

# Temporal variability drives soil chemical and biological dynamics more than grazing in a northern mixed-grass prairie

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**Abstract:** Quantification of soil health dynamics relative to grazing can inform both agriculture and conservation. We conducted an experiment near Lingle, Wyoming, USA, on a semi-arid northern mixed-grass prairie from 2017–2019. Three grazing density treatments (NG – not grazed; MRG – moderate rotationally grazed a herd of 4 Angus heifers, and UHD – ultra-high density rotationally grazed a herd of 33 Angus cow-calf pairs) were replicated four times in a randomised complete block design across twelve – 0.405 ha paddocks. Soil sampling was conducted prior to grazing in June 2017, one-week post grazing in July 2019, and six weeks post grazing in August 2019 and included a suite of forage, ground cover, soil chemical, soil physical, and soil microbiological measurements. Grazing treatment did result in lower vegetation structure but had no effect on any soil variables ( $P > 0.05$ ). Conversely, the sampling interval was more influential for predicting fluctuations in chemical (15 variables significantly different within at least one treatment) or microbiological (13 variables significantly different within at least one treatment) variables than grazing treatment. The study was conducted in an intact native prairie with initial and final values indicating "Very Good" soil health, including the saturated:unsaturated fatty acid ratio, an indicator of stress.

**Keywords:** grazing intensification; ecosystem; animal density; beef; grassland; rangeland

Livestock grazing is one of the most common agricultural practices globally. Rangelands provide the land base for a large proportion of these livestock enterprises, and most rangelands are only agriculturally suited to livestock grazing due to limited primary productivity, soil depth, and other climate and topographical constraints (Derner et al. 2017). With the consistent increase in human population, there has been an intensification of land use in order to optimise the provision of ecosystem goods and services, including livestock production and

rangeland enhancement (Derner et al. 2018). Such grazing intensification has revealed a wide range of soil, vegetation, and livestock responses (Briske et al. 2008, Teague et al. 2013). Relevant to this variation in responses is the influence of environmental context, particularly climate and soils (Derner et al. 1997, Derner and Shuman 2007).

Central to understanding how rangelands respond to grazing intensification is the need to understand soil health responses (Dormaar et al. 1989). Soil health refers to the synergistic relationship between the

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chemical, physical, and biological properties of soil driven by living soil organisms that influence plant health *via* soil nutrient cycling (Lal 2016) that ultimately provide ecosystem services that sustain plants, animals, and humans (Williams et al. 2020). When soil health is improved through mechanisms such as water retention and nutrient cycling, it is possible that greater forage production and animal health and production may also be realised (Manley et al. 1995). The processes by which grazing animals may affect soils include physical trampling, depositing faeces and urine resulting in nutrient redistribution, and defoliation of plants leading to alterations of ground cover (Van Syoc et al. 2022). These processes can then alter physical features of the soil, such as pore space, microbial niches, labile nitrogen pools, soil organic matter, vegetation composition, and ultimately cascading soil-microbe-plant interactions (Hamilton et al. 2008, Mikola et al. 2009, Damsma et al. 2015). For example, short-duration grazing/trampling resulted in lower soil bulk density and greater aboveground forage biomass when compared to continuous grazing systems (Abdel-Magid et al. 1987). Similarly, organic matter percentage, water infiltration, fertility, and penetration resistance were negatively influenced at higher rates of trampling, while the effects on vegetation were species-dependent (Ferrero 1991). Direct chemical inputs *via* faecal matter and urine with increasing grazing densities enhanced nitrogen cycling, as well as phosphorous and potassium levels (Kohandel et al. 2009). Moreover, microbial diversity and biomass may also be affected, as shown by Song et al. (2008).

However, the effects of grazing on soil health cannot be oversimplified as the application of different grazing management has the potential to influence soil health variably. This variability is attributed to the relative intensity and duration of associated foraging and trampling activity on rangelands, which dictates the degree of interaction with soil health features through both direct and indirect mechanisms (Eldridge et al. 2017). From an applied grazing management perspective, higher stocking density and rotation allow for optimisation of cattle movements relative to timing and frequency of grazing, potentially limiting selectivity and preventing repeated grazing of preferred plants (Bailey and Brown 2011). Briske and Richards (1995) noted that chronic, intensive grazing (continuous grazing) minimizes the leaf area of forage, leading to a reduction of total photosynthesis. Lower amounts of photosynthetic tissues result in lower root-to-shoot biomass leading to the degrada-

tion of rangelands. Zhang et al. (2017) demonstrated that the sensitivity of forage response to grazing is greater than that of soils. Relative to soil implications, a recent study from Australia suggested that as grazing intensity increases, strong reductions in the stability and nutrient indices of soil health were expressed, especially in low productivity environments (Eldridge et al. 2017).

This potential negative effect of grazing management intensification on soil health in low-productivity environments, coupled with some studies suggesting that more intensive grazing benefits soil health, demands more empirical assessments of the top-down effects of grazing management on soil health. In an effort to understand the effects of grazing on the soil health of cold, high-elevation, low-productivity rangelands, we conducted an empirical grazing experiment to (1) determine how grazing density, or complete exclusion, alters soil health properties and (2) quantify both the direction and magnitude of any soil health alterations relative to grazing management.

## MATERIAL AND METHODS

**Study site.** The study site was located at the University of Wyoming's James C. Hageman Sustainable Agricultural Research and Extension Center (SAREC) facility in Lingle, Wyoming, USA, in a northern mixed-grass prairie (NRCS 2001). Prior to the experiment, the pasture was used for summer season cattle grazing at a moderate utilisation level. The research plots were located in Loamy Ecological Site R067AY122WY within the Major Land Resource Area (MLRA) 67A Central High Plains North. Long-term (1895–2022) annual mean precipitation and temperature is 364 mm and 8.6 °C. Soils are of the Mitchell Series and consist of very deep, well-drained soils formed in loamy colluvial and alluvial sediments weathered from siltstone, and the mean elevation of our plots is ~1 355 m a.s.l. Soil texture with a hydrometer of the study plots indicated that the percent sand, silt, and clay were  $46.8\% \pm 1.1$ ,  $34.1\% \pm 1.3$ , and  $19.1\% \pm 0.4$ , respectively. The main forage species were native plants, including western wheatgrass (*Pascopyrum smithii*) (Rydb.) Å. Löve), needle-and-thread (*Hesperostipa comata*) (Trin. & Rupr.) Barkworth), and blue grama (*Bouteloua gracilis*) (Wild. Ex Kunth) Lag. Ex Griffiths). Annual forage production is estimated at 1 121 kg/ha in an unfavourable year, 1 682 kg/ha in an average year, and 2 242 kg/ha in above-average years (NRCS 2001).

Table 1. Grazing treatment abbreviations, definitions, and details for grazing density and soil health experiment located at the University of Wyoming's James C. Hageman Sustainable Agricultural Research and Extension Center (SAREC) facility in Lingle, Wyoming, USA in a northern mixed grass prairie. The study duration was 2017–2019, and cattle were crossbred Angus (*Bos taurus*)

Abbreviation	Definition	Details of treatment target and realised animal pressure
NG	not grazed	Completely excluded from any livestock grazing for the duration of the study.
MRG	moderate rotationally grazed	Based on the United States Department of Agriculture – Natural Resources Conservation Service (USDA-NRCS) recommendations of moderate stocking rate aiming for removal of 50% of herbaceous forage biomass with as light of animal density as possible (NRCS 2009). Grazed with 4 Angus heifers per 0.405 ha paddock, which is an approximate equivalent to 5 380 kg/ha. This number of animals was the minimum number determined for the social contentedness of the animals in an isolated paddock.
UHD	ultra-high density rotationally grazed	Based on USDA-NRCS recommendations of realising approximately 56 043 to 84 064 animal kg/ha for removal of 50% of herbaceous forage biomass (NRCS 2011). Grazed with 33 Angus cow-calf pairs (66 animals) per 0.405 ha paddock which is an approximate equivalent of 67 812 animal kg/ha.

**Experimental design and treatments.** We used a randomised complete block design (RCBD) with 3 grazing treatments (NG – not grazed; MRG – moderate rotationally grazed herd with 4 Angus heifers in 4 separate herds; UHD – ultra-high density rotationally grazed herd with 33 Angus cow-calf pairs in a single

herd; Tables 1 and 2) replicated 4 times (i.e., blocks) for a sample size ( $n$ ) = 12 total paddocks (Figure 1A; NRCS 2011). In UHD, 2 bulls were with cows during the experimental grazing period in 2017 but no bulls in 2018 or 2019. Heifers were estimated to weigh 544 kg, mature cows were estimated to weigh 635 kg,

Table 2. Grazing treatments at the University of Wyoming's James C. Hageman Sustainable Agricultural Research and Extension Center (SAREC) facility in Lingle, Wyoming, USA in a northern mixed grass prairie. The study duration was 2017–2019, and cattle were crossbred Angus (*Bos taurus*)

Year	Moderate rotationally grazed (MRG)	Ultra-high density (UHD)
2017	4 heifers per paddock	33 cow-calf pairs + 2 bulls
	Block 1: 4.5 days; June 28 <sup>th</sup> – July 2 <sup>nd</sup>	start: 7 h – Block 1 on July 5 <sup>th</sup>
	Block 2: 4.5 days; June 28 <sup>th</sup> – July 2 <sup>nd</sup>	↘ then 14 h – Block 4
	Block 3: 10.5 days; June 28 <sup>th</sup> – July 8 <sup>th</sup>	↘ then 9 h – Block 2
	Block 4: 4.5 days; June 28 <sup>th</sup> – July 2 <sup>nd</sup> mean = 6.00 days	↘ end: 14 h – Block 3 on July 7 <sup>th</sup> mean = 11.00 h
2018	4 heifers per paddock	33 cow-calf pairs per paddock
	Block 1: 7.5 days; June 28 <sup>th</sup> – July 5 <sup>th</sup>	start: 18 h – Block 1 on July 5 <sup>th</sup>
	Block 2: 7.5 days; June 28 <sup>th</sup> – July 5 <sup>th</sup>	↘ then 12 h – Block 4
	Block 3: 10.5 days; June 28 <sup>th</sup> – July 8 <sup>th</sup>	↘ then 13 h – Block 2
	Block 4: 5.5 days; June 28 <sup>th</sup> – July 3 <sup>rd</sup> mean = 7.75 days	↘ end: 24 h – Block 3 on July 8 <sup>th</sup> mean = 16.75 h
2019	4 heifers per paddock	33 cow-calf pairs per paddock
	Block 1: 11.5 days; June 18 <sup>th</sup> – June 29 <sup>th</sup>	start: 8.5 h – Block 1 on June 27 <sup>th</sup>
	Block 2: 7.5 days; June 18 <sup>th</sup> – June 25 <sup>th</sup>	↘ then 12 h – Block 4
	Block 3: 12.5 days; June 18 <sup>th</sup> – June 30 <sup>th</sup>	↘ then 14 h – Block 2
	Block 4: 4.5 days; June 18 <sup>th</sup> – June 22 <sup>nd</sup> mean = 9.00 days	↘ end: 22 h – Block 3 on June 30 <sup>th</sup> mean = 14.13 h

