**Title: Small herbivores have big effects on plant quality and quantity**

**Authors:** Julie Rebh, Ellen A. R. Welti

**Affiliation:** Smithsonian National Zoo and Conservation Biology Institute, Front Royal, VA

**Abstract**

**Introduction**

The amount of energy available to build terrestrial food webs is primarily dependent on both plant production and plant nutritional quality, with both strongly limiting herbivore populations ([Ruyle, 1993](https://www.webpages.uidaho.edu/range456/readings/NUTRITIONAL%20VALUE%20OF%20RANGE%20FORAGE%20FOR%20LIVESTOCK.pdf))([Derner et al, 2017](https://link.springer.com/article/10.1007/s10584-017-2029-6))([Milchunas et al, 2005](https://sci-hub.ru/10.1016/j.agee.2005.06.014))( [He et al, 2022](https://www.cell.com/trends/plant-science/fulltext/S1360-1385(22)00221-7)) ([White, 1978](https://pubmed.ncbi.nlm.nih.gov/28309267/)). Soil chemistry, macro and microclimate, and grazers are key drivers of plant production and quality ([Ohno and Hettiarachchi, 2018](https://sci-hub.ru/10.2134/jeq2018.08.0290)). In particular, there are a number of interesting feedbacks between plants and the effects of herbivores. Generally, grazing is expected to decrease above-ground biomass of grassland plants ([Caiyun et al, 2021](https://bioone.org/journals/journal-of-resources-and-ecology/volume-12/issue-3/j.issn.1674-764x.2021.03.002/Effects-of-Grazing-on-the-Grassland-Vegetation-Community-Characteristics-in/10.5814/j.issn.1674-764x.2021.03.002.full#:~:text=The%20VC%20of%20grassland%20in,the%20typical%20and%20meadow%20steppes.))([Borer et al,2020](https://www.nature.com/articles/s41467-020-19870-y))([An and Li, 2015](https://sci-hub.ru/10.1007/s40333-014-0049-x)). However, a loss of plant biomass through artificial or natural means can lead to compensatory plant growth due to accelerated mineralization of nutrients in the form of organic matter in the immediate vicinity of the plant ([Owen and Wiegart, 1976](https://www.jstor.org/stable/3543467?origin=crossref)). Additionally, plant nutrients, including nitrogen, phosphorus, and potassium tend to increase in plant regrowth following herbivory([Cargill and Jeffries, 1984](https://sci-hub.ru/10.2307/2403437))([Seastedt,1985](https://www.journals.uchicago.edu/doi/10.1086/284437))([Zheng et al, 2012](https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0051750))([Bi et al, 2020](https://sci-hub.ru/10.3390/ijerph17124572)).

This study will fill two key gaps in the literature on plant responses to large grazers. First, few studies examining plant responses to grazers investigate plant micronutrients, which may play a key role in herbivore nutritional needs (Prather et al, 2020). Second, little comparative work has examined responses of ANPP and plant quality to large grazer types in North American grasslands. These different species of grazers have differential impacts on plant biomass and plant quality. In tallgrass prairies , bison grazed sites have lower residual grass biomass as compared to sites that were grazed by cattle ([Towne et al, 2005](https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/04-1958)). Furthermore, grazing by prairie dogs increases plant quality by reducing leaf age and stimulating nitrogen uptake ([Whicker and Detling, 1988](https://sci-hub.ru/10.2307/1310787)). The shift from large roaming herds of bison and massive connected prairie dog colonies across the North American Great Plains to today’s cattle-dominated and disconnected landscapes likely has had strong effects on nutrient cycling, and plant and insect communities.

Here, we investigate drivers of ANPP, and plant chemistry in response to grazing by bison, cattle, and prairie dogs in a shortgrass prairie. We ask the question: What effects do bison, cattle, prairie dog, and insect grazing have on ANPP, and plant chemistry across the growing season? We hypothesize that **H1)** grazing will increase plant quality, with smaller herbivores having larger effects through faster nutrient cycling, **H2)** all grazers will decrease ANPP, and insect herbivory will equal that of large grazer herbivory, and **H3)** plant nutrient content will be greatest in the early season while biomass will peak mid-season.

Grasslands cover >25% of terrestrial Earth ([Pulungan, 2019](https://sci-hub.ru/10.1038/s41598-019-47635-1)), provide critical ecological services including carbon sequestration, erosion control, climate mitigation, and serve as habitat for a diversity of biota ([O’Mara, 2012](https://sci-hub.ru/10.1093/aob/mcs209))([Bengtsson et al, 2019](https://sci-hub.ru/10.1002/ecs2.2582)) ([Wilson and Peter, 1988](https://www.ncbi.nlm.nih.gov/books/NBK219272/)) ([Boval and Dixon, 2012](https://sci-hub.ru/10.1017/s1751731112000304)). However, grasslands are undergoing rapid changes due to human activity. The combination of grasslands’ fertile soil and flat topography has led to a massive conversion of grasslands into row-crop agriculture and rangeland, with 10.09 million acres of grassland in the United States having been converted from native grasslands to crop production in the years 2008-2016 ([Boval and Dixon, 2012](https://sci-hub.ru/10.1017/s1751731112000304))([Lark et al, 2020](https://sci-hub.ru/10.1038/s41467-020-18045-z)). Remaining grasslands are experiencing biodiversity loss (Rosenberg et al, 2019)(Seibold et al, 2019). Ongoing climate change and CO2 fertilization are expected to result in reductions in plant nutritional quality and increases in plant productivity including through woody encroachment (​​Ratajczak, Nippert, and Collins, 2012)(Welti et al, 2020).

