generate increases up to 0.28 Mg C yr⁻¹ (Conant et al., 2017).

Soil biogeochemical and physical responses to livestock grazing are regulated by complex and often interacting factors: grazing practices (Reeder et al., 2004; Derner and Schuman, 2007; Stavi et al., 2008; Steffens et al., 2008), climate (McSherry and Ritchie, 2013; Andrés et al., 2017), soil texture (Spaeth et al., 1996; Fox et al., 2015; Andrés et al., 2017), time (duration of management regime implementation; Jing et al., 2014), and plant community structure (McSherry and Ritchie, 2013; Jing et al., 2014; Qu et al., 2016). Grazing mechanisms such as plant defoliation can affect plant photosynthetic rates, root/shoot ratios, C allocation, fine root mass, and plant root exudates, all of which play principle roles in grassland biogeochemical cycles (Johnson and Matchett, 2001; Gao et al., 2008; Giese et al., 2009; Chen et al., 2015; Gong et al., 2015). For example, light to moderate grazing may increase ecosystem C through increased plant productivity by replacing aging or dead plant tissues with active photosynthetic tissues (Holland et al., 1992; Zhang et al., 2015b) and through prolonged light exposure on younger plant tissues, extending C acquisition during daylight hours (Shao et al., 2013).

Dep. of Plant Sciences, One Shields Avenue, Univ. of California, Davis, CA 95616. Assigned to Associate Editor Hero Gollany.

Abbreviations: AI, aridity index; BD, bulk density; CN, carbon/nitrogen ratio; CI, confidence interval; SOC, soil organic carbon; TN, total nitrogen.

Previous work has shown that excessive hoof trampling by grazing animals leads to soil compaction, which can result in decreased soil pore space, reduced infiltration, and less plant available water (Willatt and Pullar, 1984; Tate et al., 2004; Kotzé et al., 2013; Pulido et al., 2016). These impacts can subsequently reduce root and mycorrhizal growth (Menneer et al., 2005; Barto et al., 2010), impair soil structure (Steffens et al., 2008), decouple C and N cycles (Piñeiro et al., 2010), and reduce plant productivity. This can create positive feedback loops, amplifying the aforementioned impacts on soil structure and nutrient cycles (Houlbrooke et al., 1997; Greenwood and McKenzie, 2001). Decreased soil pore space promotes anaerobic microsites (Drewry et al., 2008), which may lead to changes in soil microbial communities that affect soil nutrient cycling (Oenema et al., 1997). Additionally, increased rates of C and N cycling may occur at livestock excreta sites (Oenema et al., 1997; Keiluweit et al., 2016; Byrnes et al., 2017), and these hotspots (particularly for N) may become greater when soils are grazed under saturated conditions (Parkin, 1987).

Evidence suggests that some grazing management strategies can positively benefit ecosystems and could even reverse negative impacts of poorly managed grasslands through enhancement of N cycling, primary production, and flow and sequestration of C (Turner et al., 1993; Soussana and Lemaire, 2014). Conant and Paustian (2002) concluded that up to 45 Tg C yr⁻¹ could be sequestered globally on restored grasslands, if grazing intensities were reduced from heavy to moderate levels. In the Northern Great Plains, historic heavy grazing and agricultural practices have previously led to negative consequences for C and N cycling, but improved grazing management since the mid-20th century has significantly recovered C and N losses, contributing in part to an offset of \sim 5.85 Mg C ha⁻¹ in CO₂-equivalent, human-derived emissions (Wang et al., 2016). Similarly, light to moderate grazing in grasslands compared with heavy grazing has been shown to lead to significant increases in soil C and improvements in soil structure (Hiernaux et al., 1999; Reeder and Schuman, 2002). Previous work also suggests grazing exclusion can decrease soil C pools, due to reduced root C inputs, decreased grazer-driven plant growth, and increased microbial respiration (Shao et al., 2013). Notably, considerable disagreement exists regarding the potential C sequestration gains and subsequent mitigation benefits to be made via specialized grazing systems (Joyce et al., 2013; Wang et al., 2015). Meeting the simultaneous demands for soil restoration (Six, 2013) and animal protein production (Thornton, 2010; Herrero et al., 2016) requires an improved understanding of the complex relationships between livestock grazing and soil function and health at regional and global scales.

We conducted a global meta-analysis to examine the effects of grazing strategy (i.e., no grazing, continuous grazing, and rotational grazing), grazing intensity (heavy, moderate, and light grazing), and site-specific environmental factors on three important contributors to soil function and health—soil C and N cycling and bulk density (BD). We specifically hypothesized that rotational grazing would improve soil function and health indicators over continuous grazing strategies, and these effects would be at least partially mediated by climate. We also hypothesized that soil function and health would decrease with increasing continuous grazing intensities compared with no grazing controls. Lastly, focusing solely on continuous grazing compared with no grazing controls, we examined the potential moderating effects of site-specific environmental and study design variables (climate, plant community, soil texture, grazing treatment intensity, and study duration) on grazing treatment effects. From these analyses, we identified key knowledge gaps and future research directions to better inform management and policy decision making.

Materials and Methods

Study Selection and Database Structure

We conducted a Scopus database (https://www.elsevier.com/ solutions/scopus) query to identify peer-reviewed articles matching predetermined title-abstract-keyword search criteria to match grazing strategies and intensities to desired response variables. The articles were then screened to include observations with:

- 1. At least one field season of treatment and control monitoring.
- 2. Experimentally manipulated ruminant livestock grazing only.
- 3. Grazing strategy (continuous and/or rotational) and intensity (heavy, moderate, and/or light) that were clearly identified either quantitatively or qualitatively.
- 4. At least one paired response of treatment (grazing strategy or intensity) and control (no grazing or continuous grazing) mean and variance for either SOC, BD, C/N ratio (CN), or total N (TN) that was extractable from text, tables, charts, or appendices.