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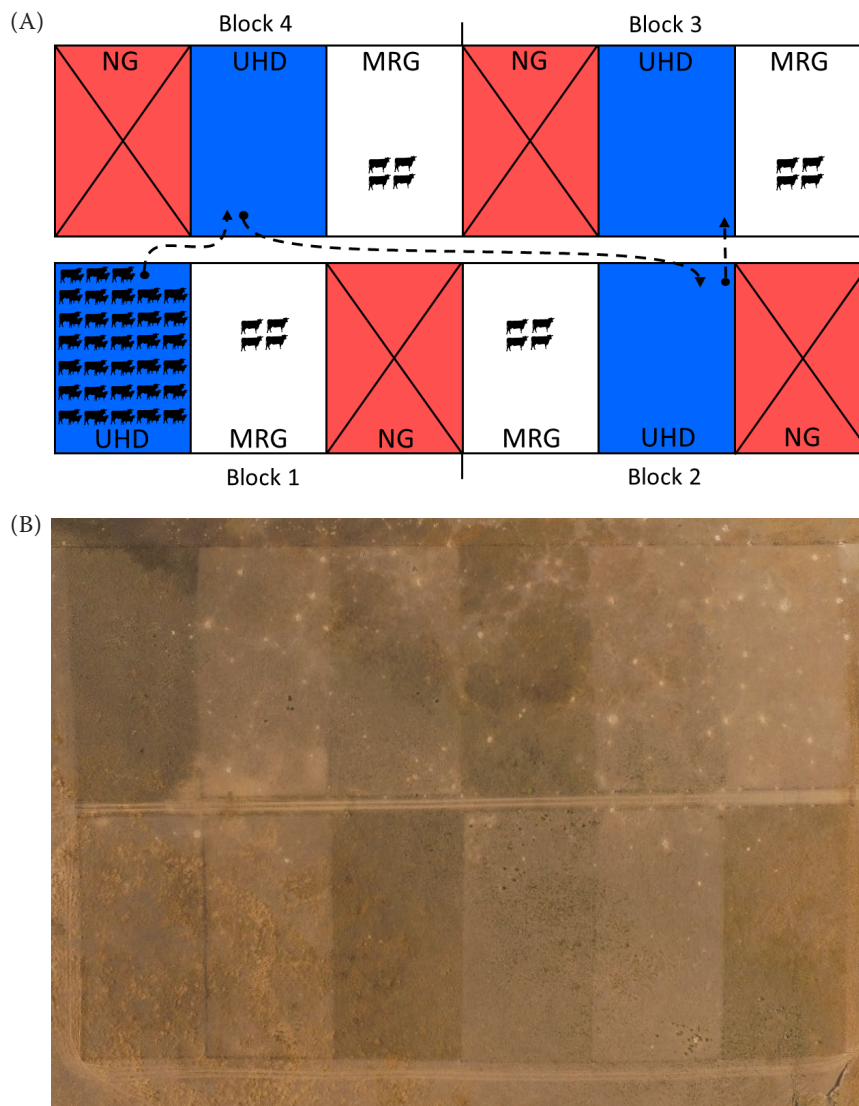


Figure 1. (A) Treatment design to for assessing the influence of grazing on soil health at the University of Wyoming's James C. Hageman Sustainable Agricultural Research and Extension Center (SAREC) facility in Lingle, Wyoming, USA. The study was a randomised complete block design (RCBD) with the 3 grazing treatments (NG – not grazed; MRG – moderate rotationally grazed with 4 herds consisting of 4 heifers each; UHD – ultra-high density rotationally grazed consisting of a single herd of 33 cows with calves) replicated 4 times (i.e., blocks). Arrows indicate the direction of movement of the UHD herd of cattle through paddocks. (B) Drone image of study site and treatment effects. Each paddock was 0.405 hectares in size and grazed with Angus crossbred cattle (*Bos taurus*) from 2017–2019

and calves were estimated to weigh 136 kg. A random number generator was used to determine the assignment of a grazing treatment within each paddock, and treatments are shown from an aerial drone image in Figure 1B.

To determine the potential annual grazing time in each paddock, we coupled the points where herbaceous biomass and vegetation visual obstruction were both measured to develop a yearly predictive linear regression equation (Figure 2) using vegetation visual obstruction- height ( $x$ ) to predict herbaceous biomass ( $y$ ) across each paddock using all vegetation visual obstruction readings. To estimate initial stocking rates (NRCS 2009), we then parameterised a grazing time model using herbaceous biomass, 50% forage allocation to cattle, and an animal unit (AU) equivalent to account for different animal types and

sizes where the total predicted biomass available using herbaceous biomass calibration equations adjusted to a 50% standard allocation of forage to animals and then relativised for the number of animals of either heifers, cows + calves, or bulls based on an AU equivalent adjusted for animal size and calf age (here considered as 1.2 for heifers, 1.7 for cows, 2.2 for bulls; Stam et al. 2018), and 11.8 kg/day is the daily forage requirement relative to body weight or in other words, 2.6% of body weight in air dry forage daily for a 454 kg cow with a calf which is the adjustment basis for an AU and then for 1 month to sustain 1 AU (i.e., an animal unit month or AUM) (Stam et al. 2018). The AUM concept is commonly applied when grazing rangelands in the western United States. Stocking details are explicitly presented in Scasta et al. (2023). The approximate



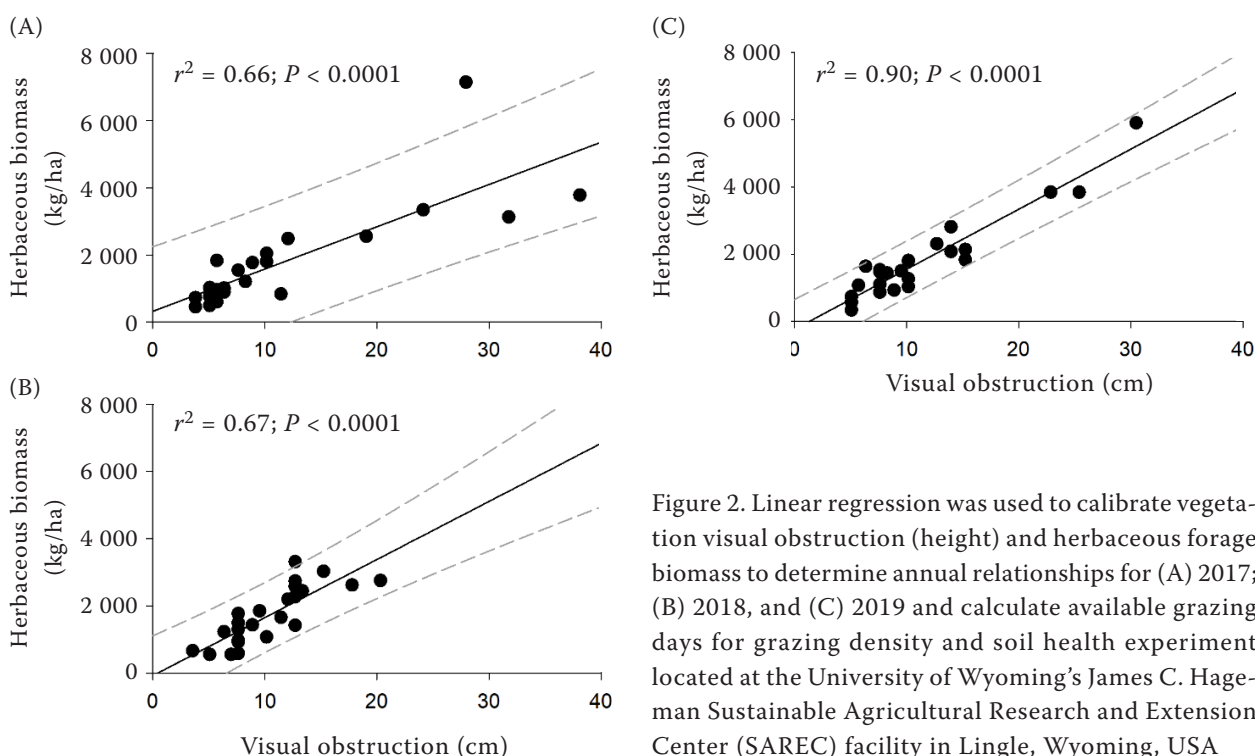


Figure 2. Linear regression was used to calibrate vegetation visual obstruction (height) and herbaceous forage biomass to determine annual relationships for (A) 2017; (B) 2018, and (C) 2019 and calculate available grazing days for grazing density and soil health experiment located at the University of Wyoming's James C. Hageman Sustainable Agricultural Research and Extension Center (SAREC) facility in Lingle, Wyoming, USA

total MRG herd (heifers) weight was 5 380 animal kg/ha, and the approximate total UHD herd (cows with calves) weight was 67 812 animal kg/ha (Grazing Treatments described in Table 1). Grazing start date, end date, and animal numbers are described in detail in Table 2.

