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

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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)(Derner et al, 2017)(Milchunas et al, 2005)(He et al, 2022) (White, 1978). Soil chemistry, macro and microclimate, and grazers are key drivers of plant production and quality (Ohno and Hettiarachchi, 2018). 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)(Borer et al,2020)(An and Li, 2015). 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). Additionally, plant nutrients, including nitrogen, phosphorus, and potassium tend to increase in plant regrowth following herbivory(Cargill and Jeffries, 1984)(Seastedt,1985)(Zheng et al, 2012)(Bi et al, 2020).

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. However, 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). Furthermore, grazing by prairie dogs increases plant quality by reducing leaf age and stimulating nitrogen uptake (Whicker and Detling, 1988). 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 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), provide critical ecological services including carbon sequestration, erosion control, climate mitigation, and serve as habitat for a diversity of biota (O'Mara, 2012)(Bengtsson et al, 2019) (Wilson and Peter, 1988) (Boval and Dixon, 2012). 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)(Lark et al, 2020). 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) and was approximately 10.45 inches over the growing season of 2022 (June-September). . The dominant soil 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 2m along two east-west oriented 58m transects, 50 m apart, each month at each site. We calibrated pasture meter measurements using 50 1 m^2 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 ($R^2 = 0.52$).

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.

Microclimate

Microclimate temperature recordings were obtained using one HOBO® Pro v2 logger at each site across the growing season. Humidity and temperature readings were recorded every 6 hours and then averaged daily. The daily averages were then further combined to reflect the monthly microclimate mean and variation for each site.

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 choose 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 with Ca (0.71), K ($r = 0.84$), Mg ($r = 0.82$), and Na ($r = 0.74$), and the section axis (29% of variation) correlating 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.

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 the 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

XX general descriptive results

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).

XX describe SEMs

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).

Describe monthly pattern of above.

List estimate amounts bison, cattle, prairie dogs, and grasshoppers ate.

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)

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…

-

Throughout the growing season, our findings showed a positive correlation between grazing and plant quality with smaller herbivores such as prairie dogs having larger effects.

Carbon:

- Ungrazed Forbs: Increased throughout season
- Ungrazed Grass: Increased throughout season
- Ungrazed Woody: Decreased throughout season

Nitrogen:

- Ungrazed Forbs: Decreased throughout season
- Ungrazed Grass:
- Ungrazed Woody:

Interpretation of results

Hypoth 1

H1) Grazing will increase plant quality, with smaller herbivores having larger effects through faster nutrient cycling,

- Higher nitrogen concentration in areas that have been more heavily grazed by prairie dogs, difference in nutrient cycling (Whicker and Detling 1988 https://sci-hub.ru/10.2307/1310787)
- Grazed plants had higher nitrogen concentrations than ungrazed plants, and had higher nitrogen levels later in the season (Cargill and Jeffries 1984)
- Vegetation nutrients (N, P, K) increased in nearly all sites after grazing (https://sci-hub.ru/10.3390/ijerph17124572) Bi, Li, Zu, Zhang (2020)
- Nutrient totals did not differ between grazed and ungrazed grassland **E. J. Chaneton, J. H. Lemcoff and R. S. Lavado (https://www.jstor.org/stable/2404751**)
- Grazing increased nitrogen content, which was determinant of plant quality (does it show a positive trend throughout growing season, or is it greater nitrogen content in comparison to ungrazed) Cargill and Jeffries, 1984)

(Seastedt,1985)(Zheng et al, 2012)(Bi et al, 2020).

Throughout a largely intact swath of the Northern Great Plains (NGP) grazing of large mammals such as bison and cattle had ___ impact on the quality of available vegetation. Small mammals such as prairie dogs had a ___ impact on this plant quality. The ANPP increased/decreased in areas that were grazed.

These findings correspond/don't correspond with previous research on the relationship between grazing and plant nutrient content. One reason for this discrepancy could be decreases in rain and increases in summer temperatures over the past several years that correspond to lower plant quality.

Our findings show ___. This is consistent/inconsistent with other findings in the field. One possible reason for this is__.

Hypoth 2

H2) All grazers will decrease ANPP, and insect herbivory will equal that of large grazer herbivory

- Grazing increased ANPP (cargill and jeffries https://www.jstor.org/stable/2403437?origin=crossref)
- Grazing increased ANPP (https://link.springer.com/article/10.1007/s11258-004-5800-5)
- Grazing increased ANPP, grazing optimization hypothesis (https://www.frontiersin.org/articles/10.3389/fpls.2019.00925/full)
- ANPP increased with grazing (https://journals.uair.arizona.edu/index.php/jrm/article/viewFile/8355/7967)
- ANPP decreased with grazing (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3855687/)

Hypoth 3

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

- Not much info

Broader Perspective

While grasslands provide important environmental and societal services, they remain one of the most threatened terrestrial ecosystems globally, facing threats such as land use change, the encroachment of invasive species, and increased climate threats 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 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.

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.

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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