In total, 64 (out of an initial 275, Supplemental Table S1) articles met our criteria for inclusion (Fig. 1). Means, sample sizes, and variances for SOC, BD, CN, and TN were collected for experimental treatment and control units. Where SOC and TN response data were available, data were extracted either on a concentration (i.e., g kg⁻¹) or mass (i.e., t ha⁻¹) basis. Data collected as a mass were then converted to a concentration using available BD and soil sampling depth. We also collected data on location (latitude and longitude), elevation (m), plant community type (annual or perennial), sand (%), clay (%), study duration (years), and soil sampling depth (cm). Soil sampling depth was noted to ensure that appropriate comparisons were made between treatments. Where climatic data and elevation were not reported, these data were collected via the WorldClim GIS database and the USGS Global Multi-Resolution Terrain Data (GMTED2010) using necessary corrections to decimal degrees data and the geographical coordinate system World Geodetic System WGS1984 (Hijmans et al., 2005).

For the experimental treatments, we recorded grazing strategy (continuous or rotational) and intensity (heavy, moderate, or light). Due to the wide range of livestock types used and units reported, we classified grazing intensities according to the authors' reporting. Due to variation in reporting of rotational grazing strategies (e.g., timing of grazing and rest periods), we could not further delineate "rotational" strategies into subclasses (e.g., intensive, extensive). For studies comparing rotational and continuous grazing, we ensured that grazing intensities were the same between paired rotational and continuous grazing treatments. This was accomplished by reviewing the authors' qualitative evaluation (light, moderate, or heavy) and/or quantitative data (i.e., animal $ha^{-1} yr^{-1}$). Where discrepancies emerged in intensity between continuous and rotational strategies, we excluded these studies from our analyses.



Aridity Index

An aridity index (AI) was used to delineate studies from similar aridity classes, where the index quantifies precipitation availability over demand:

$$Aridity index = \frac{Mean annual precipitation}{Mean annual evapotranspiration}$$
[1]

The AIs were calculated according to methods described by Spinoni et al. (2015) and Zomer et al. (2008). Each study was then classified into one of three aridity classes (Spinoni et al., 2015): arid (AI < 0.5), subhumid (AI = 0.5-0.75), and humid (AI > 0.75).

Statistical Analyses

Analyses were organized to principally examine the effects of livestock grazing strategy and intensity on indicators of soil health and function (SOC, BD, CN, and TN). Effect sizes were calculated among (i) continuous, rotational grazing, and no grazing strategies, and (ii) heavy, moderate, or light continuous grazing intensities compared with no grazing. Effect size is commonly used in meta-analyses as a tool to standardize study results, which yields a summary of the magnitude and direction of treatment effect (Gurevitch and Hedges, 1993). The effect size was estimated as the log response ratio, which was calculated as the natural log of the quotient of the reported treatment to the control response means (SOC, BD, CN, and TN):

Effect size =
$$\ln\left(\frac{\text{treatment}}{\text{control}}\right)$$
 [2]

For each effect size, 95% confidence intervals (CIs) were calculated to describe the range, and effect sizes were considered significant if their lower or upper CIs reached zero but did not overlap zero. We did not include results with less than two paired observations.

For just the continuous grazing vs. no grazing controls data subset, we performed multiple linear regression with model averaging to examine whether grazing treatment effects (effect sizes) on SOC, BD, CN, and TN were moderated by environmental (aridity, Fig. 1. Global map of livestock grazing study sites by aridity index. Low to high aridity index (see Eq. [1]) values correspond to hyper-arid to humid ecosystems, respectively. Points on the map represent each study in this analysis.

latitude, elevation, plant community, percentage sand, percentage clay) and study (study duration and grazing intensity) variables. We only included complete observations for this analysis and selected the best models using a cutoff of two Akaike information criteria (small sample size corrected) (Akaike, 1985; Ridder et al., 2005). All analyses were conducted in RStudio (R Core Team, 2016) using the metafor (Viechtbauer, 2010) and glmulti (Calcagno and de Mazancourt, 2010) packages, and standard diagnostics were used to confirm that analysis assumptions were met.

Results

Averaged across all studies and grazing intensities, continuous grazing significantly increased BD (0.06, CI [0.04, 0.07]), reduced SOC (-0.08, CI [-0.11, -0.05]), reduced CN (-0.04, (CI [-0.07, 0.00]), and reduced TN (-0.05, CI [-0.10, 0.00]) relative to no grazing controls (Fig. 2). The magnitude of SOC reduction significantly increased with continuous grazing intensity, whereas BD had apparent increases with increased grazing intensity (Fig. 3). Rotational grazing had increased BD compared with no grazing controls (0.07, CI [0.03, 0.10]), with no other significant differences revealed (Fig. 4). Rotational grazing had significantly higher SOC (0.25, CI [0.10, 0.41]) and CN (0.04, CI [0.00, 0.09]) than continuous grazing, as well as significantly reduced BD (-0.04, CI [-0.07, -0.02]) (Fig. 5). The grazing strategy comparisons were minimally conditioned by aridity class (i.e., arid, subhumid, and humid; Supplemental Figs. S1, S2, and S3). Complete observations of rotational grazing comparisons were notably missing for subhumid and humid regions, thus limiting our capacity to fully examine potential moderating effects of climate on rotational grazing outcomes (Supplemental Figs. S2 and S3).