Baseline soils, vegetation, and grazing time data were collected prior to the establishment of grazing treatments on 24–25 June 2017. Vegetation and grazing time data were again taken prior to initiation of grazing each year (specifically on 23–24 June 2018 and 14–15 June 2019 (2018 and 2019 pre-grazing soil sampling was not performed). Along the diagonal long axis of each paddock, a permanent transect stretching from northeast to southwest was established. Herbaceous biomass was clipped at 27.4 m and 54.9 m along the transect within a 20 × 50 cm quadrat. Herbaceous biomass samples were then dried at 60 °C for 48 h in a forced air oven and weighed. Along the same transect, vegetation visual obstruction readings using a modified Robel pole (Robel et al. 1970) were recorded at nine intervals (9.1, 18.3, 27.4, 36.6, 45.7, 54.9, 64.0, 73.2 and 82.3 m) with observations at each point from each of the four cardinal directions (north, south, east, and west). At each interval, the mean of the four directional readings was then calculated and recorded as the visual obstruction

value. Vegetation visual obstruction was sampled before grazing (to determine grazing time as described above). In addition, vegetation visual obstruction, ground cover classes (perennial native grass, annual exotic grass, litter, and bare ground) were estimated using a 20 × 50 cm quadrat and Daubenmire cover classes (Daubenmire 1959) at the same points along the same transect as vegetation visual obstruction readings), and surface temperatures were sampled after grazing on 8 July 2017, 8 July 2018, and 30 June 2019. Ground surface temperatures were taken using Performance Tool W89722 Infrared Thermometer by holding the instrument at waist height (0.92 m) above ground and pointing the laser at the surface of the ground which was the point of detection. Reference temperatures were also taken at each point using a white sheet of paper following Twomey et al. (1986).

Soil samples to a 10 cm depth (Bird et al. 2002) were taken at four intervals (18.3, 36.6, 54.9 and 73.2 m) along the same permanent transect used for herbaceous biomass, vegetation visual obstruction, and cover class measurements and the four soil samples per paddock were pooled into a single composite sample. Soil samples were collected at three intervals: 2017 prior to grazing, 2019 – 1 week after grazing, and 2019 – 6 weeks after grazing in order to determine if a lag in response occurred (Van Syoc et

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al. 2022). Soil samples were immediately placed in a cooler on ice until delivery to Ward Laboratories in Kearney, Nebraska, USA for analyses within 24 h. Soil chemical analyses included soil organic C the following clarification about soil organic C determination (determined with a LECO analyser; 1 g of soil treated with sulfurous acid, then ignited in oxygenated combustion chamber 1 350 °C, then assessed in infrared absorption detector), soil organic matter (determined *via* loss on ignition for 2 h in drying oven 105 °C then in asher muffle furnace), pH, salts, cation exchange capacity, ammonium, boron, calcium, copper, iron, magnesium, nitrate, nitrogen (total, available N Haney, organic N release Haney, organic N reserve Haney), phosphorous (total and available Haney), potassium (total and available Haney), sodium, sulfate, and zinc. Soil biological analyses included a suite of biological metrics including actinomycetes (biomass and %), arbuscular mycorrhiza fungi (biomass and %), saprophytes (biomass and %), gram positive (+) bacteria (biomass and %), gram negative (–) bacteria (biomass and %), protozoa (biomass and %), total bacteria (biomass and %), total fungi (biomass and %), undifferentiated (biomass and %), total phospholipid-derived fatty acids (PLFA biomass), several ratios (fungi:bacteria, gram (+):gram (–), organic C:organic N, saturated:unsaturated fatty acids, monosaturated:polyunsaturated fatty acids, and predator:prey (Protozoa:Bacteria)), Functional Group Diversity index, water extractable organic C (WEOC; H<sub>2</sub>O-OC), water extracted organic N (WEON; H<sub>2</sub>O-ON), respiration (CO<sub>2</sub>-C), and a soil health calculation. Methods used were specific to each soil metric and followed industry standards as described in the Ward Guide (2021) and in Gergeni et al. (2022).

Finally, to understand the potential role of precipitation and temperature in explaining our results, we extracted daily temperature and precipitation data for June, July, August, and September for each of the three years of the experiment (2017, 2018, and 2019) from the PRISM platform (PRISM 2023) which derives estimates at a 4 km resolution using the AN18d data set and extrapolation method that uses digital elevation models from ~10 000 weather stations (Daly et al. 2008) weighted relative to a physiographic similarity.

**Statistical analysis.** To assess stocking rate and pre- and post-graze vegetation responses, we used mixed effects analysis of variance (ANOVA) models with grazing treatment (NG, MRG, or UHD) as the

main fixed effect and block as a random effect by year. Similar models were used to assess ground temperature and ground cover responses by year. To compare the effects of grazing treatment or sampling interval on response variables, we analysed soil response variables using similar mixed-effect ANOVA models. In each model, the main fixed effect was either grazing treatment or sampling interval with block as the random effect. For the treatment analyses, each model was assessed within each sampling timing interval. For the sampling timing analyses, each model was assessed within each treatment. Each potential response variable was independently assessed for distribution using the Shapiro-Wilk W-test, where values > 0.05 indicated the normal distribution of population data. Data were transformed when needed using arcsine transformation for percentage data or log10 transformation for numerical data. The raw data were used for all visualisations and reporting of means and standard errors, while all statistical tests used transformed data as appropriate. Each pairwise test was based on the null hypothesis that soil, microbial, and soil/forage physiological response variables would not differ based on grazing treatment, with the alternative hypothesis that soil, microbial, and soil/forage physiological response variables would differ based on grazing treatment. When significance was indicated during univariate analyses, means were separated using Tukey's *HSD* (honestly significant difference) posthoc test. *P* value and standard error were reported. Significance was calculated at a *P*-value of  $\alpha = 0.05$ . All univariate analyses were run in JMP Pro (2019). We then conducted two separate constrained multivariate analyses using redundancy analysis (RDA) for the soil chemical variables and then the soil microbiology variables (Šmilauer and Lepš 2014, CANOCO 5 2017). Constraining explanatory variables were grazing treatment, sampling interval, and block and soil response data were log-transformed and centred by soil response variables. We assessed pseudo-*F* and *P*-values for the first constrained axis and all constrained axes with a permutation test with 1 000 iterations. Sample diversity was determined with the Shannon-Wiener index.

## RESULTS

**Stocking rate and vegetation structure.** Across treatments, the stocking rate averaged 2.22 ( $\pm 0.24$ ) AUMs/ha in 2017, 3.03 ( $\pm 0.21$ ) AUMs/ha in 2018, and 2.98 ( $\pm 0.31$ ) AUMs/ha in 2019, and stocking

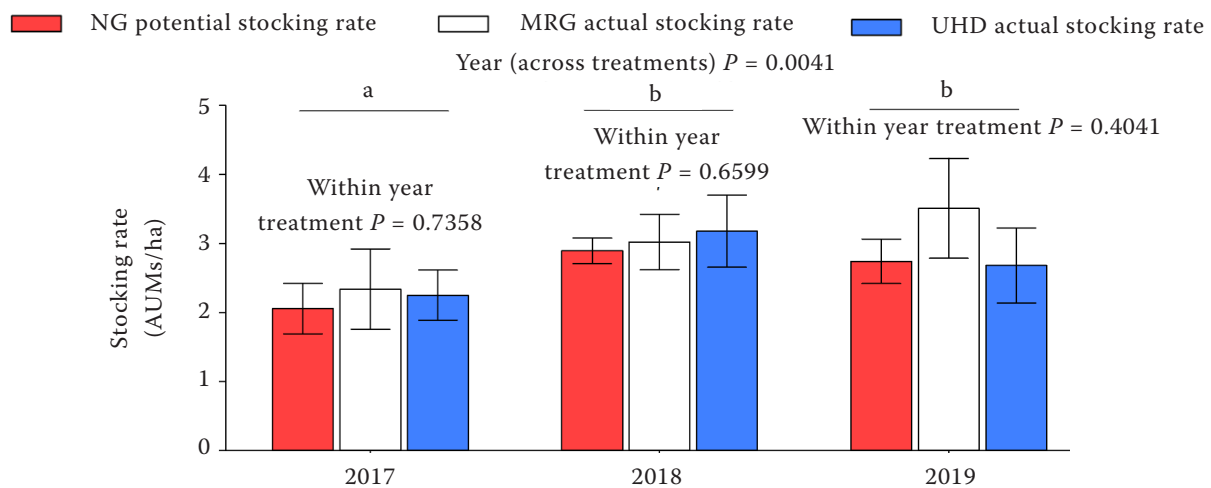


Figure 3. Comparison of annual mean stocking rates by grazed treatment for 2017–2019 at the University of Wyoming's James C. Hageman Sustainable Agricultural Research and Extension Center (SAREC) facility in Lingle, Wyoming, USA. Stocking rates were based on a parametrised grazing time model using herbaceous biomass (shown in Figure 1), 50% forage allocation to cattle, and an animal unit (AU) equivalent to account for different animal types and sizes where the total predicted biomass available using herbaceous biomass calibration equations adjusted to a 50% standard allocation of forage to animals and then relativised for the number of animals of either heifers, cows + calves, or bulls based on an AU equivalent adjusted for animal size and calf age (here considered as 1.2 for heifers, 1.7 for cows, 2.2 for bulls), and 11.8 kg/day is the daily forage requirement relative to body weight (or in other words, 2.6% of animal body weight in air dry forage daily for a 454 kg cow with a calf which is the adjustment basis for an AU and then for 1 month to sustain 1 AU (i.e., an animal unit month or AUM) (Stam et al. 2018, Scasta et al. 2023)