**Methods**

The study was conducted in the shortgrass prairie of northeast Montana, within the Northern Great Plains (NGP). The average precipitation is 12.21 inches/year ([Malta, Montana Climate - 59538 Weather, Average Rainfall, and Temperatures](http://www.worldclimate.com/climate/us/montana/malta)) and was approximately 10.45 inches over the growing season of 2022 (June-September). . The dominantsoil type is Harlake Clay **(https://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx)**. Dominant grasses in the study region include the non-native Crested wheatgrass (*Agropyron cristatum*), and natives including Western wheatgrass (*Pascopyrum smithii*), Green needle grass (*Nassella viridula*), Needle-and-thread grass (*Hesperostipa comata*), and Blue grama (*Bouteloua gracilis*). Management areas included in the study were American Prairie (including both deeded lands and areas leased from the Bureau of Land Management), the Charles M Russell National Wildlife Refuge (NWR), and Bowdoin NWR.

*Experimental design*

Our study included 15 sites divided into five grazing treatments (three replicates/treatment): bison grazed, cattle grazed, prairie dog towns within the bison grazed area that were treated with insecticide (henceforth “treated prairie dog towns”), prairie dog towns within the bison grazed area that were not treated with insecticide (henceforth “untreated prairie dog towns), and ungrazed sites. Study site coordinates are provided in Supplementary Table 1. Plant, soil, and grasshopper density sampling was conducted monthly for four months across the growing season in 2022 (June-Sept). Insecticide treatments were applied in treated prairie dog towns for flea and plague mitigation and consisted of 10 years of prior hand applications of deltamethrin (delta dust) into prairie dog burrows, and a 2022 treatment of fipronil grain, applied using a seeder in late July (between our first two and last two sampling periods).

*Sampling methods*

Estimates of aboveground plant biomass were collected using a pasture meter (Bransby and Tainton, 1977). A pasture meter is a non-destructive tool to estimate total above-ground plant biomass. Measurements were taken every 2 m along two east-west oriented 58m transects, 50 m apart, each month at each site. We calibrated pasture meter measurements using 50 1 ㎡ plots across the growing season and sites. To calibrate, we first took a pasture meter reading, then clipped all biomass below where the reading was taken, dried the biomass at 60℃ for 48 hours, weighed the biomass, and regressed pasture meter readings over dry weights to calculate the equation parameters used to estimate dry weights from pasture meter readings (R2 = 0.52).

*Clipping*

Additionally, we collected plant biomass via clipping five 0.1 x 1 m plots at each site. The location of each plot was moved 1 m each month so as not to sample the same area twice. Plants were clipped and sorted into their respective functional groups (litter, live grass, live forbs, and live woody plants). The clippings for each functional group per plot were dried in a drying oven at 60℃ for 48 hours, and the dry weight of each sample was then recorded. Samples were ground into a fine powder and for each site, month, and functional group (excluding litter), ground samples were combined (2g from each of the five plots, as available) and analyzed for elemental chemistry.

*Soil Sampling*

Soil samples were collected simultaneously at the same plot from which plant clippings were collected. Five samples were collected per site for every sampling month, and later the samples for each site for each month were combined and sent out for chemical analysis. Plant and soil elemental chemistry work was conducted at the Cornell Nutrient Analysis Lab (CNAL) using combustion analysis for C and N, and hot plate digestion and inductively coupled plasma atomic emission spectroscopy for metals.

*Grasshopper Densities*

Grasshopper density was estimated once per month at each sample site simultaneously with plant and soil sampling using ring counts. Ring counts were conducted at two 28m transects per site, with transects spaced 70 meters apart from each other and oriented east-west. Each transect included 15 rings, spaced at 5m intervals.

*Statistical Analysis*

To test our first question regarding the effects of all grazers on plant quality, we conducted two piecewise structural equation models (SEMs), for grass and forb chemistry responses. Piecewise SEM was chosen as we were interested in the individual responses of macro and micronutrients, we wished to include soil chemistry as both a driver and a response as allowed for by SEMs, and piecewise SEMs vary from traditional SEMs in that they allow lower numbers of sample collected per tested path (Lefcheck 2015). For forbs, we examined responses of the tissue concentrations of N, P, K, Mg, and Na; for grasses we additionally examined the response of Si, as Si is important as a structural defense in grass tissues. Driver variables in apriori models included the stocking rates of bison and cattle, the presence or absence of prairie dogs and insecticide treatments, the first two axes of a principal component analysis (PCA) of soil chemistry, and sampling month. The soil chemistry PCA had two significant axes when examined using a broken stick model, with the first axis explaining 40% of the variation and correlating negatively with K (r = 0.84), Mg (r = 0.82), and Na (r = 0.74), and the second axis (29% of variation) correlating positively with C (r = 0.91), N (r = 0.92), and P (r = 0.51). Month was initially included as a random variable but this resulted in many singular models; thus we included month as a fixed variable. All response variables except N were log10 transformed to meet assumptions of normal distributions and driver variables were scaled to units of standard deviation. To select for best fitting piecewise SEMs, we removed non-significant driver variables, and added relationships between elements as suggested by tests of directed separation to our apriori models until a minimum AIC was reached. The first soil chemistry PCA axis (corresponding to soil K, Mg, and Na) was not well explained by grazer driver variables, and was excluded from the final model.