Multiple linear regression and model averaging results revealed that grazing treatment effects (continuous grazing vs. no grazing effect size) were moderated by both environmental and study design variables (Table 1). Elevation, aridity, absolute latitude, percentage sand and clay, and study duration all had significant moderating effects on SOC (n = 73), BD (n = 45), and TN (n = 25) responses to grazing treatment effects (continuous grazing vs. no grazing effect size). Plant community (i.e., annual



Effect Size of Continuous Grazing to No Grazing



							95% CI
Soil Organic Carbon	Heavy Grazing (59)	L	—— —-i				-0.15 [-0.23, -0.07]
	Moderate Grazing (44)		⊢ ∎				-0.13 [-0.18, -0.08]
	Light Grazing (56)		—	•			-0.04 [-0.08, 0.01]
Bulk Density	Heavy Grazing (49)			,			0.09 [0.06, 0.12]
	Moderate Grazing (32)			H			0.09 [0.05, 0.12]
	Light Grazing (48)			HB -1	U)		0.04 [0.02, 0.06]
C:N	Heavy Grazing (11)		н	•			-0.05 [-0.11, 0.01]
	Moderate Grazing (9)						0.01 [-0.03, 0.04]
	Light Grazing (9)			-			-0.01 [-0.09, 0.08]
Total Nitrogen	Heavy Grazing (25)						-0.07 [-0.19, 0.05]
	Moderate Grazing (16)		-				-0.13 [-0.24, -0.01]
	Light Grazing (22)		H	•			-0.04 [-0.17, 0.09]
		[1	1	1		
		-0.25	-0.12	0	0.12	0.25	

Effect Size of Continuous Grazing to No Grazing

Fig. 3. Mean effect size (magnitude of grazing strategy treatment vs. the control) and 95% confidence intervals (CIs) of soil organic carbon, bulk density, C/N ratio, and total N responses to continuous grazing intensities (heavy, moderate, and light) compared with a no grazing control. Values in parentheses are total paired observations per response variable by grazing intensity combination.



Fig. 4. Mean effect size (magnitude of grazing strategy treatment compared to the control) and 95% confidence intervals (Cls) of soil organic carbon, bulk density, C/N ratio, and total N responses to rotational grazing vs. no grazing. Values in parentheses are total paired observations per response variable by grazing intensity combination.



Effect Size of Rotational Grazing to Continuous Grazing



or perennial) significantly moderated grazing treatment effects on SOC and TN; there was insufficient data to evaluate plant community effects on BD responses to grazing, as all included studies were perennial grasslands. Grazing intensity (light, moderate, and heavy) was only a significant moderator for grazing treatment effects on BD. For CN responses to continuous grazing vs. no grazing, there were insufficient data (n = 5) for analysis.

Discussion

Grazing strategies, and rotational grazing specifically, have received increasing national and global interest as potential "climate-smart" tools for sequestering SOC and enhancing soil health more broadly (Derner et al., 2016; Schulz et al., 2016). Rotational grazing strategies (e.g., high-intensity, short-duration grazing; "mob" grazing; management-intensive grazing; "MiG" grazing) have been the epicenter of an ongoing debate on the potential benefits of grazing management to improve agricultural production and natural resources (Roche et al., 2015). Although previous reviews of the experimental literature (Briske et al., 2011) have found no significant differences in agricultural production or other natural resource benefits of rotational grazing strategies, our understanding of how grazing management influences soil health is still growing.

Similar to previous work, we found increased soil compaction under all livestock grazing strategies and intensities relative to no grazing (Willatt and Pullar, 1984; Tate et al., 2004; Neff et al., 2005) (Fig. 2–4). However, it is worth noting that although BD differences were statistically significant in our meta-analysis, we do not know if these translate to functional differences in surface infiltration rates (Eastburn et al., 2017). The global meta-analysis also showed lower CN under continuous grazing relative to both rotational strategies and no grazing controls (Fig. 2 and 5), which is potentially due to greater rates of decomposition (i.e., faster nutrient cycling by the microbial community) or reduced amounts of incorporated fresh plant material under continuous grazing conditions.

Interestingly, we found that rotational grazing strategies improved SOC and BD conditions over continuous grazing strategies (Fig. 5). However, it is important to note that our analysis of rotational and continuous grazing comparisons was limited by the number of studies and observations needed to appropriately partition variation and determine effects of important covariates, such

Table 1. Environmental and study design variables moderating grazing treatment effects (i.e., effect size) on indicators of soil health and function (soil organic carbon [SOC], bulk density [BD], and total N [TN]) for continuous grazing vs. no grazing strategies. There was insufficient data (*n* = 5) for multiple linear regression analysis of C/N ratio data.

Verielele	SOC effect size†		SOC e	ffect size‡	SOC effect size§	
variable	No. of models¶	Variable importance#	No. of models	Variable importance	No. of models	Variable importance
Elevation (m)	12	1.00	2	0.21	4	0.84
Aridity index	8	0.70	4	0.52	5	0.46
Latitude (absolute)	5	0.39	6	0.78	2	0.30
Clay (%)	5	0.42	2	0.18	4	0.85
Sand (%)	4	0.28	2	0.22	4	0.85
Plant community	4	0.35	NA††	NA	2	0.32
Study duration (yr)	4	0.34	3	0.36	1	0.37
Grazing intensity	0	0.00	8	1.00	0	0.00
Intercept	12	1.00	8	1.00	5	1.00

+ n = 73; average R^2 of top models was 0.30.

 $\pm n = 45$; average R^2 of top models was 1.0.