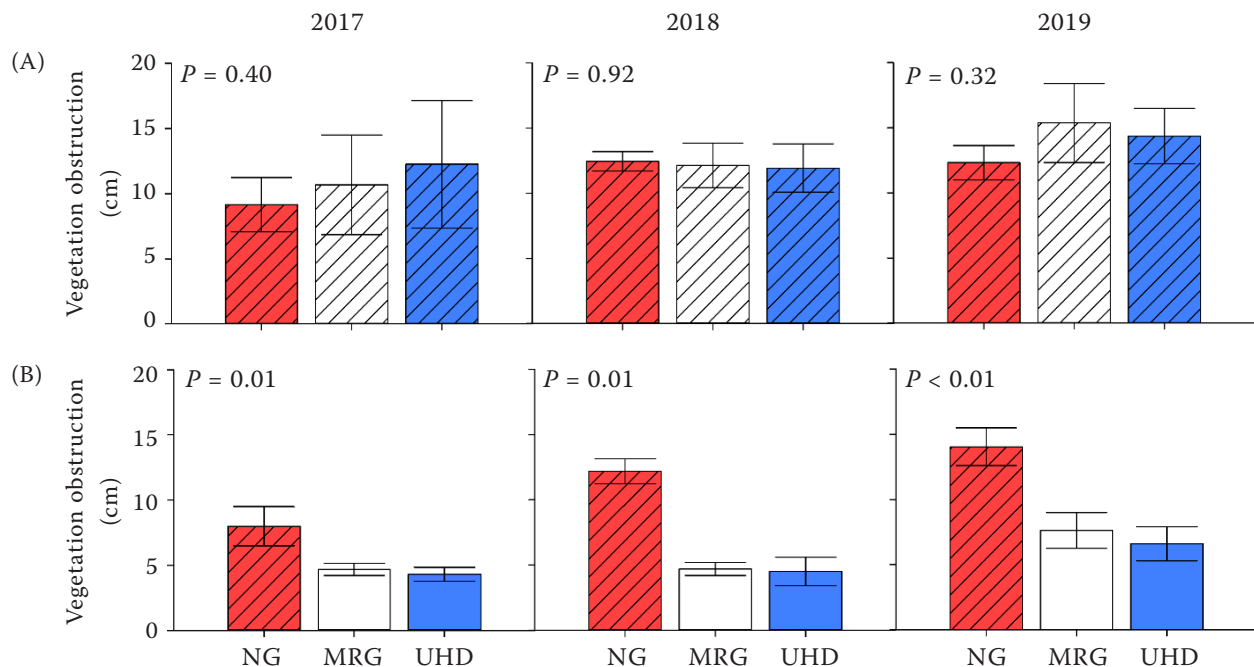


Figure 4. Comparison of the mean (A) pre- and (B) post-grazing forage visual obstruction height in 2017, 2018, and 2019 relative to grazing treatments (NG – not grazed; MRG – moderate rotationally grazed; UHD – ultra-high density rotationally grazed). The experiment was conducted from 2017–2019 to assess the influence of cattle grazing density on soil health at the University of Wyoming's James C. Hageman Sustainable Agricultural Research and Extension Center (SAREC) facility in Lingle, Wyoming, USA

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rate in 2017 was significantly lower than in 2018 and 2019 ( $P = 0.0041$ ; Figure 3). Within the year, there were no stocking rate differences for treatments for any of the years (all  $P$ -values  $> 0.05$ ; Figure 3). Prior to grazing each year, the vegetation visual obstruction was  $10.7 (\pm 2.0)$  cm in 2017,  $12.2 (\pm 0.80)$  cm in 2018, and  $14.01 (\pm 1.25)$  cm in 2019, and there were no differences in vegetation structure relative to treatment (all  $P$ -values  $> 0.05$ ; Figure 4A). After

grazing each year, vegetation structure was lower for the two grazed treatments when compared to the ungrazed control as expected (all  $P$ -values  $< 0.05$ ; Figure 4B). The vegetation visual obstruction in grazed treatments ranged from 39% to 59% (mean =  $48\% (\pm 3.7)$  of the NG treatment, which corresponds with the 50% grazing utilisation target.

**Soil surface temperature, litter, and plant cover.** Treatment was found to have no consistent effects

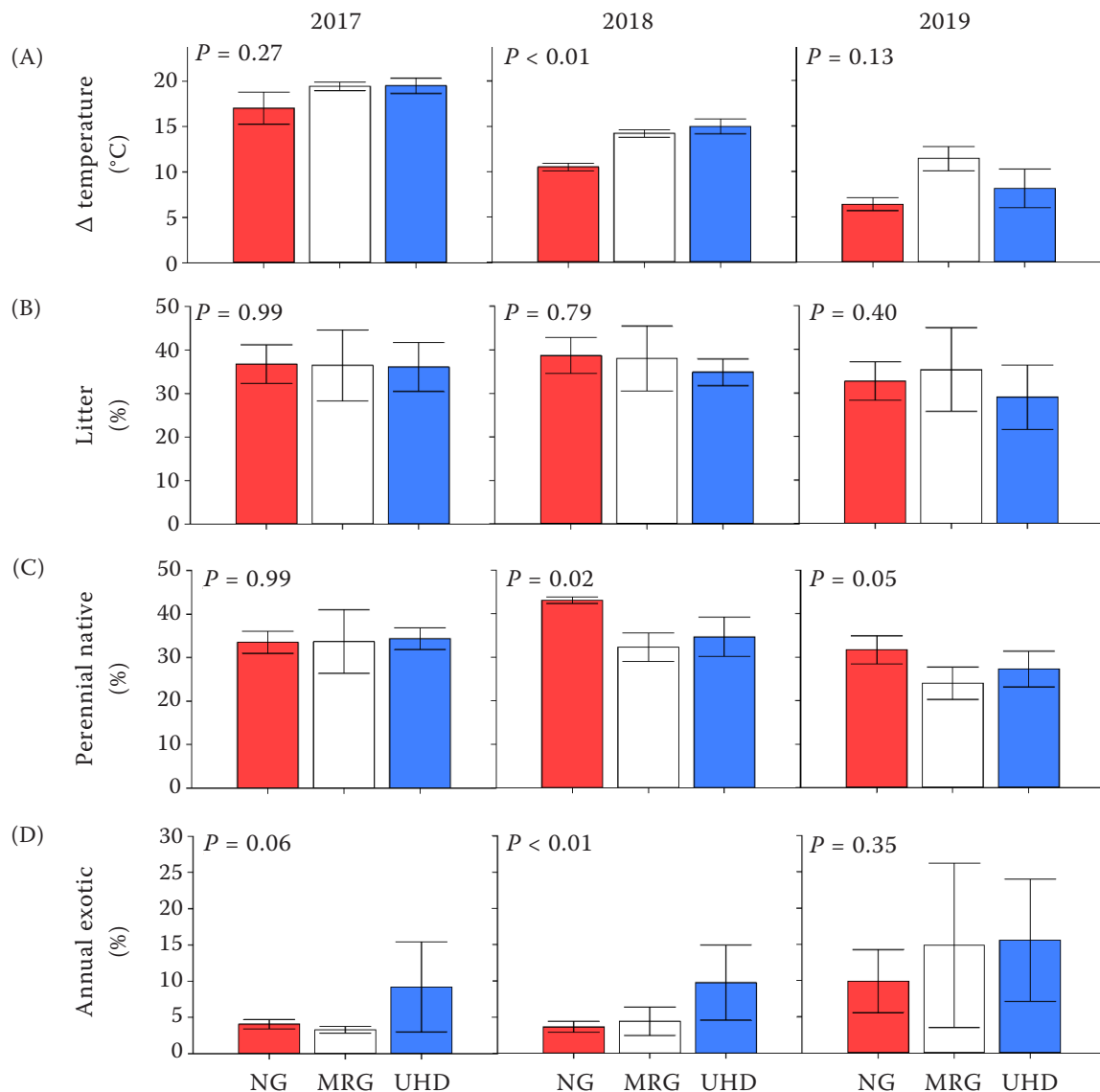


Figure 5. Ground surface temperature and plant cover classes ((A)  $\Delta$  temperature; (B) litter estimates; (C) perennial native estimates, and (D) annual exotic) measured using a  $20 \times 50$  cm quadrat and Daubenmire cover classes (Daubenmire 1959) at the same points along the same transect as vegetation visual obstruction readings) sampled after grazing on 8 July 2017, 8 July 2018, and 30 June 2019 relative to grazing treatments (NG – not grazed; MRG – moderate rotationally grazed; UHD – ultra-high density rotationally grazed). The experiment was conducted from 2017–2019 to assess the influence of cattle grazing density on soil health at the University of Wyoming’s James C. Hageman Sustainable Agricultural Research and Extension Center (SAREC) facility in Lingle, Wyoming, USA



across years on any of the soil/forage cover response variables (Figures 5A–D). Interestingly, the 2018 post-grazing mean  $\Delta$  temperature  $^{\circ}\text{C}$  was significantly greater in the MRG and UHD treatments ( $14.2 \pm 0.4$   $^{\circ}\text{C}$  and  $15.0 \pm 0.8$   $^{\circ}\text{C}$ , respectively) compared to the NG treatment that had a mean  $\Delta$  temperature  $^{\circ}\text{C}$  of  $10.5 \pm 0.4$   $^{\circ}\text{C}$  post-grazing ( $P = 0.0004$ ), 2018 pre-grazing mean perennial native cover estimates which were greater in the NG treatment ( $43.1 \pm 2.4$  %) compared to the similar MRG ( $32.3 \pm 3.2\%$ ) and UHD treatments ( $34.7 \pm 2.9\%$ ) ( $P = 0.02$ ), and 2018 pre-grazing mean annual exotic cover estimates which were greater in the UHD treatment ( $9.8 \pm 3.3\%$ ) compared to the similar MRG ( $4.5 \pm 0.9\%$ ) and NG treatments ( $3.7 \pm 0.7\%$ ) ( $P = 0.02$ ) (Figure 5). The main annual exotic species was *Bromus tectorum*. Litter cover did not differ by treatment in any of the years (Figure 5B), and bare ground was not different for any of the years (data not shown).

**Soil organic matter, organic carbon, and chemistry.** There were no significant grazing treatment effects for any of the soil chemistry variables (all  $P$ -values  $> 0.05$ ) with the exception of zinc (Table 3), however, sampling interval was significant ( $P < 0.05$ ) for all grazing treatments for 8 of the soil chemistry variables (copper, iron, magnesium, nitrate, available N, organic N release, phosphorous, and zinc), for grazed treatments only for 2 soil chemistry variables (sodium and sulfate), for the ungrazed control only for 1 soil chemistry variable (pH), and for the UHD grazing treatment only for 1 soil chemistry variable (boron). Means and treatment effects are presented in Table 3, and sampling interval effects within treatment are presented in Table 4.