To test our second question regarding the response of aboveground plant biomass to the different grazer treatments, we ran a linear mixed model with a response of our estimates of aboveground biomass (pasture measurements translated into g/m^2 using our calibration regression equation), fixed driver variables of stocking rates of bison and cattle, the presence or absence of prairie dogs and insecticide treatments, and a random variable of the identity of a line transect nested within site to account for repeated sampling over time. Biomass was log10 transformed to meet normal distribution assumptions and fixed drivers were scaled to units of standard deviation.

Lastly, to examine changes in aboveground plant biomass and nutrients over the season, we ran a series of models. We predicted that aboveground plant biomass would have a hump shaped-distribution across the season. To test this prediction, we ran a linear mixed model with log10 transformed aboveground biomass as the response variable, a second degree polynomial of sampling month as the fixed effect, and the identity of a line transect nested within site to account for repeated sampling over time. We further examined if this relationship varied with grazer type by running the sample model for data subsetted to individual treatments.

We predicted plant quality would decline over the growing season. To test this prediction, we ran simple linear models using tissue concentrations of elements as response variables and month as the predictor variable. As only one pooled sample per month and site was analyzed for chemistry, we did need to include any corrections for subsampling in this model. We further examined the same responses within individual grazer treatments.

All analyses were run in Program R v. 4.2.2 (XXcitation). R packages used included piecewiseSEM (Lefcheck 2015), vegan (XXXcitation), BiodiversityR (xxxcitation) and lme (XX citation).

**Results**

Prairie dogs had the largest effects on soils and plants, increasing soil C and N, removing aboveground plant biomass, increasing grass quality likely through fertilization, and removing high forage quality forbs. **However, their keystone effects were highly mediated by the presence of insects. Insect effects lead to greater variation and on average doubled soil C (mean = 5.81% ± 2.95 SE on untreated prairie dog towns [UPD]; mean = 2.58% ± 0.79 SE on prairie dog towns with insecticide [IPD]) and N (mean = 0.44% ± 0.21 SE on UPD; mean = 0.22% ± 0.06 SE on IPD)**. Likewise, **in the absence of insects, plant biomass increased across the growing season rather exhibiting the classic hump-shaped pattern, suggesting insect herbivory in the late growing season when many insect species are adults may drive this commonly-observed seasonal response**. Bison and cattle had only weak effects on soil, bison affecting only grass chemistry, and cattle reducing forb N, likely through selective herbivory of high N taxa or individuals.

Grazers had strong effects on plant and soil chemistry as indicated by both our model predicting the tissue concentrations of elements in grasses (Fisher’s C = 63.26, *P* = 0.7), and forbs (Fisher’s C = 53.61, *P* = 0.64) achieved good model fits (non-significant p-values indicate good fits in SEMs; Figs XX and XX, Supplementary Tables XX and XX). **Prairie dogs had the largest effects with increases in soil C and N, grass N and K, and decreases in grass P and forb N and P on prairie dog towns.** Bison had a marginally positive effect on soil C and N, increased grass Mg, decreased grass K and Na, and had no effect on forb chemistry. Cattle had no effect on soil chemistry, increased grass Mg, and decreased forb N. Finally, insecticide application led to decreases in soil C and N, a negative effect on grass Si, and a positive effect on forb N and Na.

**Across all sampling periods, aboveground plant biomass was negatively affected by the presence of prairie dogs** (Est = -0.063 +/- 0.018 SE, t = -3.36, *P* < 0.001) and cattle stocking rate (Est = -0.032 +/- 0.016 SE, t = -2.07, *P* = 0.039), but not by bison stocking rate (Est = -0.02 +/- 0.018 SE, t = -1.09, *P* = 0.27) or the presence of insecticides (Est = -0.0001 +/- 0.016 SE, t = -0.06, *P* = 0.95). Overall, plant biomass has a decidedly hump-shaped pattern across the growing season (second polynomial of month Estimate: -0.83 +/- 0.13 SE, t = -6.18, *P* < 0.001). The hump-shape pattern held in all grazing types, i.e. areas without prairie dogs that were bison grazed (Est: -0.52 +/- 0.13 SE, t = -3.84, *P* < 0.001), cattle grazed (Est: -0.3 +/- 0.1 SE, t = -3.03, *P* = 0.002), ungrazed (Est: -0.39 +/- 0.16 SE, t = -2.45, *P* = 0.014), prairie dog towns without insecticide (Est: -0.31 +/- 0.09 SE, t = -3.3, *P* < 0.001), and prairie dog towns with insecticide (Est: -0.35 +/- 0.16 SE, t = -2.13, *P* = 0.033).

On average across the growing season, aboveground plant biomass (all estimates using dry weights) was reduced compared to ungrazed areas in the presence of prairie dogs by 87.72 g/m², of cattle by 53.59 g/m², of bison by 32.77 g/m², and insects by 11.73 g/m² (contrasting UPD and IPD). While both low, the average stocking rate for cattle (0.027 cattle/acre) was nearly double that of bison (0.015 bison/acre). This calculates to an average reduction of 8,906 kg of per bison and 8030.62 kg per cow. Additionally, considering bison are stocked year-round while cattle are removed during winter months, bison consume more aboveground plant biomass per animal than cattle.

Macronutrients tended to decline across the growing season including N (Est: -0.3 +/- 0.06 SE, t = -5.04, *P* < 0.001), P (Est: -0.07 +/- 0.02 SE, t = -3.77, *P* < 0.001), and K (Est: -0.08 +/- 0.02 SE, t = -3.98, *P* < 0.001). However Na did not change with sampling month (Est: 0.004 +/- 0.0005 SE, t = 0.87, *P* = 0.39), and Si increased with month (Est: 0.41 +/- 0.06 SE, t = 6.28, *P* < 0.001). Within grazing treatments… (this should be a supplemental table)

**Discussion**

Summary of Results. Start the Discussion with a statement or paragraph that summarizes the main results of the study. The last sentence of this section should be a topic sentence that outlines the major points that will be considered in the remainder of the Discussion.