§ n = 25; average R^2 of top models was 0.91.

¶ Number of top models (all models within two Akaike information criteria [small sample size corrected] of best model) in which each variable appears. # The sum of Akaike weights for the models in which each variable appears.

++ NA, insufficient data to evaluate plant community effects on BD responses to grazing treatment effects.

as climate (Supplemental Figs. S2 and S3). Necessarily, we also combined a wide range of grazing strategies, as well as variations of these strategies (e.g., intensive and extensive rotation; Roche et al., 2015), into a single rotational grazing category. Additionally, on-ranch rotational grazing strategies are characteristically diverse (Roche et al., 2015), which further complicates generalizations for a single class of rotational grazing.

Grazing intensity is a measure of the cumulative effect of livestock use on forage and soil resources and is arguably one of the strongest predictors of agricultural and ecological outcomes, including soil function and health. Like previous work, we found evidence that greater continuous grazing intensity levels can negatively affect SOC (Fig. 3) (Zhang et al., 2015a, 2015b); Wang et al., 2016; Conant et al., 2017. Effect size analysis showed that continuous grazing intensity levels also significantly increased soil compaction over no grazing controls (Fig. 3, Table 1).

Site-specific environmental factors underpin soil function and health responses to management. In addition to grazing intensity, we found that elevation, climate, absolute latitude, soil texture, and plant community type were significant moderators of soil responses to continuous livestock grazing compared with no grazing (Table 1). In terms of soil texture effects, it has been shown that organic matter decomposition is slower in clayey (finer textured) than sandy (coarser textured) soils, which is potentially due to reduced heterotrophic microbial activity (Motavalli et al., 1995; Vogel et al., 2015) and physical protection of organic matter by clay minerals (Six el at., 2004). This means that sandier (coarser) soils may be more susceptible to organic matter losses. We also found elevation to be a significant predictor of SOC and TN responses, which is supported by previous work (Powers and Schlesinger, 2002; Wang et al., 2017). This may be due to differences in soil mineralogy and weathering across elevational gradients (Drever and Zobrist, 1992; Velbel, 1993; Szramek et al., 2007; Kramer and Chadwick, 2016). Lastly, we found that soil responses to continuous grazing vs. no grazing were dependent on study duration (Table 1), although >70% of observations were from studies that lasted <10 yr (Lundström et al., 2000; Six et al., 2004; Lawrence et al., 2015). Tate et al. (2004) found that soil BD at sites excluded from grazing for just 6 yr were significantly lower than light, continuously grazed sites, but sites excluded for 6 yr were not significantly different in BD from sites excluded from grazing for >26 yr, indicating that some soil health responses to grazing management can occur relatively quickly.

Recent trends in extreme events (e.g., severe drought) indicate that grazing lands are already being affected by climate change, and model projections suggest that these systems, as well as the millions of people who depend on them around the globe, will continue to be affected (Joyce et al., 2013). Given their global extent, even moderate management changes to protect and restore existing C pools on grazing lands could have positive long-term impacts. Our results revealed grazing management adaptation opportunities to minimize negative consequences, as well as potentially increase SOC sequestration. For example, shifting to relatively lower grazing intensity levels or adopting a rotational grazing system could partly mitigate reductions in SOC observed with continuous grazing (Fig. 3 and 5). The positive responses of SOC to rotational grazing compared with continuous grazing in subhumid and humid environments (Supplemental Figs. S2 and S3), in particular, highlight climate change mitigation opportunities, but more investigation into potential interacting effects of grazing intensity, soil characteristics, and climate within these grazing systems is warranted.

Grazing management is increasingly scrutinized for impacts on soil resources; at times, it is promoted as a panacea approach to sequestering SOC and improving soil function and health, and at others, as a driver of soil degradation. Our global meta-analysis suggests that rotational grazing could potentially improve SOC and BD over continuous grazing strategies. We found that both grazing strategy and intensity can significantly influence soil function and health outcomes; however, site-specific contextual (environmental) factors play important roles in shaping these outcomes. Unfortunately, we found very limited data to evaluate how environmental variables (e.g., climate, soil texture, plant community) potentially mediate soil responses to rotational grazing strategies. We strongly suggest that future research focus on advancing understanding of interactions among important environmental factors and grazing management and resulting soil health outcomes. Additionally, only 64 studies (23% of initial studies found) reported sufficient, comparable data for inclusion into this systematic global analysis. To address this key knowledge gap, we urge greater coordination and collaboration among scientists on regional, national, and even global efforts. We also recommend the development of consistent guidelines for soil health evaluation in grazing studies to allow for future quantitative meta-analysis of grazing management impacts on soil health.

Supplemental Material

Supplemental Table S1. General study characteristics reported by authors; author name(s), published date, study duration (yr), latitude, longitude, elevation (m), mean annual precipitation (MAP), mean annual temperature (MAT), and plot area (ha).

Supplemental Fig. S1. Mean effect size (magnitude of grazing strategy treatment compared to the control) and 95% CIs of SOC, BD, CN, and TN responses to continuous grazing compared to no grazing within aridity classes. Values in parentheses are total paired observations per response variable by climatic zone.

Supplemental Fig. S2. Mean effect size (magnitude of grazing strategy treatment compared to the control) and 95% CIs of SOC, BD, CN, and TN responses to rotational grazing compared to no grazing within aridity classes. Values in parentheses are total paired observations per response variable by grazing intensity combination.

Supplemental Fig. S3. Mean effect size (magnitude of grazing strategy treatment compared to the control) and 95% CIs of SOC, BD, CN, and TN responses to rotational grazing compared to continuous grazing strategies within aridity classes. Values in parentheses are total paired observations per response variable by grazing intensity combination.