**Soil microbiology.** There were no significant grazing treatment effects for any of the soil biological variables post-grazing (all  $P$ -values  $> 0.05$ ), however, sampling interval was significant ( $P < 0.05$ ) for all grazing treatments for 2 of the soil biological variables (respiration and the soil health calculation), for both grazed treatments only none were significant, for the ungrazed control only for 4 soil biological variables (gram (+) bacteria %, gram (–) bacteria%, gram (+):(–) bacteria ratio, and water extracted organic C [WEOC]), and for the UHD grazing treatment only for 4 soil biological variables (protozoa biomass, protozoa %, predator:prey ratio (Protozoa: Bacteria ratio), and functional group diversity index. Means and treatment effects are presented in Table 5, and sampling interval effects within treatment are presented in Table 6.

**Constrained ordination.** In the soil chemistry-constrained ordination, the first axis and all axes combined were significant (both  $P$ -values  $< 0.01$ ; Figure 6A). The first axis had an eigenvalue of 0.2892 and explained 52.95% of the fit variation, and the second axis had an eigenvalue of 0.2215 and explained an additional 40.57% of the fit variation. The first axis has a sampling interval effect with the 6-week post-grazing sampling in 2019 to the right of the biplot and the other sampling intervals to the left. In addition, there is spatial separation of the centroids for both grazing treatments compared to the NG treatment. The first axis is explained by nitrogen dynamics and specifically the organic N reserve, organic N release, and ammonium, while the second axis is explained by nitrate, pH, boron, zinc, and salts (Figure 6A).

In the soil microbiology-constrained ordination, the first axis and all axes combined were significant (both  $P$ -values  $< 0.02$ ; Figure 6B). The first axis had an eigenvalue of 0.2073 and explained 79.20% of the fit variation, and the second axis had an eigenvalue of 0.0352 and explained an additional 13.46% of the fit variation. The first axis has a sampling interval effect with the both 2019 post-grazing sampling centroids to the left of the biplot and the 2017 sampling centroid to the right. In addition, there is spatial separation of the centroids for all treatments. The first axis is explained by the fungi:bacteria ratio, the predator:prey ratio,  $\text{H}_2\text{O}$  organic C, the mono:poly ratio, and gram (+) bacteria, while the second axis is explained by arbuscular mycorrhiza fungi, the organic C:N ratio, and gram (–) bacteria (Figure 6B).

**Precipitation and temperature.** Regarding precipitation, 2017 was the driest year and 2019 the wettest year based on the cumulative precipitation for these four months, with 114.3 mm in 2017, 157.2 mm in 2018, and 197.0 mm in 2019 (Figure 7). Regarding temperature, 2017 was the warmest year, and 2019 was the coolest year based on the mean temperature for these four months, with 19.9  $^{\circ}\text{C}$  in 2017, 19.7  $^{\circ}\text{C}$  in 2018, and 19.5  $^{\circ}\text{C}$  in 2019 (Figure 7). From a monthly perspective, the final year of sampling (2019) had the wettest July and August, the coolest June and July, and the hottest August and September of the months in the study. Based on the results above, it does not appear that extremely anomalous precipitation may have driven results; however, relative responses of some variables could be explained by the drier and warmer conditions at the beginning of the experiment as opposed to the wetter and cooler conditions at the end.

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Table 3. Soil chemical response variables at pre- (2017) and post-grazing (2019 measured 1 week and 6 weeks after grazing) sampling intervals

Soil chemical variable	2017 pre-grazing			2019 1 week post-grazing			2019 6 weeks post-grazing		
	NG	MRG	UHD	NG	MRG	UHD	NG	MRG	UHD
Carbon (organic C %)	1.40 ± 0.08	1.42 ± 0.07	1.40 ± 0.10	1.33 ± 0.10	1.29 ± 0.05	1.44 ± 0.12	1.36 ± 0.09	1.34 ± 0.07	1.45 ± 0.11
Organic matter %	3.28 ± 0.18	3.50 ± 0.23	3.58 ± 0.26	3.38 ± 0.17	3.23 ± 0.13	3.38 ± 0.21	3.45 ± 0.18	3.75 ± 0.17	3.55 ± 0.18
pH	7.8 ± 0.1	7.7 ± 0.1	7.8 ± 0.1	8.3 ± 0.1	8.1 ± 0.2	8.2 ± 0.2	7.9 ± 0.1	7.8 ± 0.1	7.9 ± 0.1
Salts	0.14 ± 0.02	0.12 ± 0.01	0.13 ± 0.01	0.09 ± 0.01	0.09 ± 0.01	0.08 ± 0.01	0.18 ± 0.06	0.12 ± 0.03	0.10 ± 0.02
Cation exchange capacity (CEC)	18.3 ± 0.6	17.2 ± 1.3	18.0 ± 0.8	17.5 ± 1.3	17.3 ± 2.0	17.0 ± 1.1	16.7 ± 0.4	17.0 ± 1.6	16.3 ± 1.3
Ammonium	<b>1.8 ± 0.3</b>	<b>3.0 ± 0.3</b>	<b>2.0 ± 0.3</b>	1.1 ± 0.1	1.4 ± 0.2	1.6 ± 0.3	0.1 ± 0.0	0.7 ± 0.2	0.7 ± 0.3
Boron	<b>0.42 ± 0.01</b>	<b>0.45 ± 0.03</b>	<b>0.48 ± 0.03</b>	0.40 ± 0.03	0.37 ± 0.01	0.40 ± 0.02	0.43 ± 0.05	0.46 ± 0.02	0.44 ± 0.03
Calcium	3 111 ± 119	2 887 ± 278	3 065 ± 201	3 046 ± 257	2 991 ± 400	2 951 ± 249	2 849 ± 97	2 902 ± 339	2 783 ± 263
Copper	0.24 ± 0.01	0.26 ± 0.01	0.24 ± 0.01	0.15 ± 0.02	0.15 ± 0.01	0.15 ± 0.01	0.16 ± 0.01	0.21 ± 0.01	0.15 ± 0.02
Iron	2.9 ± 0.2	3.2 ± 0.5	3.0 ± 0.4	1.8 ± 0.5	1.6 ± 0.3	1.5 ± 0.5	1.7 ± 0.2	1.9 ± 0.3	1.6 ± 0.4
Magnesium	211 ± 5	210 ± 11	207 ± 20	177 ± 6	178 ± 9	170 ± 18	193 ± 4	197 ± 6	181 ± 15
Nitrate	0.10 ± 0.00	0.14 ± 0.03	0.13 ± 0.03	2.17 ± 0.53	2.45 ± 0.30	2.55 ± 0.28	0.52 ± 0.06	0.51 ± 0.10	0.84 ± 0.18
Nitrogen (total N)	1 392 ± 63	1 454 ± 61	1 450 ± 86	1 456 ± 142	1 407 ± 97	1 481 ± 104	1 338 ± 51	1 371 ± 55	1 446 ± 89
Nitrogen (available N Haney)	20.4 ± 1.7	23.1 ± 1.3	24.2 ± 1.9	8.6 ± 1.4	10.0 ± 1.2	9.6 ± 1.1	11.4 ± 1.9	14.9 ± 2.4	15.7 ± 1.9
Nitrogen (organic N release Haney)	7.9 ± 0.9	9.2 ± 0.9	8.8 ± 1.0	6.1 ± 1.1	6.1 ± 0.7	6.1 ± 0.6	2.9 ± 0.9	3.2 ± 1.2	4.2 ± 1.0
Nitrogen (organic N reserve Haney)	0.8 ± 0.8	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 0.4	0.6 ± 0.4	0.3 ± 0.2	1.1 ± 0.8	0.9 ± 0.3	1.4 ± 0.5
Phosphorous	9.2 ± 1.2	9.8 ± 0.5	10.8 ± 1.4	4.1 ± 0.2	3.9 ± 0.1	4.4 ± 0.3	3.2 ± 0.3	3.7 ± 0.4	4.4 ± 0.4
Phosphorous (available P Haney)	33.4 ± 9.6	52.4 ± 13.5	49.4 ± 13.2	25.8 ± 5.9	32.8 ± 13.7	39.5 ± 14.9	49.8 ± 11.7	50.6 ± 16.1	59.7 ± 18.5
Potassium	369 ± 24	393 ± 35	373 ± 45	301 ± 27	329 ± 25	288 ± 21	301 ± 18	320 ± 17	320 ± 26
Potassium (available K Haney)	137 ± 12	146 ± 21	132 ± 21	143 ± 16	162 ± 22	130 ± 11	143 ± 18	156 ± 13	155 ± 11
Sodium	6.0 ± 1.1	5.5 ± 1.2	5.8 ± 1.1	5.3 ± 0.6	5.0 ± 0.4	4.8 ± 0.3	13.0 ± 4.4	9.5 ± 1.2	10.3 ± 1.3
Sulfate	6.3 ± 0.5	6.5 ± 1.0	5.5 ± 0.6	4.7 ± 0.3	3.9 ± 0.5	3.9 ± 0.5	33.1 ± 21.9	13.7 ± 3.3	17.9 ± 5.2
Zinc	0.29 ± 0.02	0.32 ± 0.04	0.28 ± 0.03	0.17 ± 0.02	0.14 ± 0.01	0.17 ± 0.02	<b>0.20 ± 0.02</b>	<b>0.22 ± 0.03</b>	<b>0.27 ± 0.04</b>

Means (± standard error) and treatment *P*-values are presented. Treatments were: NG – not grazed; MRG – moderate rotationally grazed; UHD – ultra-high density rotationally grazed using *Bos taurus* cattle in a northern mixed-grass prairie near Lingle, Wyoming, USA. Significantly different means are bolded and shaded. All units are ppm, except salts are in mmho/cm, CEC is the sum of cations mol/100 g, and available N,P, and K are lbs/ac