Our findings show…

Summary of Main Results

Throughout the growing season, the impact of grazers on plant productivity and quality as well as soil quality produced variable results. Prairie dogs had a substantial impact on soil and plant nutrients, with increases in soil C and N, grass N and K, and decreases in grass P and forb N and P on prairie dog towns. The absence of insect herbivory, as seen in prairie dog towns that had been treated with insecticide, proved to have the greatest impact on soils and plants, with the prairie dog towns that were untreated with insecticides having double the amount of soil C and N as compared to the treated prairie dog towns. Another key finding is that in the absence of insect herbivory, plant biomass continued to increase across the growing season, suggesting that herbivory by adult insects may be the cause of the hump shaped pattern seen in all other plot types.

Hypothesis 1: **H1)** grazing will increase plant quality, with smaller herbivores having larger effects through faster nutrient cycling,

Grazers did not influence plant quality in a uniform manner. P**rairie dogs had the largest effects with increases in soil C and N, grass N and K, and decreases in grass P and forb N and P on prairie dog towns.** This was supported/refuted by….

Bison had a marginally positive effect on soil C and N, increased grass Mg, decreased grass K and Na, and had no effect on forb chemistry. Other studies found…

Cattle had no effect on soil chemistry, increased grass Mg, and decreased forb N. Other studies found…

Finally, insecticide application led to decreases in soil C and N, a negative effect on grass Si, and a positive effect on forb N and Na. Other studies found…

* Variable, some grazers increased some didnt, varied across plant type as well (forb vs grass)
* Smaller herbivores did have greater impacts, PD and insects

Hypothesis 2: **H2)** all grazers will decrease ANPP, and insect herbivory will equal that of large grazer herbivory,

* Grazers decreased ANPP (PD and cattle) but not bison.
* All grazer types led to hump shaped distribution, only one that didn’t was insecticide treated, which shows that insects would have decreased ANPP

Hypothesis 3: **H3)** plant nutrient content will be greatest in the early season while biomass will peak mid-season.

* Macronutrients tended to decline across the growing season including N, P, and K . However Na did not change with sampling month , and Si increased with month

Wrap up

While grasslands provide important environmental and societal services, they remain one of the most threatened terrestrial ecosystems globally, facing issues such as land use change, the encroachment of invasive species, and increased changes in climate in these regions (Hendrickson et al, 2019)(Miniat et al, 2021)(Leidinger et al, 2017). The short and mixed grass prairies of the Northern Great Plains (NGP) face many of the same threats common to grasslands globally. The NGP is a particularly important region for food security in the United States, containing 218 million acres of farmland, accounting for 23.8% of the total farmland in the country and supporting crops such as corn, wheat, barley, soybeans , and around 21.9% of the national supply of beef cattle (4th National Climate Assessment). This region is especially vulnerable to the impacts of climate change, which is predicted to alter climate patterns through rising temperatures and reduced snowpack. This shift to warm and dry summers has the potential to alter the plant growth of both native plants and croplands in the region (Derner et al, 2016)(Adams et al, 2020). With imminent changes to forage quality and quantity in the NGP due to climate change, this study is an important step towards understanding how the pressures of modern grazing impact the health of the plants and soil in this region.

**Herbivore and Insecticide effects on Plant Nutrients**

Grass

Cattle did not have a strong effect on grass nutrients, only causing increases in grass Mg levels. Prairie dog grazing had a slightly greater impact on grass nutrients, leading to increases in grass N levels, and decreases in grass P levels. Bison grazing had the greatest impact on grass nutrients, leading to increases in grass Mg, and decreases in grass K and Na levels. The impact of Bison on plant quality has been found in other studies, showing an increase in plant quality in areas that have been grazed by Bison ([Geremia et al, 2019](https://www.pnas.org/doi/10.1073/pnas.1913783116))([Joern, 2005](https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/04-0135))([McNaughton, 1984](https://www.jstor.org/stable/2461305)). Our findings showing Bison having no significant impact on N levels differ from past studies which find that Bison grazing increases N mineralization in plants and soil ([Knapp et al, 1999](https://www.jstor.org/stable/10.1525/bisi.1999.49.1.39)) ([Ozment, Welti, Shaffer, Kaspari, 2021](https://onlinelibrary.wiley.com/doi/abs/10.1002/ece3.7435))([Johnson and Matchett, 2001](https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/0012-9658%282001%29082%5B3377%3AFAGRBP%5D2.0.CO%3B2)).

Forbs

Cattle grazing led to decreases in forb N levels. Bison grazing had no impact on forb nutrients. This is thought to be because bison prefer to graze on grasses, and do not typically graze on forbs (source). Prairie dog grazing led to a slight (indirect?) decrease in forb N levels.

**Insecticide**

The presence of insecticide in a plot led to strong decreases in grass Si levels. This is thought to be due to plants not needing to increase their defense mechanisms to protect against insect grazing (source). The presence of insecticide in a plot had strong effects on forb chemistry, leading to increases in forb Na, N, and P levels. (This may suggest that the presence of insects leads to declines in plant quality.) These findings contradict other studies such as [Shen et al, 2013](https://swfrec.ifas.ufl.edu/hlb/database/pdf/5_Shen_13.pdf), which found that insecticide treatment decreased plant nutrient content (Shen et al, 2013). This study is one of the first studies documenting the impacts of insecticide application in a grassland environment, and further studies are needed to elucidate the true impact of these treatments.