References

- Akaike, H. 1985. Prediction and entropy. In: E. Parzen, et al., editors, Selected papers of Hirotugu Akaike. Springer, New York. p. 387–410. doi:10.1007/978-1-4612-1694-0_30
- Andrés, P., J.C. Moore, F. Cotrufo, K. Denef, M.L. Haddix, R. Molowny-Horas, et al. 2017. Grazing and edaphic properties mediate soil biotic response to altered precipitation patterns in a semiarid prairie. Soil Biol. Biochem. 113:263–274. doi:10.1016/j.soilbio.2017.06.022
- Barto, E.K., F. Alt, Y. Oelmann, W. Wilcke, and M.C. Rillig. 2010. Contributions of biotic and abiotic factors to soil aggregation across a land use gradient. Soil Biol. Biochem. 42:2316–2324. doi:10.1016/j.soilbio.2010.09.008
- Briske, D.D., J.D. Derner, D.G. Milchunas, and K.W. Tate. 2011. An evidencebased assessment of prescribed grazing practices. In: D. Briske, editor, Conservation benefits of rangeland practices: Assessment, recommendations, and knowledge gaps. USDA Natl. Resour. Conserv. Serv., Lawrence, KS. p. 21–74.

- Byrnes, R.C., J. Nùñez, L. Arenas, I. Rao, C. Trujillo, C. Alvarez, et al. 2017. Biological nitrification inhibition by *Brachiaria* grasses mitigates soil nitrous oxide emissions from bovine urine patches. Soil Biol. Biochem. 107:156– 163. doi:10.1016/j.soilbio.2016.12.029
- Calcagno, V., and C. de Mazancourt. 2010. glmulti: An R package for easy automated model selection with (generalized) linear models. J. Stat. Softw. 34:1–29. doi:10.18637/jss.v034.i12
- Cameron, D.R., J. Marty, and R.F. Holland. 2014. Whither the rangeland?: Protection and conversion in California's rangeland ecosystems. PLoS One 9:e103468. doi:10.1371/journal.pone.0103468
- Chen, W., D. Huang, N. Liu, Y. Zhang, W.B. Badgery, X. Wang, and Y. Shen. 2015. Improved grazing management may increase soil carbon sequestration in temperate steppe. Sci. Rep. 5:10892. doi:10.1038/srep10892
- Conant, R.T., C.E.P. Cerri, B.B. Osborne, and K. Paustian. 2017. Grassland management impacts on soil carbon stocks: A new synthesis. Ecol. Appl. 27:662–668. doi:10.1002/eap.1473
- Conant, R.T., and K. Paustian. 2002. Potential soil carbon sequestration in overgrazed grassland ecosystems. Global Biogeochem. Cycles 16:90-1–90-9. doi:10.1029/2001GB001661
- Derner, J.D., L. Hunt, K.E. Filho, J. Ritten, J. Capper, and G. Han. 2017. Livestock production systems. In: D. Briske, editor, Rangeland systems. Springer, New York. p. 347–372. doi:10.1007/978-3-319-46709-2_10
- Derner, J.D., and G.E. Schuman. 2007. Carbon sequestration and rangelands: A synthesis of land management and precipitation effects. J. Soil Water Conserv. 62:77–85.
- Derner, J.D., C. Stanley, and E. Chad. 2016. Usable science: Soil health. Rangelands 38:64–67. doi:10.1016/j.rala.2015.10.010
- Drever, J.I., and J. Zobrist. 1992. Chemical weathering of silicate rocks as a function of elevation in the southern Swiss Alps. Geochim. Cosmochim. Acta 56:3209–3216. doi:10.1016/0016-7037(92)90298-W
- Drewry, J.J., K.C. Cameron, and G.D. Buchan. 2008. Pasture yield and soil physical property responses to soil compaction from treading and grazing: A review. Soil Res. 46:237–256. doi:10.1071/SR07125
- Eastburn, D.J., A.T. O'Geen, K.W. Tate, and L.M. Roche. 2017. Multiple ecosystem services in a working landscape. PLoS One 12:e0166595. doi:10.1371/ journal.pone.0166595
- Fabricius, C., M. Burger, and P.A.R. Hockey. 2003. Comparing biodiversity between protected areas and adjacent rangeland in xeric succulent thicket, South Africa: Arthropods and reptiles. J. Appl. Ecol. 40:392–403. doi:10.1046/j.1365-2664.2003.00793.x
- FAO, IFAD, and WFP. 2015. The state of food insecurity in the world 2015. Meeting the 2015 international hunger targets: Taking stock of uneven progress. FAO, Rome.
- Fox, H.V., O. Bonnet, J.P.G.M. Cromsigt, H. Fritz, and A.M. Shrader. 2015. Legacy effects of different land-use histories interact with current grazing patterns to determine grazing lawn soil properties. Ecosystems 18:720–733.
- Fuhlendorf, S.D., and D.M. Engle. 2001. Restoring heterogeneity on rangelands: Ecosystem Management based on evolutionary grazing patterns. Bioscience 51:625–632. doi:10.1641/0006-3568(2001)051[0625:RH OREM]2.0.CO;2
- Gao, Y.Z., M. Giese, S. Lin, B. Sattelmacher, Y. Zhao, and H. Brueck. 2008. Belowground net primary productivity and biomass allocation of a grassland in Inner Mongolia is affected by grazing intensity. Plant Soil 307:41–50. doi:10.1007/s11104-008-9579-3
- Giese, M., Y.Z. Gao, Y. Zhao, Q. Pan, S. Lin, S. Peth, and H. Brueck. 2009. Effects of grazing and rainfall variability on root and shoot decomposition in a semiarid grassland. Appl. Soil Ecol. 41:8–18. doi:10.1016/j.apsoil.2008.08.002
- Glenn, E., V. Squires, M. Olsen, and R. Frye. 1993. Potential for carbon sequestration in the drylands. In: J. Wisniewski and R.N. Sampson, editors, Terrestrial biospheric carbon fluxes quantification of sinks and sources of CO₂. Springer, Dordrecht, the Netherlands. p. 341–355. doi:10.1007/978-94-011-1982-5_22
- Gong, X.Y., N. Fanselow, K. Dittert, F. Taube, and S. Lin. 2015. Response of primary production and biomass allocation to nitrogen and water supplementation along a grazing intensity gradient in semiarid grassland. Eur. J. Agron. 63:27–35. doi:10.1016/j.eja.2014.11.004
- Greenwood, K.L., and B.M. McKenzie. 2001. Grazing effects on soil physical properties and the consequences for pastures: A review. Aust. J. Exp. Agric. 41:1231–1250. doi:10.1071/EA00102
- Gurevitch, J., and L. Hedges. 1993. Meta-analysis: Combining the results of independent experiments. In: S. Scheiner and J. Gurevitch, editors, Design and analysis of ecological experiments. Chapman and Hall, New York. p. 378–398.
- Havstad, K.M., D.P.C. Peters, R. Skaggs, J. Brown, B. Bestelmeyer, E. Fredrickson, et al. 2007. Ecological services to and from rangelands of the United States. Ecol. Econ. 64:261–268. doi:10.1016/j.ecolecon.2007.08.005