Table 4. Significance of treatment and sampling interval (*P*-values) for soil chemical responses within treatment across the study period (2017–2019)

Soil chemical variable	Treatment effect ( <i>P</i> -value)			Sampling interval ( <i>P</i> -value)			Sampling interval effect
	2017 Pre Grazing	2019 1 week post	2019 6 week post	NG	MRG	UHD	
Carbon (organic C %)	0.8114	0.2351	0.4731	0.6628	0.24	0.8963	
Organic matter %	0.4293	0.4879	0.5078	0.5869	0.1143	0.7444	
pH	0.8143	0.6917	0.3125	<b>0.0003</b>	0.1683	0.1126	highest in 2019-1w
Salts	0.8432	0.317	0.2157	0.166	0.4455	0.0994	
Cation exchange capacity (CEC)	0.7665	0.9171	0.8967	0.356	0.9507	0.3349	
Ammonium	<b>0.0317</b>	0.3355	0.1241	<b>0.0007</b>	<b>0.0015</b>	0.1027	highest in 2017
Boron	0.0893	0.6802	0.8199	0.7979	0.109	<b>0.0419</b>	highest in 2017 and 2019-6w
Calcium	0.7662	0.9374	0.9324	0.4472	0.8332	0.4715	
Copper	0.3909	0.9059	0.0905	<b>0.0003</b>	<b>0.0013</b>	<b>0.0085</b>	highest for all treatments in 2017
Iron	0.6611	0.8993	0.8196	<b>0.026</b>	<b>0.0027</b>	<b>0.0004</b>	highest for all treatments in 2017
Magnesium	0.9556	0.8722	0.4985	<b>0.0005</b>	<b>0.0134</b>	<b>0.0464</b>	highest in 2017; lowest in 2019-1w
Nitrate	0.3097	0.7863	0.0903	<b>0.0083</b>	<b>0.0003</b>	<b>0.0002</b>	highest in 2019-1w; lowest in 2017
Nitrogen (total N)	0.6122	0.8491	0.3041	0.3679	0.5693	0.9039	
Nitrogen (available N Haney)	0.2725	0.7304	0.1442	<b>0.0021</b>	<b>0.0009</b>	<b>0.0026</b>	highest in 2017; lowest in 2019-1w
Nitrogen (organic N release Haney)	0.4255	0.9997	0.437	<b>0.0039</b>	<b>0.0007</b>	<b>0.0128</b>	highest in 2017; lowest in 2019-6w
Nitrogen (organic N reserve Haney)	0.4219	0.502	0.6961	0.8877	0.0947	<b>0.023</b>	highest in 2019-6w
Phosphorous	0.5888	0.425	0.0616	<b>0.002</b>	<b>&lt; 0.0001</b>	<b>0.0053</b>	highest for all treatments in 2017
Phosphorous (available P Haney)	0.4905	0.4964	0.8209	0.081	0.1238	0.1472	
Potassium	0.7049	0.4842	0.7563	<b>0.0134</b>	0.074	<b>0.0358</b>	highest in 2017
Potassium (available K Haney)	0.6442	0.3846	0.79	0.8587	0.7058	0.1094	
Sodium	0.6699	0.6141	0.4847	0.134	<b>0.0465</b>	<b>0.0268</b>	highest in 2019-6w
Sulfate	0.2093	0.4106	0.5237	0.2719	<b>0.0437</b>	<b>0.0413</b>	highest in 2019-6w
Zinc	0.5094	0.3309	<b>0.0131</b>	<b>&lt; 0.0001</b>	<b>0.0114</b>	<b>0.0317</b>	highest in 2017; lowest in 2019-1w

Treatments were: NG – not grazed; MRG – moderate rotationally grazed; UHD – ultra-high density rotationally grazed using *Bos taurus* cattle in a northern mixed-grass prairie near Lingle, Wyoming, USA. Significantly different means are bolded and shaded. All units are ppm, except salts are in mmho/cm, CEC is the sum of cations mol/100 g, and available N, P, and K are lbs/ac

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Table 5. Soil microbiological response variables at pre- (2017) and post-grazing (2019 measured 1 week and 6 weeks after grazing) sampling intervals

Soil biological variable	2017 pre-grazing			2019 1 week post-grazing			2019 6 weeks post-grazing		
	NG	MRG	UHD	NG	MRG	UHD	NG	MRG	UHD
Actinomycetes biomass	257 ± 29	238 ± 17	327 ± 34	331 ± 50	302 ± 20	330 ± 35	323 ± 33	371 ± 37	357 ± 14
Actinomycetes %	7.3 ± 0.9	8.5 ± 1.1	8.2 ± 1.0	8.7 ± 0.4	8.4 ± 0.4	9.9 ± 0.4	8.8 ± 0.2	10.0 ± 0.5	8.7 ± 0.5
Arbuscular mycorrhiza fungi (AMF) biomass	<b>125 ± 22</b>	<b>104 ± 11</b>	<b>159 ± 13</b>						
Arbuscular mycorrhiza fungi (AMF) %	3.4 ± 0.5	3.8 ± 0.7	4.1 ± 0.7	5.1 ± 0.6	4.2 ± 0.4	5.4 ± 0.3	5.1 ± 0.4	5.2 ± 0.7	4.5 ± 0.1
Saprophytes biomass	431 ± 104	338 ± 67	515 ± 45	336 ± 90	236 ± 35	263 ± 97	338 ± 98	383 ± 122	383 ± 58
Saprophytes %	11.1 ± 0.8	11.6 ± 2.0	13.0 ± 1.7	8.6 ± 1.4	6.6 ± 0.9	7.2 ± 1.8	8.7 ± 1.3	9.3 ± 2.6	9.0 ± 0.8
Gram positive (+) bacteria biomass	712 ± 71	686 ± 30	855 ± 97	978 ± 147	953 ± 77	933 ± 54	1 028 ± 92	1 073 ± 75	1 113 ± 57
Gram positive (+) bacteria %	20.4 ± 2.6	24.4 ± 2.7	21.1 ± 2.1	25.8 ± 0.8	26.5 ± 0.8	28.7 ± 2.3	28.2 ± 1.4	29.4 ± 2.6	26.8 ± 0.9
Gram negative (–) bacteria biomass	787 ± 174	590 ± 86	908 ± 142	833 ± 103	744 ± 65	710 ± 115	653 ± 105	704 ± 157	905 ± 68
Gram negative (–) bacteria %	20.5 ± 1.1	20.3 ± 2.0	21.8 ± 1.3	22.2 ± 0.5	20.8 ± 1.7	21.0 ± 1.1	17.5 ± 0.7	17.9 ± 2.6	21.8 ± 0.9
Protozoa biomass	47 ± 14	29 ± 9	65 ± 8	25 ± 13	14 ± 4	9 ± 3	22 ± 10	42 ± 5	21 ± 5
Protozoa %	1.2 ± 0.2	1.0 ± 0.4	1.6 ± 0.2	0.6 ± 0.3	0.4 ± 0.1	0.2 ± 0.1	0.5 ± 0.2	1.0 ± 0.1	0.5 ± 0.1
Bacteria biomass (total)	1 498 ± 236	1 275 ± 74	1 762 ± 238	1 810 ± 250	1 697 ± 131	1 643 ± 163	1 681 ± 192	1 777 ± 220	2 017 ± 123
Bacteria %	40.9 ± 2.3	44.7 ± 2.8	42.9 ± 3.3	48.0 ± 1.0	47.3 ± 2.3	49.6 ± 1.5	45.7 ± 1.2	47.3 ± 1.0	48.6 ± 1.7
Fungi biomass (total)	556 ± 121	442 ± 73	673 ± 57	530 ± 127	385 ± 46	411 ± 149	527 ± 130	587 ± 167	570 ± 72
Fungi %	14.5 ± 1.0	15.4 ± 2.5	17.0 ± 2.4	13.7 ± 1.9	10.8 ± 1.2	11.3 ± 3.0	13.8 ± 1.6	14.6 ± 3.3	13.5 ± 0.7
Undifferentiated biomass	1 651 ± 383	1 167 ± 274	1 814 ± 623	1 407 ± 171	1 497 ± 167	1 288 ± 130	1 466 ± 158	1 374 ± 140	1 563 ± 147
Undifferentiated %	43.4 ± 2.7	38.8 ± 5.0	38.4 ± 5.9	37.7 ± 2.9	41.5 ± 3.5	38.9 ± 2.0	40.0 ± 1.5	37.4 ± 3.5	37.4 ± 0.9
Phospholipid-derived fatty acids biomass (total)	3 752 ± 732	2 913 ± 362	4 314 ± 920	3 772 ± 517	3 593 ± 230	3 349 ± 431	3 695 ± 473	3 769 ± 503	4 172 ± 330
Fungi:bacteria	0.36 ± 0.03	0.34 ± 0.05	0.39 ± 0.03	0.28 ± 0.04	0.23 ± 0.02	0.23 ± 0.07	0.30 ± 0.04	0.31 ± 0.07	0.28 ± 0.02
Gram (+):gram (–)	1.01 ± 0.17	1.27 ± 0.26	0.96 ± 0.04	1.16 ± 0.04	1.29 ± 0.10	1.40 ± 0.19	1.62 ± 0.12	1.88 ± 0.57	1.24 ± 0.04
Organic carbon:organic nitrogen	<b>14.7 ± 1.1</b>	<b>12.9 ± 0.6</b>	<b>11.1 ± 0.5</b>	13.7 ± 0.7	12.2 ± 1.1	12.5 ± 1.3	15.6 ± 0.5	16.2 ± 1.8	14.6 ± 1.6
Saturated:unsaturated fatty acids	1.23 ± 0.07	1.23 ± 0.08	1.09 ± 0.07	1.37 ± 0.16	1.71 ± 0.30	1.71 ± 0.35	1.66 ± 0.17	1.88 ± 0.66	1.36 ± 0.06
Monounsaturated:polyunsaturated fatty acids	4.9 ± 0.7	5.3 ± 0.8	4.5 ± 0.4	12.5 ± 3.4	12.9 ± 0.7	27.6 ± 13.0	10.5 ± 1.4	17.2 ± 9.5	11.2 ± 2.7
Predator:prey (Protozoa:Bacteria)	0.029 ± 0.006	0.023 ± 0.007	0.038 ± 0.004	0.012 ± 0.005	0.008 ± 0.003	0.005 ± 0.001	0.011 ± 0.004	0.021 ± 0.001	0.010 ± 0.002
Functional group diversity index	1.58 ± 0.03	1.57 ± 0.05	1.64 ± 0.02	1.51 ± 0.03	1.47 ± 0.02	1.43 ± 0.08	1.53 ± 0.02	1.50 ± 0.08	1.50 ± 0.01
Water extractable organic C (WEOC; H <sub>2</sub> O-OC)	127 ± 12	118 ± 11	98 ± 13	91 ± 9	81 ± 3	77 ± 4	80 ± 9	96 ± 7	87 ± 8
Water extracted organic N (WEON; H <sub>2</sub> O-ON)	8.7 ± 0.6	9.2 ± 0.9	8.8 ± 1.0	6.7 ± 0.7	6.8 ± 0.5	6.4 ± 0.5	5.2 ± 0.7	6.1 ± 0.5	6.0 ± 0.2
Respiration CO <sub>2</sub> -C	100 ± 19	102 ± 19	70 ± 19	32 ± 13	30 ± 10	26 ± 7	23 ± 6	25 ± 5	28 ± 9
Soil health calculation	9.1 ± 1.4	10.0 ± 1.6	8.0 ± 1.7	5.6 ± 1.5	5.3 ± 1.0	4.8 ± 0.7	4.4 ± 0.7	5.0 ± 0.6	5.2 ± 0.8