**Herbivore and Insecticide effects on ANPP**

All grazers had a negative effect on ANPP. The only site in which a positive trend in ANPP was observed throughout the growing season was in the prairie dog colony that had been treated with insecticide. This suggests that the presence of insects leads to decreases in ANPP (equal to herbivores?).

**Herbivore effects on biomass**

Biomass peaked mid-season for all plots that were grazed by herbivores. The only exception was the prairie dog colony that was treated with insecticide. Grazing led to decreases in biomass throughout the season in all plots except for insecticide treated prairie dog colonies. This finding is consistent with that of Hao, 2019. ([Effects of grazing patterns on grassland biomass and soil environments in China: A meta-analysis - PMC](https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6476490/#:~:text=As%20discussed%20above%2C%20grazing%20can,was%20reduced%20by%20livestock%20feeding)). Other studies have found that biomass decreases as grazing intensity decreases ( [Effects of different intensities of long-term grazing on plant diversity, biomass and carbon stock in alpine shrubland on the Qinghai-Tibetan Plateau - PMC](https://www.ncbi.nlm.nih.gov/pmc/articles/PMC8760858/)). While our findings also show a general trend of grazing decreasing biomass throughout the growing season, the decrease is more severe in bison grazed plots than cattle grazed plots which have a higher stocking density.

**Grass nutrients throughout growing season**

Grass nutrients N decreased throughout the growing season, while Mg and Si increased throughout the growing season. For forbs, N decreased throughout the growing season, while Na increased throughout the growing season.

**Impact on soil**

Our findings show that the impact of grazing on plant quality can not be defined in a singular manner. While large herbivores such as cattle and bison impact plant quality, the impacts vary in significance as well as direction. Smaller herbivores such as prairie dogs and insects seem to have more of an impact on plant quality, but again the directionality and significance varies depending on the nutrient. These findings contradict studies that have shown that

Cattle stocking rates and the presence of prairie dogs decreased ANPP, while bison stocking rates and insecticide did not decrease ANPP. Plant biomass peaked in mid season, and plant quality declined throughout the growing season with the exception of Si.

These findings are consistent with… studies showing the grazing does not increase plant quality

We found… These results are consistent/inconsistent with…

Does grazing impact ANPP

* ANPP negatively impacted by PD and cattle stocking rate but not bison stocking rate or insecticide

Does grazing increase plant quality?

-It really depends

When are plant nutrients highest vc when is plant biomass highest?

* Biomass peaks mid season in all plots except treated pd
* Nitrogen is higher in early months in grasses, but silica increases in later months

Interpretation

* Grazing

Broader Perspective

While grasslands provide important environmental and societal services, they remain one of the most threatened terrestrial ecosystems globally, facing issues such as land use change, the encroachment of invasive species, and increased changes in climate in these regions (Hendrickson et al, 2019)(Miniat et al, 2021)(Leidinger et al, 2017). The short and mixed grass prairies of the Northern Great Plains (NGP) face many of the same threats common to grasslands globally. The NGP is a particularly important region for food security in the United States, containing 218 million acres of farmland, accounting for 23.8% of the total farmland in the country and supporting crops such as corn, wheat, barley, soybeans , and around 21.9% of the national supply of beef cattle (4th National Climate Assessment). This region is especially vulnerable to the impacts of climate change, which is predicted to alter climate patterns through rising temperatures and reduced snowpack. This shift to warm and dry summers has the potential to alter the plant growth of both native plants and croplands in the region (Derner et al, 2016)(Adams et al, 2020). With imminent changes to forage quality and quantity in the NGP due to climate change, it is integral to understand how the pressure of grazing impacts the health of the plants and soil in this region.

Large mammal grazing had varying effects on plant nutrient content, with cattle grazing and bison grazing both increasing and decreasing plant nutrients throughout the growing season. The impact of small mammal grazing was as predicted, with prairie dogs increasing nit

**Questions:**

* **Hypoth 1:** H1) Grazing will increase plant quality, with smaller herbivores (PD, Insects?) having larger effects through faster nutrient cycling,
  + **(What nutrients make up quality?) P, K, N, Mg, Na (increase)? Si grass, defensive compound (decrease)**

**Is this correct? Are there trends?**

* + Cattle decreased forb N
  + Bison decreased Grass K
  + PD increased grass K and N and decreased grass P, decreased forb N
  + Insecticide increased forb P and decreased forb N

**Seems like this is opposite of most other studies, and most other studies account for grazing intensity. Should I stay away from those studies as support/contradictions?**

**Are there broad conclusions to draw about plant quality and grazers, seems dependent on grazer and plant type**

H2) All grazers will decrease ANPP, and insect herbivory will equal that of large grazer herbivory (is this from pasture meter figure?)

Yes, everywhere except treated pd→ so really just shows that insects also would decrease ANPP

* Studies seem to be mixed on this, is that accurate?

Hypoth 3

H3) Plant nutrient content will be greatest in the early season while biomass will peak mid-season.

* For nutrients→ Depends on nutrient and plant type→ are there general conclusions to draw?
* Biomass does peak mid season?
* Not much info lit wise

Interpretation. When interpreting the Results, try to be even-handed. Do not make conclusions that the data do not support or fail to address. Present alternative explanations if caveats are appropriate. Being self-critical takes this option away from a reviewer. Keep in mind that sample sizes and the size of the differences between your treatments may be small.

Broader perspective. Conclude the Discussion by addressing the broader implications of the research. This can include: questions that remain unanswered, suggestions of areas where further research is necessary, implications of the results for problems in other taxa or areas of theory, development of new hypotheses, or implications for management and conservation.