- Herrero, M., B. Henderson, P. Havlík, P.K. Thornton, R.T. Conant, P. Smith, et al. 2016. Greenhouse gas mitigation potentials in the livestock sector. Nat. Clim. Chang. 6:452–461. doi:10.1038/nclimate2925
- Hiernaux, P., C.L. Bielders, C. Valentin, A. Bationo, and S. Fernández-Rivera. 1999. Effects of livestock grazing on physical and chemical properties of sandy soils in Sahelian rangelands. J. Arid Environ. 41:231–245. doi:10.1006/jare.1998.0475
- Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25:1965–1978. doi:10.1002/joc.1276
- Holland, E.A., W.J. Parton, J.K. Detling, and D.L. Coppock. 1992. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. Am. Nat. 140:685–706. doi:10.1086/285435
- Houlbrooke, D.J., E.R. Thom, R. Chapman, and C.D.A. McLay. 1997. A study of the effects of soil bulk density on root and shoot growth of different ryegrass lines. N. Z. J. Agric. Res. 40:429–435. doi:10.1080/00288233.1997.9513265
- Jing, Z., J. Cheng, J. Su, Y. Bai, and J. Jin. 2014. Changes in plant community composition and soil properties under 3-decade grazing exclusion in semiarid grassland. Ecol. Eng. 64:171–178. doi:10.1016/j.ecoleng.2013.12.023
- Johnson, L.C., and J.R. Matchett. 2001. Fire and grazing regulate belowground processes in tallgrass prairie. Ecology 82:3377–3389. doi:10.1890/0012-9658(2001)082[3377:FAGRBP]2.0.CO;2
- Joyce, L.A., D.D. Briske, J.R. Brown, H.W. Polley, B.A. McCarl, and D.W. Bailey. 2013. Climate change and North American rangelands: Assessment of mitigation and adaptation strategies. Rangeland Ecol. Manage. 66:512– 528. doi:10.2111/REM-D-12-00142.1
- Keiluweit, M., P.S. Nico, M. Kleber, and S. Fendorf. 2016. Are oxygen limitations under recognized regulators of organic carbon turnover in upland soils? Biogeochemistry 127:157–171. doi:10.1007/s10533-015-0180-6
- Kotzé, E., A. Sandhage-Hofmann, J.A. Meinel, C.C. du Preez, and W. Amelung. 2013. Rangeland management impacts on the properties of clayey soils along grazing gradients in the semi-arid grassland biome of South Africa. J. Arid Environ. 97:220–229. doi:10.1016/j.jaridenv.2013.07.004
- Kramer, M.G., and O.A. Chadwick. 2016. Controls on carbon storage and weathering in volcanic soils across a high-elevation climate gradient on Mauna Kea, Hawaii. Ecology 97:2384–2395. doi:10.1002/ecy.1467
- Lawrence, C.R., J.W. Harden, X. Xu, M.S. Schulz, and S.E. Trumbore. 2015. Long-term controls on soil organic carbon with depth and time: A case study from the Cowlitz River Chronosequence, WA USA. Geoderma 247–248:73–87. doi:10.1016/j.geoderma.2015.02.005
- LeCain, D.R., J.A. Morgan, G.E. Schuman, J.D. Reeder, and R.H. Hart. 2002. Carbon exchange and species composition of grazed pastures and exclosures in the shortgrass steppe of Colorado. Agric. Ecosyst. Environ. 93:421–435. doi:10.1016/S0167-8809(01)00290-0
- Lundström, U.S., N. van Breemen, and D. Bain. 2000. The podzolization process: A review. Geoderma 94:91–107. doi:10.1016/S0016-7061(99)00036-1
- McSherry, M.E., and M.E. Ritchie. 2013. Effects of grazing on grassland soil carbon: A global review. Glob. Change Biol. 19:1347–1357. doi:10.1111/gcb.12144
- Menneer, J.C., S.F. Ledgard, C.D.A. McLay, and W.B. Silvester. 2005. The effects of treading by dairy cows during wet soil conditions on white clover productivity, growth and morphology in a white clover–perennial ryegrass pasture. Grass Forage Sci. 60:46–58. doi:10.1111/j.1365-2494.2005.00450.x
- Morgan, J.A., W. Parton, J.D. Derner, T.G. Gilmanov, and D.P. Smith. 2016. Importance of early season conditions and grazing on carbon dioxide fluxes in Colorado shortgrass steppe. Rangeland Ecol. Manage. 69:342–350. doi:10.1016/j.rama.2016.05.002
- Motavalli, P.P., C.A. Palm, E.T. Elliott, S.D. Frey, and P.C. Smithson. 1995. Nitrogen mineralization in humid tropical forest soils: Mineralogy, texture, and measured nitrogen fractions. Soil Sci. Soc. Am. J. 59:1168–1175. doi:10.2136/sssaj1995.03615995005900040032x
- Neff, J.C., R.L. Reynolds, J. Belnap, and P. Lamothe. 2005. Multi-decadal impacts of grazing on soil physical and biogeochemical properties in southeast Utah. Ecol. Appl. 15:87–95. doi:10.1890/04-0268
- Oenema, O., G.L. Velthof, S. Yamulki, and S.C. Jarvis. 1997. Nitrous oxide emissions from grazed grassland. Soil Use Manage. 13:288–295. doi:10.1111/j.1475-2743.1997.tb00600.x
- Parkin, T.B. 1987. Soil microsites as a source of denitrification variability. Soil Sci. Soc. Am. J. 51:1194–1199. doi:10.2136/ sssaj1987.03615995005100050019x
- Piñeiro, G., J.M. Paruelo, M. Oesterheld, and E.G. Jobbágy. 2010. Pathways of grazing effects on soil organic carbon and nitrogen. Rangeland Ecol. Manage. 63:109–119. doi:10.2111/08-255.1
- Powers, J.S., and W.H. Schlesinger. 2002. Relationships among soil carbon distributions and biophysical factors at nested spatial scales in rain forests of northeastern Costa Rica. Geoderma 109:165–190. doi:10.1016/ S0016-7061(02)00147-7