Means (± standard error) and treatment *P*-values are presented. Treatments were: NG – not grazed; MRG – moderate rotationally grazed; UHD – ultra-high density rotationally grazed using *Bos taurus* cattle in a northern mixed-grass prairie near Lingle, Wyoming, USA. Significantly different means are bolded and shaded. All units are ng/g except WEOC and WEON as ppm unless otherwise noted

Table 6. Significance of treatment and sampling interval (*P*-values) for soil biological responses within treatment across the study period (2017–2019)

Soil biological variable	Treatment effect ( <i>P</i> -value)				Sampling interval ( <i>P</i> -value)			Sampling interval effect
	2017 pre-grazing	2019 1 week post	2019 6 week post	2019	NG	MRG	UHD	
Actinomycetes biomass	0.0527	0.8499	0.4727	0.4950	<b>0.0424</b>	0.7497		increased through time
Actinomycetes %	0.7886	0.0879	0.0843	0.1410	0.2659	0.2569		
Arbuscular mycorrhiza fungi (AMF) biomass	<b>0.0216</b>	0.2233	0.9156	0.4100	0.1116	0.4817		
Arbuscular mycorrhiza fungi (AMF) %	0.813	0.176	0.5207	0.0586	0.0870	0.2183		
Saprophytes biomass	0.3837	0.6759	0.9191	0.8081	0.5261	0.186		
Saprophytes %	0.7788	0.5919	0.8717	0.4670	0.4887	0.0922		
Gram positive (+) bacteria biomass	0.3238	0.9403	0.5075	0.2541	<b>0.0184</b>	0.1716		increased through time
Gram positive (+) bacteria %	0.633	0.3273	0.5976	<b>0.0470</b>	0.4615	0.0851		lowest in 2017; highest in 2019-6w
Gram negative (-) bacteria biomass	0.4018	0.718	0.1064	0.7014	0.7068	0.5014		
Gram negative (-) bacteria %	0.7354	0.6777	0.1614	<b>0.0031</b>	0.5969	0.6282		highest in 2017 and 2019-1w
Protozoa biomass	0.1117	0.42	0.1841	0.4614	0.0530	<b>0.0015</b>		highest in 2017
Protozoa %	0.4293	0.7957	0.1601	0.4100	0.1585	<b>0.0039</b>		highest in 2017
Bacteria biomass (total)	0.3632	0.8272	0.1824	0.6372	0.0974	0.3697		highest in 2017
Bacteria %	0.7281	0.6083	0.4137	0.0539	0.6506	0.1763		
Fungi biomass (total)	0.2804	0.6945	0.9355	0.9889	0.4791	0.3429		
Fungi %	0.7731	0.6544	0.9822	0.9071	0.5197	0.2611		
Undifferentiated biomass	0.5917	0.653	0.6764	0.7903	0.5306	0.6301		
Undifferentiated %	0.6774	0.6269	0.4102	0.3349	0.6314	0.9015		
Phospholipid-derived fatty acids biomass (total)	0.41	0.7709	0.7225	0.9953	0.2952	0.515		
Fungi:bacteria	0.6618	0.5966	0.9163	0.4911	0.2557	0.1057		
Gram (+):gram (-)	0.5331	0.4209	0.3593	<b>0.0104</b>	0.5001	0.0821		highest in 2019-6w
Organic carbon:organic nitrogen	<b>0.0424</b>	0.3175	0.7197	0.2428	0.0912	0.1785		
Saturated:unsaturated fatty acids	0.3892	0.6307	0.5800	0.2484	0.5552	0.1195		
Monounsaturated:polyunsaturated fatty acids	0.6951	0.3891	0.6970	0.1475	0.3744	0.2019		
Predator:prey (Protozoa:bacteria)	0.2424	0.4255	0.1096	0.1657	0.0897	<b>0.0012</b>		highest in 2017
Functional group diversity index	0.3996	0.6017	0.9240	0.2847	0.4103	<b>0.0419</b>		highest in 2017
Water extractable organic C (WEOC; H <sub>2</sub> O-OC)	0.1298	0.2483	0.0647	<b>0.0414</b>	0.0706	0.4181		highest in 2017
Water extracted organic N (WEON; H <sub>2</sub> O-ON)	0.8215	0.8939	0.5199	<b>0.0078</b>	<b>0.0131</b>	0.0551		highest for all treatments in 2017
Respiration CO <sub>2</sub> -C	0.1413	0.9306	0.7048	<b>0.0037</b>	<b>0.0007</b>	<b>0.0132</b>		highest for all treatments in 2017
Soil health calculation	0.5119	0.8835	0.5408	<b>0.0106</b>	<b>0.0044</b>	<b>0.0381</b>		highest for all treatments in 2017

Treatments were: NG – not grazed; MRG – moderate rotationally grazed; UHD – ultra-high density rotationally grazed using *Bos taurus* cattle in a northern mixed-grass prairie near Lingle, Wyoming, USA. Significantly different means are bolded and shaded. All units are ng/g except WEOC and WEON as ppm unless otherwise noted



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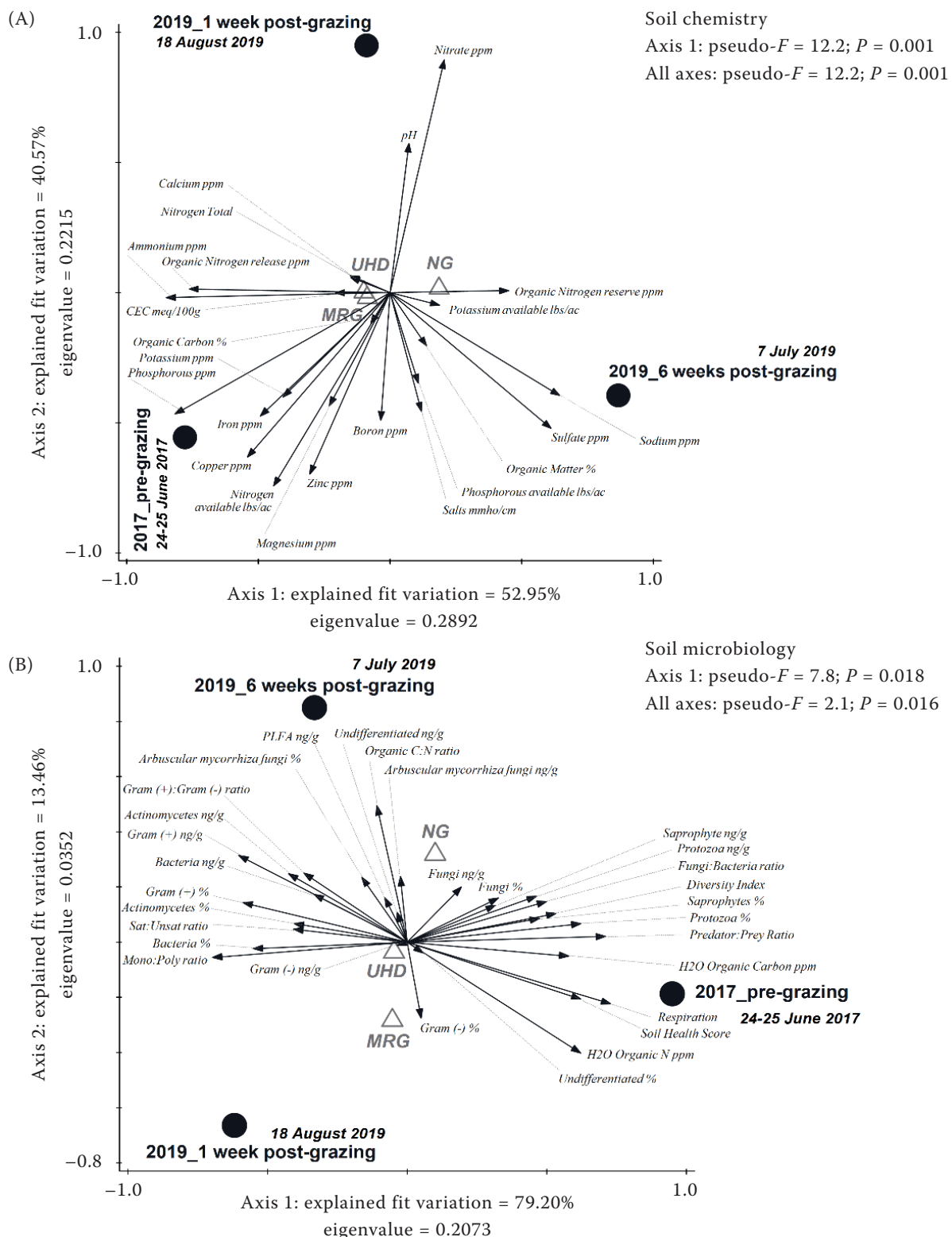