**Acknowledgements**

Ben Allgire greatly assisted with field and lab work for this study. We are grateful to land managers and organization personnel at American Prairie, BLM, Bowdoin National Wildlife Refuge, and the Charles M Russell National Wildlife Refuge, especially Danny Kinka, Damien Austin, and Jessica Larson, for providing support, guidance, and allowing this project to be conducted on their lands.

**References**

**Notes from Reading:**

Belovsky (1987)

* **Main theme: People think that herbivory is good for plants, but not enough evidence--> this is in 1987 though**
* For plants-> reduction in biomass of one area leads to reduction of biomass in another area→ reduction in size limits a plants’ ability to be competitive→ therefore it is assumed that herbivory has a negative impact on
* Studies claim that herbivory has a positive impact on plants→ does not provide sufficient evidence→ has this changed since 1987?
* Cargill and Jeffries(1984) found grazing of snow goose has positive impact on above ground biomass→ doesn’t say anything about below ground biomass
* Does pruning/mowing vegetation mean it will come back more full? → mixed reviews
* There is an impact of biases on if grazing has a positive or negative impact
* Concludes that more studies need to be done→ assuming that this work has been built on in subsequent decades

Chew (1974)

* **Referenced in Belovsky (1987) as showing evidence that herbivory may, or actually does, increase the total productivity, reproductive output, or fitness of some plant species.**
* Consumers are beneficial to ecosystems as regulators and not energy movers
* States that herbivores don’t do much to move energy and matter around→ this is done mostly by microorganisms→ herbivores consume very little of the primary production of most systems
* Asks the question of whether animals are truly important to an ecosystem→ how do they regulate ecosystem processes
* **“Wherever plant processes are nutrient limited, the consumers which accelerate mineralization will increase primary productivity, a benefit by my criteria.”** → consumers eating plants will increase primary productivity in areas where plant processes are nutrient limited
* Herbivores add feces to areas in which plants are growing which is beneficial→ allows recycling of nutrients in one growing season
* Herbivores can increase productivity by increasing the production:respiration ratio of plants→ grazing removed leaf area to reach optimum level and allowed for the death of old and shaded leaves
* When almost all flowers on plants are eaten→ yield of seed and fiber increased. When all flowers are eaten→ photosynthesis decreased
* In grasslands→ grazing animals make the environment heterogenous and make plant populations more complex→ help generate diversity (Harper 1969, Janzen 1971b, Harris, 1972)
* Impacts of herbivores on vegetation diversity varies according to the feeding behavior of the animal, time of feeding, and nature of plant dominants
  + If herbivore is generalist→ simplifies vegetation

Owen and Wiegart (1976)

* **Referenced in Belovsky (1987) as showing evidence that herbivory may, or actually does, increase the total productivity, reproductive output, or fitness of some plant species.**
* **Hypothesis is developed that consumers are much like pollinators in that they have a mutualistic relationship with plants**. Examples of this include:
  + Nitrogen is often a limiting factor in plants productivity and reproductive success. Aphids as an example may stimulate nitrogen fixation with the sugary excretion they provide to a plant. If a plant can produce surplus sugar, and this can be fed to the soil by aphids then plants and aphids benefit
  + Cercopids can release water from trees which might increase the uptake of nutrients by near surface roots in dry conditions
  + Grazing can result in premature leaf fall and extend cycle of decomposition beneath a plant, which increases the conservation of nutrients
* Suggests that we re-examine the idea that plants are constantly trying to defend themselves from consumers, they may be actually encouraging consumers to eat them
* Some people suggest that since some plants have developed means to deter consumers this must mean that chewing and sucking of living plant tissue only has detrimental effects
* Perhaps we need to think of consumers more like pollinators in that plants are not discouraging them but rather regulating them→ find the most efficient ones and encourage them
* Availability of nitrogen is important and the productivity of a plant is dependent on the efficiency with which is can acquire and recycle nutrients→ think of consumers as regulators of production (not necessarily reducing it)
* This theory is most applicable to trees
* Biggest evidence is honeydew production and aphids→ increases sugar for free nitrogen fixing organisms in soil→ more production of nitrogen which is a limiting factor in plants productivity

Owen (1980)

* **Referenced in Belovsky (1987) as showing evidence that herbivory may, or actually does, increase the total productivity, reproductive output, or fitness of some plant species.**
* **The ability to photosynthesize of a plant is limited if growth and reproduction are limited by nutrients→ plants could enlist help of a consumer to facilitate nutrient cycling and increase supply of nutrient**
* Talks about aphids again and how aphids deposit sugary honeydew beneath a plant which can increase rate of nitrogen fixation by providing an energy source for free living nitrogen fixing bacteria that live in the soil
* Grasses survive best when cropped→ may have co-evolved with grazers
* States that paper is speculative but also that if any of the speculations are correct than the idea that plants defend themselves from consumers must be amended
* Case of vitamin D3 existing in some grasses→ author thinks this to attract grazers which require this vitamin (much like nectar in a flower) → author asks why else would a grass synthesize vitamin d3?