- Pulido, M., S. Schnabel, J.F. Lavado Contador, J. Lozano-Parra, and F. González. 2016. The impact of heavy grazing on soil quality and pasture production in rangelands of SW Spain. Land Degrad. Dev. 29:216–230. doi:10.1002/ ldr.2501
- Qu, T., W. Du, X. Yuan, Z. Yang, D. Liu, D. Wang, and L. Yu. 2016. Impacts of grazing intensity and plant community composition on soil bacterial community diversity in a steppe grassland. PLoS One 11:e0159680. doi:10.1371/journal.pone.0159680
- R Core Team. 2016. R: A language and environment for statistical computing. R Found. Stat. Comput., Vienna, Austria.
- Reeder, J.D., and G.E. Schuman. 2002. Influence of livestock grazing on C sequestration in semi-arid mixed-grass and short-grass rangelands. Environ. Pollut. 116:457–463. doi:10.1016/S0269-7491(01)00223-8
- Reeder, J.D., G.E. Schuman, J.A. Morgan, and D.R. LeCain. 2004. Response of organic and inorganic carbon and nitrogen to long-term grazing of the shortgrass steppe. Environ. Manage. 33:485–495. doi:10.1007/ s00267-003-9106-5
- Ridder, F.D., R. Pintelon, J. Schoukens, and D.P. Gillikin. 2005. Modified AIC and MDL model selection criteria for short data records. IEEE Trans. Instrum. Meas. 54:144–150. doi:10.1109/TIM.2004.838132
- Roche, L.M., B.B. Cutts, J.D. Derner, M.N. Lubell, and K.W. Tate. 2015. On-ranch grazing strategies: Context for the rotational grazing dilemma. Rangeland Ecol. Manage. 68:248–256. doi:10.1016/j. rama.2015.03.011
- Sayre, N.F. 2007. A history of working landscapes: The Altar Valley, Arizona, USA. Rangelands 29:41–45. doi:10.2111/1551-501X(2007)29[41:AHOWLT]2.0.CO;2
- Schlesinger, W.H., T.J. Ward, and J. Anderson. 2000. Nutrient losses in runoff from grassland and shrubland habitats in southern New Mexico: II. Field plots. Biogeochemistry 49:69–86. doi:10.1023/A:1006246126915
- Schulz, K., K. Voigt, C. Beusch, J.S. Almeida-Cortez, I. Kowarik, A. Walz, and A. Cierjacks. 2016. Grazing deteriorates the soil carbon stocks of Caatinga forest ecosystems in Brazil. For. Ecol. Manage. 367:62–70. doi:10.1016/j. foreco.2016.02.011
- Schuman, G.E., J.D. Reeder, J.T. Manley, R.H. Hart, and W.A. Manley. 1999. Impact of grazing management on the carbon and nitrogen balance of a mixed-grass rangeland. Ecol. Appl. 9:65–71. doi:10.1890/1051-0761(1999)009[0065:IOGMOT]2.0.CO;2
- Scurlock, J.M.O., and D.O. Hall. 1998. The global carbon sink: A grassland perspective. Glob. Change Biol. 4:229–233. doi:10.1046/j.1365-2486.1998.00151.x
- Shao, C., J. Chen, and L. Li. 2013. Grazing alters the biophysical regulation of carbon fluxes in a desert steppe. Environ. Res. Lett. 8:025012. doi:10.1088/1748-9326/8/2/025012
- Six, J. 2013. Conservation: Spare our restored soil. Nature 498:180–181. doi:10.1038/498180a
- Six, J., S.M. Ogle, F.J. Breidt, R.T. Conant, A.R. Mosier, and K. Paustian. 2004. The potential to mitigate global warming with no-tillage management is only realized when practised in the long term. Glob. Change Biol. 10:155– 160. doi:10.1111/j.1529-8817.2003.00730.x
- Soussana, J.-F., and G. Lemaire. 2014. Coupling carbon and nitrogen cycles for environmentally sustainable intensification of grasslands and croplivestock systems. Agric. Ecosyst. Environ. 190:9–17. doi:10.1016/j. agee.2013.10.012
- Spaeth, K.E., T.L. Thurow, W.H. Blackburn, and F.B. Pierson. 1996. Ecological dynamics and management effects on rangeland hydrologic processes. In: K. Spaeth, et al., editors, Grazing land hydrology issues: Perspectives for the 21st century. Soc. Range Manage., Denver, CO. p. 25–51.