Figure 6. Constrained ordination using redundancy analysis (RDA) of (A) 23 soil chemical responses and (B) 30 soil biological responses measured in 2017 (pre-grazing) and 2019 (post-grazing week 1 and week 6) relative to grazing treatments (NG – not grazed; MRG – moderate rotationally grazed; UHD – ultra-high density rotationally grazed). The experiment was conducted from 2017–2019 to assess the influence of cattle grazing density on soil health at the University of Wyoming's James C. Hageman Sustainable Agricultural Research and Extension Center (SAREC) facility in Lingle, Wyoming, USA

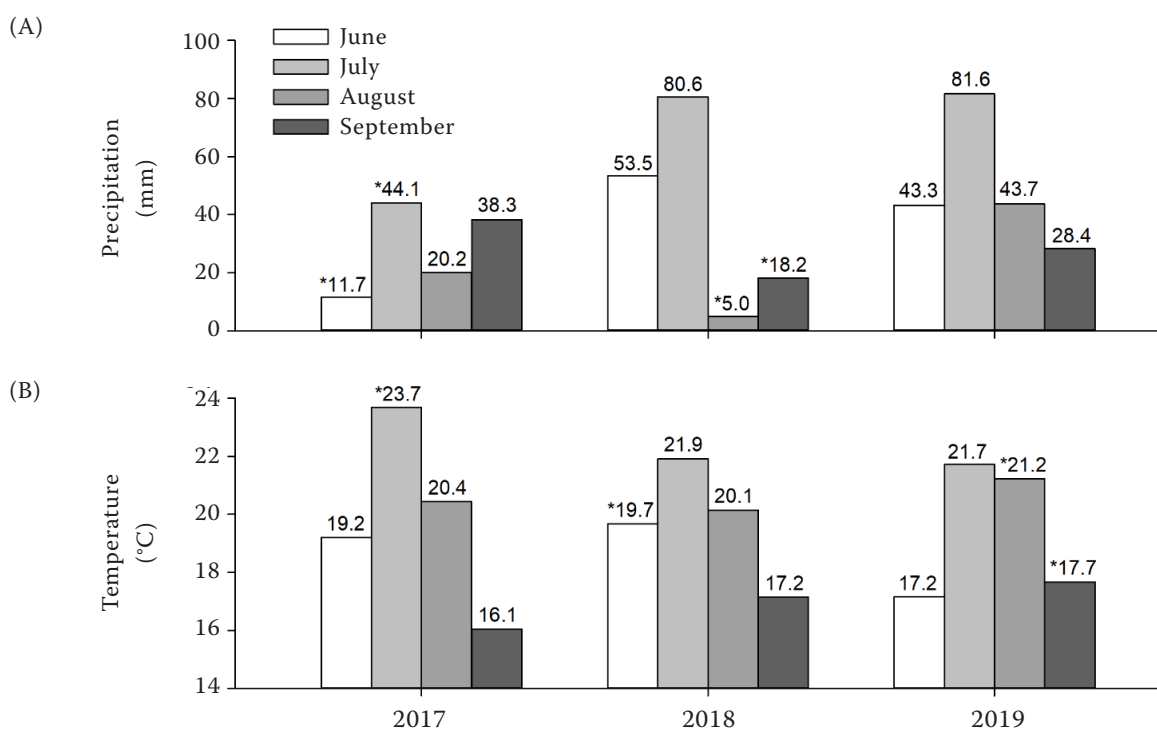


Figure 7. Monthly (A) cumulative precipitation and (B) mean temperature for June, July, August, and September for each of the three years of the experiment (2017, 2018, and 2019) from the PRISM weather data platform, which derives estimates at a 4 km resolution using the AN18d data set and extrapolation method that uses digital elevation models from ~10 000 weather stations weighted relative to a physiographic similarity. \*indicate the driest month or hottest month for the period of study

## DISCUSSION

A multitude of grazing studies have resulted in claims that animal rotation, stocking rate, density, or grazing exclusion may enhance soil properties (Teague et al. 2011, 2013, Steffens et al. 2011, Wiesmeier et al. 2019), but with changes to forage species functional groups (Frank et al. 1995, Reeder and Schuman 2002, Ingram et al. 2008). However, in our study, we found minimal changes for a broad suite of soil and ground cover response variables relative to grazing but a strong influence of sampling timing (Badgery et al. 2017, Van Syoc et al. 2022). Importantly, stocking rate and vegetation structure outcomes in our two contrasting grazing treatments were similar as time was allowed to vary to achieve similar utilisation levels while animal density was different (Scasta et al. 2023). Our findings of no response of soil organic carbon to grazing were similar to Henderson et al. (2004), Li et al. (2012), Shrestha and Stahl (2008), Derner et al. (2018), and Briske et al. (2008, 2011) but in contrast with those of Teague et al. (2011). Importantly, the context of the study site was an intact native prairie with initial values that did not

change relative to treatment or sampling interval, indicating "Very Good" soil health rating including mean total PLFA biomass of 3 703 ng/g, mean functional group diversity of 1.53, mean organic C: organic N of 13.7, and the fungi:bacteria ratio which is an indicator of community composition (Ward Guide 2021). Similarly, the lack of change relative to treatment or sampling interval in the saturated: unsaturated fatty acid ratio is insightful because this is an indicator of stress and community activity where stressed soil communities will increase the proportion of unsaturated fatty acids (Norris et al. 2023). Thus, the lack of any discernible directional (negative or positive) or magnitudinal change relative to the different grazing treatments on soil health properties, coupled with the information above, suggests that this northern mixed-grass prairie may be considered highly functioning and resilient to the rational intensification of animal density (Seó et al. 2017).

Similar to Banerjee et al. (2000) and Raiesi and Riahi (2014), who found little difference in soil biochemical properties in grazed non-woody rangelands, treatment had no effect in the northern mixed-grass

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prairie site in our study. When 2019 post-grazing soil analyses on AMF biomass and organic C:N were analysed, ((both were found to be good indicators of soil health practices/management (Bedini et al. 2007, Hagny 2018))), the effect of the three grazing treatments were insignificant. Our results of little response of soil biological properties to grazing were similar to Kieft (1994). These results differ from many published studies that found soil biological response variables were enhanced by grazing (Song et al. 2008, Teague et al. 2011), the removal of grazing (Bai et al. 2013), negatively affected by grazing (Holt 1997), or increased soil respiration but decreased microbial biomass (Zhou et al. 2017). Our non-significant treatment results could be partly explained by the variable responses of soil surface temperature, litter, and plant functional groups, which did not differ between treatments after grazing all years. In regards to soil chemical responses, grazing has been shown to have a minimal impact as compared to catastrophic disturbances such as fire or weather and subsequently, inter- and intra-annual weather patterns in our study seemed to be the primary driver (Helliwell et al. 2010, Boudjabi and Chenchouni 2022).

The results reported herein have application for livestock producers on how environmental factors such as temperature and moisture at the time of sampling can lead to false conclusions about treatment effect on response variables (Dormaar et al. 1977, Banerjee et al. 2000, Segoli et al. 2015) if soil monitoring is used as a management indicator. For example, some metrics are more stable and consistent through time, such as soil organic carbon, but any changes can be slow relative to management expectations. In contrast, many soil measurement metrics can fluctuate relative to temperature and soil moisture, such as respiration and may fluctuate independently of management. This temporal aspect of soil response to management is critical to quantify because changes in soil properties may take decades to detect with different grazing management treatments (Liebig et al. 2006, Derner and Schuman 2007). From a range management perspective, stocking rate, animal distribution, and their relationship to current environmental conditions could be considered the most important rangeland production and conservation tool and need to be placed in such context when a livestock producer is striving to achieve desired outcomes or draw accurate conclusions about grazing management (Briske et al. 2011, Sanderson et al.

2016). For example, the effect of grazing intensity on soil carbon must be contextualised with climate, soil type, and grazing history (Floate 1981, Potter et al. 2001, Eyles et al. 2015, Abdalla et al. 2018), and couched within the appropriate aridity frame of reference (Teague et al. 2011, Teutschnerová et al. 2020). In addition, the importance of developing quantitative baseline information is critical to understanding both storage and accumulation relative to land use history, the environment, and management (Wiesmeier et al. 2019).

For livestock producers to appropriately and accurately assess grazing management and its effects on soil and forage properties, affordable and comprehensive field-derived data must be collected (Gergeni and Scasta 2019) relative to the current proper stocking rate. It is equally important for producers to account for and understand the effect of environmental conditions on sampling results and accurately differentiate between management or environmental outcomes. More regional, replicated, long-term studies (Banerjee et al. 2000, Teague et al. 2011, Teague et al. 2013, Sanderson et al. 2016, Basche and DeLonge 2017, Derner et al. 2018, 2019), an established appropriate baseline (Fernandez et al. 2008, McSherry and Ritchie 2013, Derner et al. 2019), consistent monitoring (Sanderson et al. 2020), similar sampling procedures, soils knowledge (Schuman et al. 1999), and quantitative data on stocking metrics (Allen et al. 2013) are needed to draw accurate conclusions about the effects of grazing on rangeland properties. Only then can the dissemination of grazing information on rangeland soil health become useful to producers. Because the temporal scale of this study could be considered short relative to changes in soil properties in cold, arid steppes (Shrestha and Stahl 2008, Eyles et al. 2015), additional years of data may help to elucidate potential enhancements to soil properties over the long-term which will yield insights for additionality in soil carbon contracts. Finally, because soil organic matter and organic carbon were unaffected by sampling interval suggests that they may be less sensitive to inter- and intra-annual climate and weather variability, rendering them as useful indicators of management effects over longer time scales (Banerjee et al. 2000), particularly for grazing management on rangelands.

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