Stenseth (1978)

* **Concludes that the fitness of short lived plant species is enhanced when grazed**
* Mutualism is more likely for r-strategists than k-strategists → and also more likely in terrestrial systems as well as in early successional stages
  + R-selected have short lifespans and low survival rate from birth until maturation. Grazing is more likely to maximize plant fitness here
* Plants using defense mechanisms to deter consumers is more likely in long-lived species
* Provides model-based evidence to support Owen and Weigert (1976) which stated that grazers can increase plant fitness→ says it is possible from theoretical view
* Hypothesis → grazing reduces individual survival but increases reproductive output of the individual by recycling nutrients which are in short supply and stimulating growth

Borer et al (2020)

* Excessive richness of nutrients -eutrophication
* Exclusion of herbivores (ungrazed)--> leads to increases in above ground biomass→ what is the impact on nutrients though?
* Both the exclusion of herbivores and fertilization led to an increase in biomass (exclusion→ 12% and fertilizer→ 58%) → this seems to be consistent short term and semi long term (8 or more years)
* Herbivores consumed more biomass from extra fertilization at areas where domestic and wild herbivores were present → what constitutes a wild herbivore? → Are bison in the American prairie wild?
* Main finding→ in contrast to past data synthesis, this study finds that grassland biomass and nutrients around the world is limited by vertebrate herbivores (What is a non-vertebrate herbivore?) → this is similar to findings in marine and freshwater ecosystems
* **Main finding→ herbivores did not keep up with fertilized biomass production→ study does not provide support for herbivores removing additional biomass due to greater nutritional quality→ study shows constant proportional biomass reduction by herbivores→ if there is more fertilization, herbivores will eat more, but biomass accumulation outpaces herbivory**
* Soil nutrient composition seems to also have an impact on herbivore consumption of biomass
* Greatest im[act of vertebrate herbivores was seen in sites with low precipitation→ this could be relevant for american prairie region

Hao and He (2019)

* Study is based on findings from grasslands in china
* **Findings→ grazing significantly decreased the total biomass, aboveground biomass, belowground biomass, soil organic matter, soil total nitrogen, soil total phosphorus and soil water content. Grazing also increased the root to shoot ratio, soil available nitrogen, soil pH, and bulk density.**
* As grazing intensity increased, so did the impacts of grazing
* Smallest effects were seen in light grazing and areas with cattle grazing only
* Grazing in the non-growing season increased above ground biomass while annual grazing and growing season grazing decreased above ground biomass
* Conclusions→ cattle grazing alone and grazing in the non-growing season are beneficial for improving grassland quality→ what other animals were cattle being compared to?→ what does “quality” mean?

Peden et al (1974)

* Bison have greater preference for warm-season grasses and may feed less selectively than cattle in shortgrass areas
* Bison have greater digestive power when consuming poor quality forage
* Bison may exploit more fully than cattle the vegetation resources

Sitters et al (2019)

* Studies how herbivores can cause a shift between nitrogen and phosphorus limitations
* Findings→ an increase in grazing intensity by reindeer aided a shift towards phosphorus limited conditions→ they think this is because there is a large Phosphorus demand for antler production→ is this transferable to cows/bison?
* **Study shows that it is possible for large mammalian herbivores to influence nutrient limitation of plant growth**

Sitters et al (2020)

* Grassland soils are important reservoirs of carbon and nitrogen→ herbivores can impact these pools which can interact with increases in soil nutrient availability
* **If there are extra nutrient levels, then herbivore exclusion caused nutrient pools to shrink**
* Highest pools of nutrients found in grazed and fertilized plots
* Highlights importance of conserving mammalian herbivore populations in grasslands

Yu et al (2020)

* Grazing by ungulates can alter nitrogen and phosphorus concentrations in plant and soil
* **Grazing increased leaf nitrogen and phosphorus but decreased total and available soil levels for same compounds**
* Grazing increased leaf N:P ratios while decreasing root and total soil ratios
* Intensive grazing (long term or heavy) had more positive impacts on plant N:P stoich and negative on soil N:P stoich than light grazing→ varied by plant functional group
* Phosphorus is more important for plant growth

Belsky (1985)

* Focuses on grazers and grasses
* Two sides of the argument are that grazing is not beneficial to plants→ that's why they have defense mechanisms. The other argument is that grazing is beneficial to plants→ this paper focuses on that.
* Compensatory growth→ positive response of plants to injury. Partial replacement of lost tissue or a net productivity increase compared to uninjured plants
  + Overcompensation→ cumulative dry weight of grazed plants is greater than dry weight of control plants
  + Exact Compensation→ cumulative dry weight of the treated plants equals that of the controls
  + Undercompensation→ cumulative dry weight of plants is less than controls
  + Partial compensation→ undercompensating species produce more biomass than would be expected if no increase in growth rate occurs
  + No Compensation→ no increase in growth rate or increase in biomass
* **Herbivore Optimization Curve**→ net primary or above ground productivity of grazed plants increases at low to moderate levels of herbivory until productivity is maximized at an optimal grazing level where it then begins to fall
  + High grazing levels means productivity falls below ungrazed
* It is speculated that some plant populations have a higher fitness due to grazing and therefore evolve traits to maintain a certain level of grazing
  + High palatability
  + Basal meristems
  + Increased longevity
  + Increased shoot production
  + Production of D3→ needed for animal growth, but has no known function in plants
* **Suggested that herbivores have substances in their saliva that promotes plant growth**
* Competitive fitness→ increased fitness a plant gains when its neighbors are grazed in conjunction with them being grazed→ some plant species disappear when herbivores disappear
* Overcompensation in grass species has never been reported, but partial compensation is common
* Increases in dry weight of aboveground grass biomass after tissue removal have been reported
* McNaughton (1979a) showed that moderate grazing stimulated aboveground productivity in the serengeti plains to twice that of ungrazed plots
* Non-grass Grazer Systems
  + Sedges→ sedges have been found to overcompensate up to 300% for removed tissue
  + Dicots→studies are conflicted
  + Algae→ little effect
  + Crop Species→ increased productivity of neighboring but uninjured plants
* Only two papers (McNaughton et al 1983, Wallace et al 1985) showed that a non-crop species could overcompensate in total biomass for tissue lost to clipping
* Studies that support the herbivore optimization curve have limited validity
* Grassland species need grazing as they are evolved to an open landscape
* Hard evidence for the positive impacts of grazing in natural systems is lacking
* **Main idea→ in growth chamber conditions, clipping has increased plant biomass, not a lot of support in natural systems, herbivores may reduce competition or remove dead tissue prematurely which may be beneficial**