- Spinoni, J., J. Vogt, G. Naumann, H. Carrao, and P. Barbosa. 2015. Towards identifying areas at climatological risk of desertification using the Köppen–Geiger classification and FAO aridity index. Int. J. Climatol. 35:2210–2222. doi:10.1002/joc.4124
- Stavi, I., E.D. Ungar, H. Lavee, and P. Sarah. 2008. Grazing-induced spatial variability of soil bulk density and content of moisture, organic carbon and calcium carbonate in a semi-arid rangeland. Catena 75:288–296. doi:10.1016/j.catena.2008.07.007
- Steffens, M., A. Kölbl, K.U. Totsche, and I. Kögel-Knabner. 2008. Grazing effects on soil chemical and physical properties in a semiarid steppe of Inner Mongolia (P.R. China). Geoderma 143:63–72. doi:10.1016/j.geoderma.2007.09.004
- Szramek, K., J.C. McIntosh, E.L. Williams, T. Kanduc, N. Ogrinc, and L.M. Walter. 2007. Relative weathering intensity of calcite versus dolomite in carbonate-bearing temperate zone watersheds: Carbonate geochemistry and fluxes from catchments within the St. Lawrence and Danube river basins. Geochem. Geophys. Geosyst. 8:Q04002. doi:10.1029/2006GC001337
- Tate, K.W., D.M. Dudley, N.K. Mcdougald, and M.R. George. 2004. Effect of canopy and grazing on soil bulk density. J. Range Manage. 57:411–417. doi:10.2307/4003867
- Thornton, P.K. 2010. Livestock production: Recent trends, future prospects. Philos. Trans. R. Soc. Lond. B Biol. Sci. 365:2853–2867. doi:10.1098/ rstb.2010.0134
- Turner, C.L., T.R. Seastedt, and M.I. Dyer. 1993. Maximization of aboveground grassland production: The role of defoliation frequency, intensity, and history. Ecol. Appl. 3:175–186. doi:10.2307/1941800
- Velbel, M.A. 1993. Temperature dependence of silicate weathering in nature: How strong a negative feedback on long-term accumulation of atmospheric CO₂ and global greenhouse warming? Geology 21:1059–1062. doi:10.1130/0091-7613(1993)021<1059:TDOSWI>2.3.CO;2
- Viechtbauer, W. 2010. Conducting meta-analyses in R with the metafor package. J. Stat. Softw. 36:1–48. doi:10.18637/jss.v036.i03
- Vogel, C., K. Heister, F. Buegger, I. Tanuwidjaja, S. Haug, M. Schloter, and I. Kögel-Knabner. 2015. Clay mineral composition modifies decomposition and sequestration of organic carbon and nitrogen in fine soil fractions. Biol. Fertil. Soils 51:427–442. doi:10.1007/s00374-014-0987-7
- Wang, S., Q. Zhuang, Q. Wang, X. Jin, and C. Han. 2017. Mapping stocks of soil organic carbon and soil total nitrogen in Liaoning Province of China. Geoderma 305:250–263. doi:10.1016/j.geoderma.2017.05.048
- Wang, T., W.R. Teague, S.C. Park, and S. Bevers. 2015. GHG mitigation potential of different grazing strategies in the United States southern Great Plains. Sustainability 7:13500–13521. doi:10.3390/su71013500
- Wang, X., B.G. McConkey, A.J. VandenBygaart, J. Fan, A. Iwaasa, and M. Schellenberg. 2016. Grazing improves C and N cycling in the Northern Great Plains: A meta-analysis. Sci. Rep. 6:33190. doi:10.1038/srep33190
- Willatt, S.T., and D.M. Pullar. 1984. Changes in soil physical properties under grazed pastures. Soil Res. 22:343–348. doi:10.1071/SR9840343
- Zhang, K., H. Dang, Q. Zhang, and X. Cheng. 2015a. Soil carbon dynamics following land-use change varied with temperature and precipitation gradients: Evidence from stable isotopes. Glob. Change Biol. 21:2762–2772. doi:10.1111/gcb.12886
- Zhang, T., Y. Zhang, M. Xu, J. Zhu, M.C. Wimberly, G. Yu, et al. 2015b. Lightintensity grazing improves alpine meadow productivity and adaption to climate change on the Tibetan Plateau. Sci. Rep. 5:srep15949. doi:10.1038/ srep15949
- Zomer, R.J., A. Trabucco, D.A. Bossio, and L.V. Verchot. 2008. Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. Agric. Ecosyst. Environ. 126:67–80. doi:10.1016/j.agee.2008.01.014