Maestre et al (2022)

* In warmer and species poor drylands→ increased grazing pressure has decreased benefits on ecosystem
* In colder and species-rich areas, grazing had a positive impact on ecosystem

Taddesse et al (2002)

* Quantified changes in plant species richness, biomass, plant cover and soil physical and hydrological properties
* Grazing regimes were moderate, heavy, and no grazing
  + Biomass yield in non grazed was higher than grazed but the biomass yield in grazed plots improved over time
  + Species richness was better in medium grazed plots
  + Soil compaction higher in heavily grazed plots

**Prairie Dog Specific:**

Beals et al (2014)

* In urban areas, prairie dog movement is restricted and the impacts of these animals on the environment is different than previous studies in remote areas
* In areas without prairie dogs, native grasses declined and increases in forbs (native and non-native) were seen
* When prairie dogs were introduced these same changes we seen but in higher magnitudes
* Areas with prairie dogs had lower richness, and diversity of plant species

Weltzin et al (1997)

* Black tailed prairie dogs influence ecosystems by increasing plant species diversity in comparison to uncolonized portions
* This was not found in this study→ found that prairie dog activity reduced crop and plant species richness and diversity and increased homogeneity of vegetation→ called for further studies

**Bison Specific**

Varriano et al (2020)

* Field study in tall grass prairie that manipulated arthropod abundance in bison grazed and ungrazed areas following a prescribed burn
  + Total plant biomass was unchanged but individual biomass of forbs and grasses was changed
  + Forb biomass in bison grazed/arthropod reduced plots was 2-3x higher than other treatments
  + Grass biomass was higher in bison grazed plots where arthropods were unmanipulated
  + Bison grazing and arthropod herbivory work in complementary way
    - Bison reduce grass biomass→ allows forbs to increase
    - Herbivorous arthropods reduced forb biomass→ allow grass to increase

Hillenbrand et al (2019)

* Measured impacts of bison and cattle on plant growth, reproduction, and species abundances
* Grazing regimes were : ungrazed, cattle grazed and bison grazed
* Results varied greatly. Some forbs increased in growth and reproduction in grazed sites while some reduced performance at grazed sites

**Cattle Specific**

Vermeire et al (2018)

* Compared areas that were moderately grazed by livestock with those that had excluded livestock for 15 years.
  + Livestock exclusion increased C3 perennial grass, forbs and reduced C4 perennial grass

Bork et al (2019)

* Looks at how long term cattle grazing in northern temperate grasslands impacts above and below ground biomass
  + Uses dataset of 73 grasslands to understand the impact of grazing
  + Uses areas that are grazed and those that are not
* Findings:
  + Forb biomass was greater in areas that were grazed
  + Grass and total aboveground herbage biomass did not differ with grazing
  + Forb crude protein concentrations were lower in grazed communities
  + Grasslands that had grazing had 56% less litter mass
  + Root biomass remained similar in areas with and without grazing
  + Moderate cattle grazing had minimal impact on grassland biomass (above and below ground)

**Insect Herbivory**

Carson and Root (1999)

* Suppressed above ground insects using insecticide for 3 years
* Insect herbivory substantially reduced plant biomass at all three sites

Dyer and Bokhari (1976)

* **Referenced in Belovsky (1987) as showing evidence that herbivory may, or actually does, increase the total productivity, reproductive output, or fitness of some plant species.**
* Measured impacts of grasshoppers feeding on lab grown blue gramma
  + Experiment shows that there are plant processes that are triggered by grasshopper feeding which results in increased energy transport levels in the plant
  + Regrowth potentials of plants that grasshoppers fed on is higher than if plants had just been clipped
  + Insect grazers may have greatest impact by increasing belowground respiration of plants and root exudation
* **This paper challenges the idea of insect/plant interactions as primarily benefiting the insects→ hypothesizes that since plants are active participants in the evolution of this relationship, there must be some benefit to grazing**
* One of the benefits may be in regrowth→when a plant is fed upon, there is a stimulus for translocating materials quickly from aboveground into roots→ this was seen in an increase in root activity
* Main Finding→ grasshoppers grazing on plants produce two events:
  + Physical event that is akin to clipping
  + Physiological one that provides a stimulus by injecting saliva on plant which can have impacts on regrowth
* There was a change in pH of root medium on plants that were fed by grasshoppers and those that were not→ grasshopper fed leads to more respiration by roots and lower pH?

Harris (1974)

* **Referenced in Belovsky (1987) as showing evidence that herbivory may, or actually does, increase the total productivity, reproductive output, or fitness of some plant species.**
* Some literature shows that insect attacks do not cause loss in plant yield but rather an increase→ this can be mimicked by pruning apical buds
* Pruning apical buds→ damage to plants leads to redirection of limiting resources to areas of plant that are not damaged→ stimulates growth so the idea goes
* **Idea that plants synthesize with less efficiency than environment allows until it is “woken up” by chewing insect**
* Yield increases have been reported when damage is done early in the growing season and was moderate with little growing competition